UNIVERSITE PIERRE ET MARIE CURIE – PARIS VI
Ecole Doctorale Diversité du Vivant
Laboratoire Fonctionnement et Evolution des Systèmes Ecologiques (UMR 7625)

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Présentée par
Elodie VERCKEN

Pour obtenir le titre de Docteur de l'Université Pierre et Marie Curie

Polymorphisme de couleur et stratégies alternatives chez les femelles du lézard vivipare

Soutenue le 27 Avril 2007

Devant le jury composé de :

Bernard Cazelles	Président du jury
Alexandre Roulin	Rapporteur
Erik Svensson	Rapporteur
Dominique Pontier	Examinateur
Jacominus Van Baalen	Examinateur
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Barry Sinervo	Co-Directeur de Thèse (absent)

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PhD
Ecology

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Colour polymorphism and alternative strategies in female common lizards

Defended on April 27th 2007

Jury:

Bernard Cazelles	President
Alexandre Roulin	Examiner
Erik Svensson	Examiner
Dominique Pontier	Examiner
Jacominus Van Baalen	Examiner
Jean Clobert	Supervisor
Barry Sinervo	Co-Supervisor (absent)

Sur la planète aux mille et une couleurs
Des enfants gais jouent dans les fleurs
Y'en a des verts, des roses, des jaunes, des bleus
[…]
A chaque couleur, son caractère
Les bleus sont joyeux et les verts solitaires
Les roses composent des chansons, les marrons les écoutent
Et les rouges jouent au foot

Les Wriggles, *Planète* (Ah Bah Ouais Mais Bon, Universal, 2002)

Je remercie tout d'abord Jean, évidemment, pour m'avoir fait confiance pendant presque cinq ans, et m'avoir laissé une grande liberté à la fois dans la réalisation de mes expériences, et dans le développement de mes propres idées. Grâce à lui, j'ai appris à me connaître mieux, à valoriser mes talents et corriger mes faiblesses, et surtout à prendre du plaisir à chercher des explications, et à partager mes réflexions. Je remercie également Barry, pour son soutien, sa patience, et son implication dans la rédaction des articles. C'est lui qui est à l'origine du sujet de cette thèse, et il fut pour moi une source d'inspiration constante. Je remercie aussi chaleureusement Alexandre Roulin et Erik Svensson pour avoir accepté de rapporter cette thèse, ainsi que Bernard Cazelles, Dominique Pontier et Minus Van Baalen pour avoir accepté de faire partie du jury.

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INTRODUCTION

La variation phénotypique est ce qui permet de différencier et de reconnaître des organismes entre eux, à l'échelle individuelle, populationnelle, ou spécifique. L'existence d'une variation déterminée génétiquement est nécessaire à l'action des processus évolutifs, en particulier la sélection naturelle. En effet, toute différence phénotypique entre individus peut potentiellement induire une différence de valeur sélective ou **fitness**, et donc avoir des conséquences majeures à l'échelle évolutive en favorisant certains variants alléliques aux dépens d'autres. Un des buts de l'écologie évolutive est donc de décrire la variation existant au sein des systèmes naturels et d'étudier ses implications fonctionnelles, afin de comprendre et de prédire au mieux l'évolution de ces systèmes (Fox et al. 2001). Ainsi, l'étude du degré d'héritabilité d'un phénotype ou d'un caractère permet de déterminer son potentiel évolutif. Ensuite, l'étude des caractéristiques écologiques associées aux différents phénotypes (capacité à acquérir des ressources, à éviter la prédation, et à se reproduire) permet de mesurer leur fitness respective, et de prédire les changements de la distribution des phénotypes dans les générations futures. Enfin, la mesure de la fitness des différents phénotypes dans différents environnements permet de déterminer si les différences observées entre populations ou entre espèces sont le résultat d'un processus évolutif (Mazer et Damuth 2001). Dans ce contexte, les polymorphismes ont souvent fait l'objet d'une attention particulière, car ils permettent une mesure qualitative et quantitative précise de la variation phénotypique.

I. Etude des polymorphismes au sein des populations naturelles

1) Qu'est-ce qu'un polymorphisme ? Pourquoi l'étudier ?

Un polymorphisme correspond à la coexistence, au sein d'un sexe ou d'une classe d'âge, de variants phénotypiques discrets pour un caractère donné ou **morphes**. Les polymorphismes sont des modèles de choix en biologie : ils ont été entre autres à l'origine des premières découvertes en génétique (étude de la texture des graines de Pois *Pisum sativum* par Mendel en 1866, étude de la couleur des yeux et de la forme des ailes de la Drosophile *Drosophila melanogaster* par Morgan en 1911) car il était possible de décrire facilement l'état des caractères au cours des générations.

En écologie, les polymorphismes sont caractérisés par la distribution de fréquence des différents morphes, qui peut varier selon les populations et les milieux. La fréquence des morphes au cours des générations peut être mesurée précisément et permet de tester de nombreuses hypothèses évolutives (Mazer et Damuth 2001). De plus, l'héritabilité des caractères discrets est souvent plus simple que celle des caractères quantitatifs (petit nombre de gènes impliqués), et les interprétations évolutives s'en trouvent facilitées. Les premières études d'écologie évolutive ont ainsi cherché à mettre en relation les variations de fréquence des différents morphes et les variations d'un facteur du milieu (étude du mélanisme industriel chez la phalène du bouleau *Biston betularia* par Kettlewell en 1955, étude du polymorphisme anti-prédation chez l'Escargot des bois *Cepea nemoralis* par Lamotte en 1959).

2) Pourquoi observe-t-on des polymorphismes ? Quelles sont les implications évolutives ?

Un polymorphisme peut être sous contrôle **génétique**, ou bien **condition-dépendant**. Dans le cas d'un polymorphisme condition-dépendant, le phénotype d'un individu dépend de la valeur d'un autre trait ou d'un facteur de l'environnement. Par exemple, la taille larvaire détermine le développement des cornes chez les bousiers mâles (Emlen 1994), la présence de prédateurs induit le développement d'un casque et d'une épine chez les daphnies (Woltereck 1909), et une forte densité locale déclenche la production d'individus dispersants ailés chez les pucerons (Johnson 1965). Les polymorphismes strictement condition-dépendants n'ont pas de conséquences évolutives sur les populations, car il ne s'agit pas de caractères transmissibles aux descendants. Nous nous intéresserons donc plus particulièrement aux polymorphismes d'origine génétique, même si l'héritabilité n'est pas toujours totale et que les phénotypes sont souvent partiellement condition-dépendants (ce sont alors les différences de sensibilité aux variations de l'environnement, ou **normes de réaction** qui définissent les morphes). Dans le cas d'un polymorphisme génétique, la biologie des populations prédit que la variation présente dans les populations résulte d'un équilibre entre la création de nouveaux variants par mutation, et la fixation de certains variants par sélection ou dérive génétique (Fisher 1930). Par conséquent, si l'on observe dans les populations plusieurs variants à des fréquences supérieures à ce que l'on attendrait par le simple fait de mutations aléatoires, cela signifie que la variation est maintenue par sélection. Il existe plusieurs mécanismes sélectifs favorisant le maintien d'une variation génétique dans les populations isolées (détaillés dans Barton et Turelli 1989) :

- **L'overdominance** : les hétérozygotes ont une fitness supérieure aux homozygotes (Krueger et al. 2001, Reusch et al. 2001). En effet, les hétérozygotes bénéficient en général d'une plus faible consanguinité, ils expriment plus rarement des allèles délétères, et ils possèdent une plus grande diversité protéique, ce qui peut leur permettre de s'adapter à davantage de conditions différentes (Roulin 2004a).
- La sélection **disruptive**, ou variation de niche : les différents phénotypes sont avantagés dans différents micro-habitats (Galeotti et al. 2003, Formica et al. 2004, Roulin 2004b).
- La sélection **fréquence-dépendante négative** : le phénotype le plus rare détient un avantage sélectif. Par exemple il peut être préféré par l'autre sexe, ou être moins facilement repéré par les prédateurs ou les proies (Rohwer et Paulson 1987, Hughes et al. 1999, Olendorf et al. 2006).

L'étude de la fitness des morphes dans différents environnements où leur fréquence relative varie peut permettre de déterminer quels mécanismes sélectifs sous-jacents sont à l'origine du maintien du polymorphisme dans les populations. Ainsi, dans le cas d'une overdominance, la fitness des hétérozygotes doit être supérieure à celle des homozygotes dans tous les environnements. Dans le cas d'une variation de niche, la fitness d'un morphe doit être supérieure dans les populations ou les environnements où il est naturellement le plus fréquent, car il est localement mieux adapté. Enfin, dans le cas d'une fréquence-dépendance négative, la fitness d'un morphe doit être supérieure dans les environnements où il est rare.

La signification évolutive d'un polymorphisme pourra quant à elle être inférée à partir de l'étude des traits corrélés au trait polymorphe. En effet, dans le cas d'un polymorphisme lié aux variations de l'environnement non-social (climat, habitat, prédation,…), l'avantage sélectif obtenu par les différents morphes dans différents milieux est conféré par la valeur même du trait polymorphe, ce qui permet d'expliquer directement l'évolution et le maintien du polymorphisme. Ainsi, certaines formes mélaniques de reptiles sont favorisées dans des régions où l'ensoleillement et la température sont peu élevés car leur thermorégulation est plus efficace (Pearse and Pogson 2000). Au contraire, dans le cas d'un polymorphisme en relation avec l'environnement social, le trait polymorphe en lui-même ne porte pas d'avantage sélectif, mais sert de marqueur pour un ensemble d'autres traits corrélés qui définissent des stratégies alternatives et qui vont affecter la fitness des différents morphes.

II. Polymorphisme et stratégies alternatives

1) Qu'est-ce qu'une stratégie ?

Une **stratégie** correspond à un ensemble de traits associés par le biais de corrélations génétiques ou physiologiques appelées **trade-offs** ou compromis évolutifs (Stearns 1992), qui définissent un phénotype particulier. Un trade-off génétique est causé par un déséquilibre de liaison génétique entre allèles, ou par l'existence d'une pléiotropie (un même gène affectant l'expression de plusieurs autres). Un trade-off physiologique est dû à l'action pléiotrope de certaines hormones sur un grand nombre de caractères, ou au conflit énergétique entre plusieurs fonctions. Par exemple, l'existence d'un trade-off entre l'investissement reproducteur et la survie adulte est à l'origine de l'émergence de deux types de stratégies : les stratégies semelpares , où les individus vont investir toutes leurs ressources dans un événement de reproduction unique ; les stratégies itéropares, où les individus réalisent plusieurs événements de reproduction avec un investissement ponctuel plus réduit. Etant donné qu'un organisme ne peut pas investir toute son énergie à la fois dans sa reproduction et sa survie, l'une ou l'autre stratégie sera sélectionnée selon les caractéristiques de l'espèce considérée (longévité, survie des stades juvéniles…). Ainsi, la plupart des insectes sont semelpares, et les mammifères plutôt itéropares.

Dans certaines conditions cependant, plusieurs stratégies peuvent coexister au sein d'une même espèce ou d'une même population. La variabilité spatiale ou temporelle de l'environnement biotique et abiotique génère une variabilité des pressions de sélection, face auxquelles certaines stratégies vont être avantagées. Plus précisément, d'un point de vue théorique, l'existence d'une structure de l'environnement (génétique, physiologique, temporelle ou spatiale) augmente sa dimensionnalité, c'est-à-dire le nombre minimal de variables nécessaires pour décrire l'environnement dans les équations de la dynamique de la population. Dans un environnement mono-dimensionnel, une seule stratégie peut émerger. Par contre, si la dimension de l'environnement est supérieure à deux, alors des stratégies alternatives peuvent évoluer (Heino et al. 1998). Par exemple, dans un milieu instable ou perturbé, les stratégies démographiques de type r (faible survie adulte et fécondité élevée) vont être sélectionnées. Au contraire, dans un milieu stable, les stratégies de type K (forte survie adulte et fécondité réduite) vont être avantagées (Begon et al. 1996). Différents phénotypes vont donc être plus ou moins performants selon les conditions locales, et une hétérogénéité spatiale ou temporelle de l'environnement peut alors favoriser le maintien de ces phénotypes alternatifs dans une population. Dans l'exemple ci-dessous (Figure 1), deux stratégies existent qui diffèrent pour deux traits A et B négativement corrélés. Dans un environnement donné (environnement I), la stratégie 1 (faible valeur de A, forte valeur de B) est avantagée, tandis que dans un autre environnement (environnement II) la stratégie 2 (forte valeur de A, faible valeur de B) est sélectionnée.

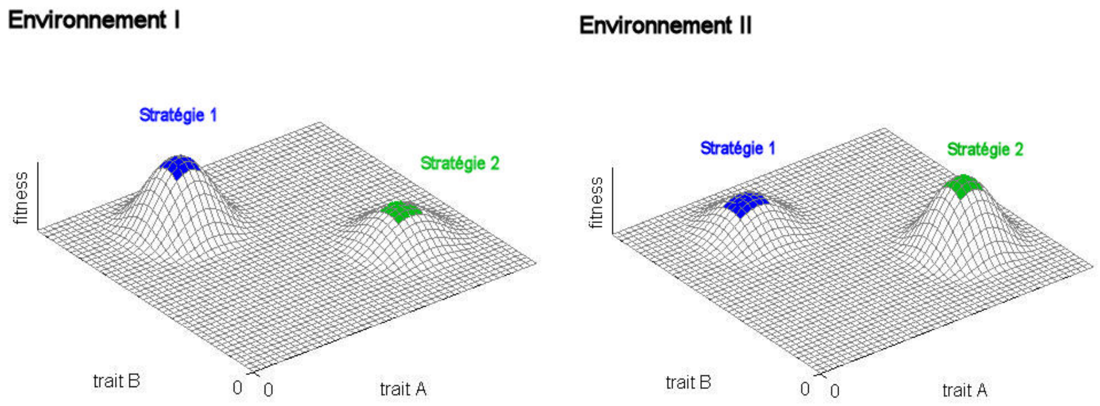


Figure 1 : Surfaces de fitness en fonction des valeurs prises par les traits A et B dans différents environnements.

Si l'environnement est variable et change régulièrement d'état, les deux stratégies ont une fitness moyenne égale et sont maintenues dans la population. Ainsi, chez le lézard à flancs tachetés (*Uta stansburiana*), des femelles adoptant une stratégie de type r (nombreux descendants, de petite taille) coexistent avec des femelles adoptant une stratégie de type K (moins de descendants, de plus grande taille) dans des populations où l'intensité de la compétition locale varie fortement entre les années (Sinervo et al. 2000a).

D'autre part, les organismes peuvent également être capables de produire des réponses plastiques aux variations de l'environnement qui leur permettent de conserver une fitness élevée dans une large gamme de conditions différentes. A un même problème, différentes solutions sont souvent possibles. Si différents génotypes varient dans leur réponse plastique aux variations de l'environnement, différents phénotypes adaptatifs peuvent être produits, dont la combinaison des traits (fixes et plastiques) définit des optimaux de fitness alternatifs (Leimar 2005). Dans ce cas, la variation entre les individus se traduit par différentes voies d'exploration du paysage adaptatif et différents pics adaptatifs locaux qui correspondent à des stratégies alternatives. Dans l'exemple ci-dessous (Figure 2), deux génotypes diffèrent par la valeur d'un trait A. Ces génotypes peuvent développer différentes valeurs pour le trait B, mais certaines valeurs sont plus avantageuses pour l'un des génotypes que pour l'autre. Les deux génotypes vont donc explorer différentes zones du paysage adaptatif et développer des phénotypes alternatifs pour le trait B en fonction des variations de l'environnement.

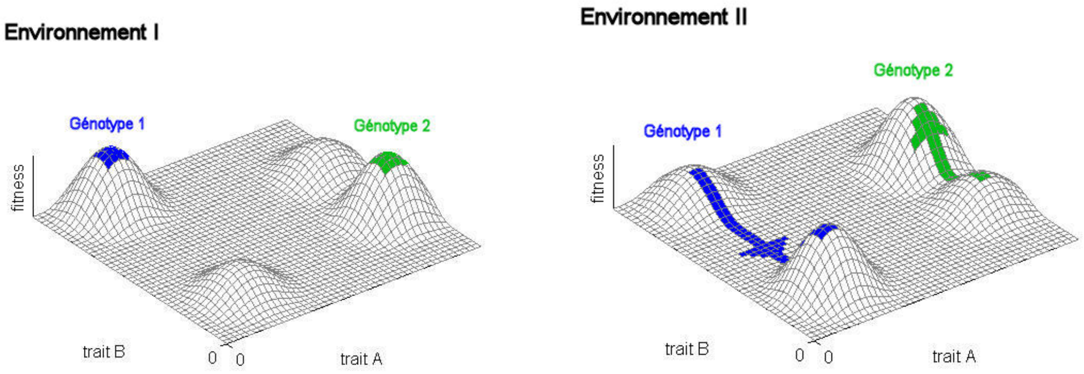


Figure 2 : Surfaces de fitness pour les génotypes 1 et 2 en fonction des valeurs prises par les traits A et B dans différents environnements.

Si la structuration de l'environnement est une condition nécessaire à l'émergence de différentes stratégies, les variations de l'environnement social en particulier, comme les variations de densité, semblent avoir le potentiel de générer facilement l'évolution de stratégies alternatives (Doebeli et Ruxton 1997). Le contexte social semble donc être au cœur de la dynamique des stratégies alternatives, dont la fitness va être affectée par la présence d'autres stratégies dans la population. Les résultats de telles interactions sociales ont été étudiés au niveau théorique à l'aide de modèles issus de la Théorie des Jeux. Ces modèles ont fourni de nombreux apports quant aux conditions écologiques nécessaires à l'évolution et au maintien des stratégies alternatives, en particulier l'existence de signaux sociaux jouant le rôle de marqueurs de stratégies.

2) Stratégies alternatives et interactions sociales

La notion de **stratégie** a été définie par John Maynard-Smith en 1982 : une stratégie correspond à un phénotype particulier, et décrit comment un individu réagit à une situation donnée. Ce concept de stratégie a été défini dans le contexte de l'étude du comportement animal mais il peut être étendu à tous les traits d'histoire de vie, comme nous l'avons vu ci-dessus. Dans le cadre de la Théorie des Jeux, le gain de fitness obtenu par un individu adoptant une stratégie est affecté par le résultat des interactions sociales avec les autres stratégies, et l'environnement social est donc déterminant dans le succès remporté par une stratégie particulière. Une stratégie peut être condition-dépendante, c'est-à-dire que la stratégie adoptée par l'individu sera déterminée par une (ou plusieurs) de ses caractéristiques. Dans ce cas, toutes les stratégies ne sont pas équivalentes en fitness, mais un individu adoptera la meilleure stratégie possible compte tenu de son phénotype (« Best of a Bad Situation », Dawkins 1980). Différentes stratégies peuvent également être déterminées génétiquement (**stratégies alternatives vraies**), et un mécanisme de fréquence-dépendance négative assure l'égalité moyenne des fitness entre stratégies. Dans un système diploïde à reproduction sexuée, des stratégies ayant une fitness moyenne inégale peuvent également coexister de façon stable s'il y a overdominance (Maynard-Smith 1982).

L'exemple le plus classique de stratégies alternatives est le système Faucon-Colombe. Un Faucon va défendre activement une ressource de valeur V, éventuellement jusqu'à l'affrontement (qui entraîne un coût C en cas de défaite), et la probabilité de remporter l'affrontement est égale à 0,5. Une Colombe fuira devant un Faucon, et partagera la ressource avec une autre Colombe. Le tableau 1 résume les gains associés à chaque stratégie pour chaque situation.

Adversaire Individu	Faucon	Colombe
Faucon	½ (V-C)	V
Colombe	0	½ V

Tableau 1 : Gains associés à chaque stratégie dans le système Faucon-Colombe

Dans ce système, si le gain V est supérieur au coût de l'affrontement C, la fitness moyenne de la stratégie Faucon est supérieure à celle de la stratégie Colombe : la stratégie Faucon est donc sélectionnée, et la population devient monomorphe. Par contre, si le coût de l'affrontement est supérieur au gain apporté par la ressource, il existe une valeur de fréquence de la stratégie Faucon pour laquelle la fitness moyenne des deux stratégies est égale, et elles peuvent donc coexister de manière stable dans la population. Pour que le système fonctionne, il faut que les individus puissent reconnaître la stratégie adoptée par leurs adversaires. Ici, la Colombe change de comportement en fonction de la stratégie de son adversaire : elle s'enfuit si elle reconnaît un Faucon, mais elle reste si elle reconnaît une Colombe. Plus généralement, les stratégies qui font intervenir une **règle de décision** dépendante du phénotype de l'adversaire sont toujours sélectionnées, comme la stratégie Assesseur : jouer Faucon si l'on détient un avantage compétitif, qui l'emporte sur les stratégies « fixes » Faucon et Colombe. Du point de vue de l'adversaire, il est également avantageux de **signaler honnêtement** sa stratégie car un signal inapproprié peut se révéler coûteux pour son porteur (Maynard-Smith 1982). Ainsi, chez le bruant à face noire (*Zonotrichia querula*), la couleur du plumage au printemps signale le statut de dominance: les individus dominants arborent un plumage sombre, et les dominés un plumage clair. La manipulation expérimentale de ce signal engendre des coûts de fitness importants pour toutes les catégories sociales : les individus dominants peints en clair doivent s'engager dans de nombreux affrontements afin de maintenir leur statut, tandis que les individus dominés peints en sombre sont violemment agressés par les « vrais » dominants (Rohwer 1977). Ainsi, l'accès à l'**information** est nécessaire pour que les stratégies soient adaptatives : les individus doivent correctement estimer la situation afin d'adopter le comportement qui leur assurera le meilleur gain de fitness. Les stratégies alternatives sont donc souvent associées à des traits polymorphes visibles, qui jouent le rôle de signaux sociaux.

3) Les stratégies alternatives sont signalées par un polymorphisme

Les traits polymorphes sont en général associés à de nombreux autres traits discrets ou continus, par le biais de trade-offs génétiques ou physiologiques. Ainsi, la plupart des polymorphismes concernent en réalité un ensemble de caractères plus ou moins observables, et les morphes constituent des **syndromes phénotypiques**, qui se distinguent aussi bien au niveau morphologique que physiologique et/ou comportemental. Ainsi, chez le Tétrix des clairières (*Tetrix undulata*), différents morphes de couleur génétiquement déterminés se distinguent par de nombreux autres traits (taille corporelle, reproduction, choix du micro-habitat, plasticité du taux de croissance, Ahnesjö et Forsman 2003). Chez le criquet des sables (*Gryllus firmus*), plusieurs traits participant à la fonction de migration sont corrélés génétiquement (présence d'ailes, masse musculaire, comportement de vol), de telle sorte qu'une modification du taux de dispersion se répercutera sur tous les traits associés (Roff and Fairbairn 2001). Les corrélations entre un trait polymorphe visible et un certain nombre d'autres caractères définissent donc des stratégies alternatives, où différents individus adoptent différentes tactiques d'histoire de vie en fonction de leur propre génotype afin de maximiser leur fitness.

La **compétition sociale** au sens large, qui regroupe toutes les interactions entre un individu et ses congénères pour accéder à une ressource (qu'elle quelle soit : territoire, nourriture, partenaires sexuels), est une force sélective qui favorise l'apparition de polymorphismes visibles jouant le rôle de signaux (West-Eberhard 1983). Ces polymorphismes peuvent traduire des différences de potentiel compétitif (Kingston et al. 2003), de statut de dominance (Johnson 1988, Berglund and Rosenqvist 2001), ou de qualité individuelle (Johnsen et al. 1996, Amundsen et al. 1997, Weiss 2006) et donc être associés à des stratégies alternatives (Amundsen 2000, Roulin 2004a). Chez les mâles, l'existence d'une forte compétition pour l'accès aux partenaires sexuels est ainsi à l'origine de l'évolution de stratégies alternatives de reproduction. Par exemple, les mâles du poisson porte-épée *Xiphophorus nigrensis* utilisent trois tactiques de reproduction : courtiser les femelles, « voler » des copulations, ou un mélange des deux (Ryan et al. 1992). De même, les mâles du bruant à gorge blanche *Zonotrichia albicollis* exhibent deux types de comportement : un morphe est agressif et recherche les copulations hors-couple, l'autre investit davantage dans la garde des femelles et les soins parentaux (Tuttle 2003). Chez les femelles, les relations avec les mâles (harcèlement sexuel) et la compétition intra-sexuelle pour l'accès aux ressources vitales a dans certains cas favorisé l'apparition de stratégies alternatives liées à la reproduction (femelles andromorphes ou gynomorphes chez la demoiselle *Ischnura elegans*, Svensson et al. 2005) ou au comportement social (les femelles du lézard à flancs tachetés souffrent plus ou moins de la présence d'autres femelles dans leur voisinage, Comendant et al. 2003).

Par ailleurs, les signaux intervenant dans la communication sociale sont souvent également impliqués dans la **sélection sexuelle** (Amundsen 2000), car ils se révèlent plus fiables que des signaux à vocation uniquement sexuelle. En effet, les coûts associés à une tricherie (usurpation d'un signal) devraient être beaucoup plus élevés lors d'une interaction compétitive (affrontement physique et blessure possible, Rohwer 1977, Rohwer et Ewald 1981) que lors d'une tentative de séduction d'un partenaire (perte d'une occasion de reproduction, Berglund et Rosenqvist 2001). Les signaux intervenant dans la reconnaissance de stratégies alternatives sont donc soumis à une forte pression de sélection, car ils sont impliqués à la fois dans la communication intra-sexuelle (évaluation des compétiteurs) et dans la communication inter-sexuelle (choix d'un partenaire). Chez de nombreuses espèces, des signaux colorés ont évolué pour identifier des stratégies alternatives, et sont aussi utilisés par les individus pour sélectionner leurs partenaires (Alonzo et Sinervo 2001, Krueger 2001, Formica et al. 2004). De tels signaux peuvent en effet véhiculer des messages complexes, en reflétant non seulement des caractéristiques génétiques fixes des individus, mais également certaines composantes plus variables du phénotype.

III. Polymorphisme de couleur et communication intra-spécifique

1) La couleur, un signal composite

La coloration peut être impliquée dans les fonctions de thermorégulation, de camouflage, et de **communication intraspécifique** (Endler 1990). Dans les deux premiers cas, la coloration des individus varie entre populations selon le climat, l'habitat et le type de prédateurs. Par contre, dans le cas d'une fonction de communication, la coloration exprime une forte variation au sein des populations, afin de refléter au mieux **l'hétérogénéité individuelle** (Galeotti et al. 2003). Pour étudier le rôle de la couleur individuelle dans la communication intraspécifique, il est alors nécessaire de mesurer les variations dans le signal émis afin de le mettre en relation avec un message éventuel (corrélation avec des caractéristiques individuelles, effet de l'environnement…).

Pendant longtemps, les études portant sur les variation de couleur entre individus ont utilisé une mesure qualitative de la couleur, qui s'avérait être subjective (différents observateurs pouvant avoir différentes sensibilités à la couleur) et peu répétable (effet de la fatigue, de la lumière ambiante, de la couleur de l'environnement…). De plus, cette estimation était réalisée sur la base de la perception humaine des couleurs, alors que selon l'espèce considérée, sa perception peut être très différente car la vision des couleurs dépend de la quantité de cônes sensibles au vert, au bleu ou au rouge dans la rétine. Ainsi, les chats sont incapables de distinguer le rouge et les chiens ont une vision basée autour du vert. Par contre, les oiseaux ont en général une perception très développée de la couleur, et réagissent davantage à celle-ci qu'à la lumière ou la forme. Enfin, les poissons seraient capables de distinguer toutes les couleurs, y compris des longueurs d'onde dans l'ultraviolet. La généralisation des méthodes de **spectrophotométrie** permet aujourd'hui d'effectuer des mesures quantitatives fiables de la couleur en intégrant toutes ses composantes. La couleur d'un objet est alors décrite par son spectre de réflectance, c'est à dire la part de la lumière qui est réfléchie par l'objet en direction du récepteur pour différentes longueurs d'onde (Endler 1990). La couleur qui est perçue par les individus est en réalité composée de deux éléments :

- la **brillance**, qui correspond à l'intensité totale de lumière réfléchie qui atteint le récepteur. La brillance dépend de l'interaction entre le spectre de la lumière incidente et celui de l'objet. Ainsi, sous une lumière à fortes composantes verte et jaune, les objets les plus brillants seront ceux qui réfléchissent principalement ces longueurs d'onde.
- la couleur proprement dite, qui est déterminée par la forme du spectre de réflectance. La description de la couleur s'appuie sur deux variables complémentaires : la **teinte**, qui correspond au sens quotidien de la couleur (bleu, jaune, rouge, …), et qui est corrélée à la longueur d'onde pour laquelle la pente du spectre est maximale ; le **chroma**, qui correspond à la pureté ou saturation de la couleur, et qui dépend de la rapidité avec laquelle l'intensité change avec la longueur d'onde (c'est-à-dire l'étroitesse du spectre).

Cependant, ces mesures ne prennent pas en compte les capacités de perception propres à chaque espèce, et une variation mesurée par spectrophotométrie peut ne pas être fonctionnelle en tant que signal intraspécifique si elle n'est pas réellement perçue par les individus. De telles mesures doivent donc être complétées par des expériences comportementales visant à estimer la réponse des individus à ces signaux de couleur, afin d'identifier les signaux socialement pertinents, notamment les signaux indicateurs de stratégies alternatives.

2) La couleur comme marqueur de stratégie

Les différents éléments de la couleur vont pouvoir répondre indépendamment à différents facteurs, et véhiculer un **message complexe** intégrant différentes sources d'information. Certaines composantes vont être déterminées **génétiquement** (en général les éléments de la couleur, c'est-à-dire la teinte et le chroma), et vont pouvoir identifier les sexes, ou bien des stratégies alternatives, de façon fiable. Ainsi, les deux morphes mâles (sombre ou clair) chez le bruant à gorge blanche sont déterminés par un inversion chromosomique et le polymorphisme est donc strictement génétique (Tuttle 2003). De même, chez le lézard arboricole *Urosaurus ornatus,* l'expression de stratégies de reproduction alternatives signalées par la couleur de la gorge (orange ou bleue) est sous contrôle essentiellement génétique (Thompson et al. 1993). D'autres composantes vont être plus **plastiques** (en général la brillance), et répondre à des variations ponctuelles de facteurs internes ou externes. Par exemple, chez le lézard agamidé *Ctenophorus ornatus,* la brillance des femelles est un indicateur de leur réceptivité sexuelle (LeBas et Marshall 2000). De même, la brillance des mâles est un indicateur de la qualité individuelle chez l'épinoche (condition physique et immunitaire, Milinski et Baker 1990). La combinaison de ces différents signaux va donc véhiculer un message précis sur le phénotype de l'individu, en intégrant à la fois des **traits fixes** et des **traits variables**. L'ensemble de ces informations pourra être utilisé par ses congénères afin de prendre une décision adaptative. Ainsi, les mâles du gorge-bleue à miroir *Luscinia svecica* préfèrent s'accoupler avec des femelles plus colorées (Amundsen et al. 1997), et les femelles du cichlide zébré *Cichlasoma nigrofasciatum* vont être plus agressives envers des femelles à coloration orange vive (Beeching et al. 1998).

De plus, la couleur est un signal accessible à longue distance, au contraire d'un signal chimique ou comportemental, et peu coûteux en termes de prédation s'il se limite à une zone réduite ou **badge**, au contraire de certains ornements extravagants impliqués dans la sélection sexuelle uniquement, comme les bois des cervidés ou la queue des paons. L'existence de badges colorés d'origine génétique chez une espèce serait donc un indicateur de l'existence de stratégies alternatives, et celles-ci seraient à rechercher en priorité chez les espèces montrant un polymorphisme de couleur localisé.

IV. Caractériser un polymorphisme de stratégies : l'exemple du lézard vivipare

Chez le lézard vivipare, les femelles présentent une variation de la coloration ventrale, allant du jaune à l'orange, avec des phénotypes intermédiaires (coloration mixte). Ce polymorphisme étant situé au niveau de la couleur ventrale, il est peu probable qu'il joue un rôle dans le camouflage ou la thermorégulation. Un polymorphisme non lié à la prédation ou à l'habitat au sens strict (climat, milieu) étant probablement impliqué dans les interactions sociales, le trait polymorphe (ici, la couleur ventrale) est donc susceptible d'agir comme un marqueur de stratégies, et covarier avec d'autres traits morphologiques, physiologiques, comportementaux ou d'histoire de vie (Roulin 2004a). Au cours de cette thèse, nous avons cherché à tester cette hypothèse, en couplant différentes approches corrélatives et expérimentales, afin de comprendre la signification évolutive du polymorphisme de couleur ventrale chez les femelles du lézard vivipare, et les mécanismes sélectifs permettant son maintien dans les populations naturelles.

1) Etude des différences entre morphes : existence de stratégies ?

En premier lieu, il était nécessaire de vérifier si le trait en question est sous déterminisme génétique, au moins partiel. Nous avons donc réalisé une étude de la stabilité et de l'héritabilité de la couleur ventrale chez les lézards femelles (détaillée dans le chapitre Méthodes). Ensuite, nous avons étudié les différences d'histoire de vie entre morphes afin d'identifier des stratégies alternatives. Nous avons analysé les corrélations entre la couleur ventrale et la reproduction, la survie et la dispersion natale, et plus particulièrement les réponses morphes-spécifiques de ces traits d'histoire de vie à un certain nombre de facteurs internes et externes. En effet, une différence génétique dans les normes de réaction est précisément ce qui définit des stratégies alternatives. Les résultats de ces analyses sont présentés dans le chapitre I (Coloration ventrale et stratégies d'histoire de vie).

Les interactions sociales étant à l'origine de l'évolution des stratégies alternatives, nous avons également étudié la réponse comportementale en laboratoire d'une femelle confrontée à une autre femelle en fonction de leur couleur respective, afin d'identifier des stratégies sociales. Le rôle de la couleur ventrale en tant que signal social a été spécifiquement testé. Les conclusions de ces expériences sont détaillées dans le chapitre II (Réponses comportementales à la couleur de l'environnement social).

Ces deux études nous ont donc permis de caractériser des stratégies alternatives associées à la couleur ventrale chez les femelles du lézard vivipare. Nous nous sommes ensuite demandé si la fitness des individus pouvait être affectée par leur environnement social, et quels étaient les mécanismes à l'origine du maintien du polymorphisme de stratégies, en utilisant une approche expérimentale en populations naturelles.

2) Etude de la valeur sélective associée aux stratégies alternatives : quel scénario adaptatif ?

Pour que les différentes stratégies coexistent, elles doivent obtenir des fitness moyennes égales (éventuellement par le biais d'une fréquence-dépendance négative), ou les hétérozygotes doivent être sélectionnés par un mécanisme d'overdominance. Afin d'estimer la fitness associée à chaque stratégie en fonction de la fréquence des autres stratégies, nous avons fait varier expérimentalement la fréquence de certains morphes dans plusieurs populations naturelles, et étudié la réponse des traits d'histoire de vie définissant les stratégies alternatives (reproduction et dispersion natale) à cette variation de l'environnement social. Cette manipulation expérimentale a modifié les pressions de sélection locales agissant sur les femelles, et a induit des modifications morphes-spécifiques de leurs traits d'histoire de vie et de leur fitness. Afin de tester le caractère adaptatif de ces réponses, nous avons également estimé la fitness des jeunes (croissance et survie) issus de mères de différentes couleurs dans les différents environnements. Cette approche expérimentale nous a permis d'estimer l'effet de l'environnement social sur la fitness respective des différents morphes, et de poser des hypothèses sur leur maintien dans les populations par sélection de micro-environnements différents. Les résultats de ces expériences sont décrits dans le chapitre III (Variation de l'environnement social et fitness des stratégies). La fitness des individus étant affectée par leur environnement social, nous avons cherché si les femelles pouvaient maximiser leur fitness en choisissant les femelles avec lesquelles elles interagissent, c'est-à-dire si les femelles de différentes couleurs adoptaient des stratégies d'association spatiale différentes.

3) Effet du polymorphisme sur la structuration de l'environnement social : y a-t-il une distribution non aléatoire des morphes ?

Pour finir, nous avons testé si les morphes adoptaient une stratégie adaptative en réponse à une hétérogénéité spatiale dans les pressions de sélection sociales due à l'existence de différentes stratégies au sein d'une population. Pour cela, nous avons testé si les différents morphes se répartissaient de façon non aléatoire dans la population, en fonction de leur propre couleur et de la couleur de leurs voisins, et si les différentes stratégies se caractérisaient par différents profils d'association entre apparentés, traduisant par exemple l'existence de stratégies territoriales ou coopératives. Les résultats de cette analyse sont présentés dans le chapitre IV (Compétition sociale et stratégies de distribution spatiale).

METHODES

I. Le modèle d'étude : le lézard vivipare

1) Le cycle de vie

Le lézard vivipare (*Lacerta vivipara*) est un petit lacertidé (longueur museau-anus ou LMA : 50 à 70 mm) dont l'aire de répartition s'étend à l'ensemble de l'Europe et de l'Asie, à l'exception des zones les plus méridionales. Le lézard vivipare est donc une espèce ubiquiste, capable de s'adapter à des conditions environnementales très différentes. En France, on le trouve essentiellement dans les lieux humides à sol acide : prairies, landes et tourbières (Lorenzon et al. 2001). Les populations étudiées se trouvent dans le Parc National des Cévennes, sur le Mont Lozère.

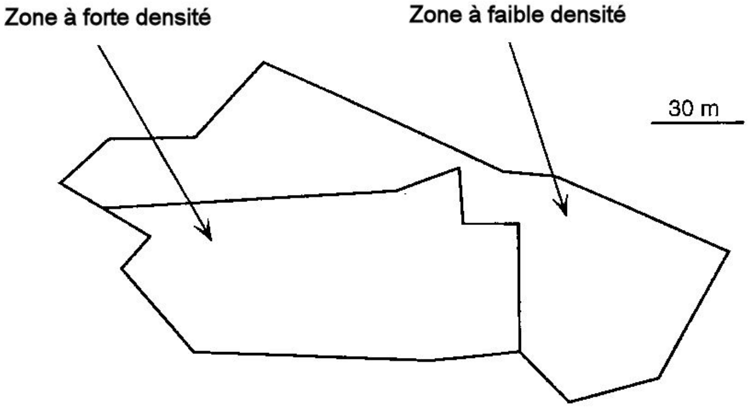
Lézards vivipares femelles en cours de gestation (photos B. Mauroy)

Comme pour tous les reptiles des régions tempérées, le cycle annuel du lézard vivipare comporte deux phases : une phase d'activité pendant la saison chaude durant laquelle les individus se reproduisent, et une phase d'hibernation pendant la saison froide où les individus sont en vie ralentie. Dans les populations des Cévennes, la phase active dure environ six mois, d'avril à fin septembre. Les mâles sortent d'hibernation les premiers, au début du mois d'avril, les femelles et les subadultes émergent ensuite vers la fin du mois d'avril, et la reproduction a lieu immédiatement. Chez cette espèce, les mâles entrent en compétition pour l'accès à la reproduction, tandis que les femelles entrent en compétition pour l'accès aux ressources vitales (Massot 1992).

Les populations étudiées sont ovovivipares : le développement des embryons se fait de façon interne, et la gestation dure entre deux et trois mois (mais certaines populations méridionales sont ovipares). En juillet, les femelles pondent de 1 à 12 œufs entourés d'une membrane coquillière fine et souple, que les jeunes rompent ensuite, généralement en moins d'une heure. Les nouveaux-nés mesurent de 20 à 25 mm et sont immédiatement indépendants de leur mère.

2) Populations d'étude

ROB est une population située sur le versant Sud du Mont Lozère, à la station du Mas de la Barque. Dans cette population, l'habitat est hétérogène, et on peut distinguer une zone de grande diversité structurale et à forte densité (zone de bonne qualité), et une zone de faible diversité structurale et à faible densité (zone de moins bonne qualité, Clobert et al. 1994).



Carte de la population ROB (d'après Clobert et al. 1994)

Chaque année, des femelles gestantes sont capturées à ROB, et ramenées au laboratoire. Elles sont alors soumises à un traitement expérimental de nourrissage jusqu'à la mise bas : un traitement « bien nourri », où les femelles sont nourries une fois par semaine ; un traitement « mal nourri », où les femelles sont nourries toutes les deux semaines. Cette population est suivie annuellement depuis 1989, et offre donc la possibilité d'étudier des effets en s'affranchissant des variations annuelles, et d'analyser des variations à long terme.

Sur le versant Nord du Mont Lozère se trouvent quatre populations distantes de moins de 2km deux à deux : Chalet, Bigoudou, Barnassac et Finiels. Ces populations sont utilisées pour mener des expérimentations à l'échelle populationnelle, sur une durée de quelques mois à plusieurs années.

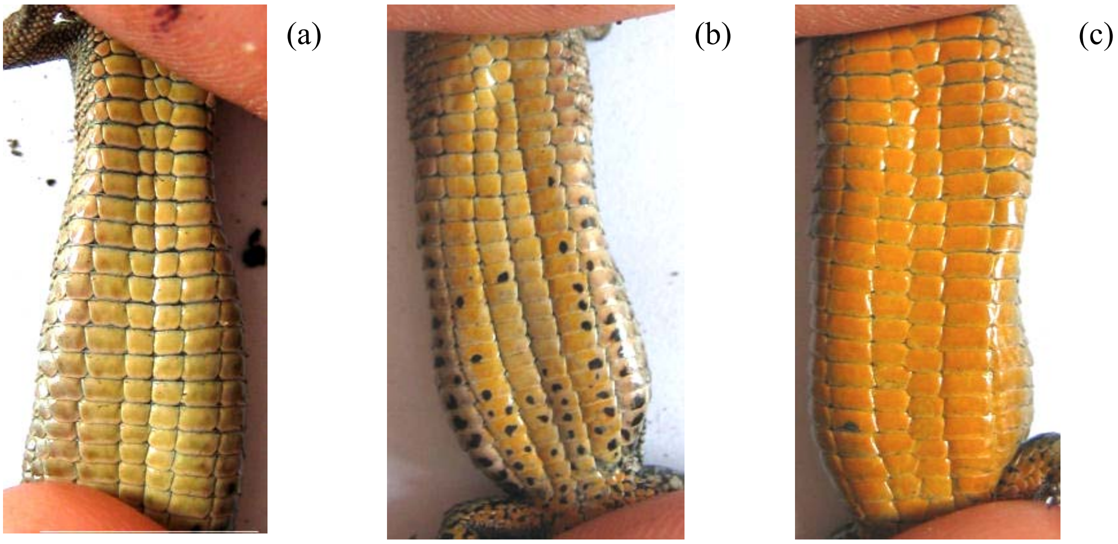
3) Estimation des paramètres : reproduction, survie et dispersion

Chaque année, des femelles gestantes sont capturées dans les différents populations du Mont Lozère à la fin du mois de juin et ramenées au laboratoire jusqu'à la mise bas. A la capture, les femelles sont mesurées et pesées. Les femelles sont ensuite gardées dans des terrariums individuels, avec de la terre de bruyère, un abri et de l'eau à volonté. Elles sont nourries une fois par semaine (ou une fois toutes les 2 semaines dans le cadre du traitement expérimental de ROB) avec une larve de *Pyralis farinalis* (teigne). Les femelles sont éclairées 6h par jour par des ampoules électriques (de 9h à 12h et de 14h à 17h pour mimer les conditions naturelles, où les femelles s'abritent durant les heures les plus chaudes). Lors de la mise bas, les jeunes vivants ou mort-nés sont comptés afin d'estimer la fécondité de la femelle, et son succès de ponte (nombre de jeunes vivants sur le nombre total d'œufs ou de jeunes produits). La taille et le poids des jeunes sont également mesurés, et la condition physique est calculée (résidus de la régression linéaire poids/taille). Les jeunes sont sexés en comptant les écailles ventrales, les femelles ayant un nombre supérieur d'écailles ventrales (Lecomte et al. 1992), ce qui permet d'estimer le sexe-ratio des pontes (proportion de mâles).

Les mères et les jeunes sont marqués individuellement par amputation partielle des phalanges, puis relâchés au point de capture de la mère. Au mois de septembre suivant, et au mois de mai de l'année suivante, les jeunes sont recapturés sur le terrain, mesurés et pesés. Les taux de survie sont estimés par des modèles de capture-marquage-recapture (modèle de Cormack-Jolly-Seber). Le statut de dispersion des individus (philopatrique ou dispersant) est estimé en comparant leur point de recapture avec leur point de lâcher d'origine. Chez le lézard vivipare, la dispersion a lieu dans les 10 jours suivant la naissance, et est définitive (Léna et al. 1998). La taille moyenne du territoire d'une femelle étant de 20m de diamètre (Clobert et al. 1994), les individus recapturés à moins de 15m de leur point de lâcher sont considérés comme philopatriques, ceux recapturés à plus de 30m de leur point de lâcher sont considérés comme dispersants. Les individus s'étant éloignés de leur point de lâcher d'une distance comprise entre 20 et 30m ne se voient pas attribuer de statut, et sont exclus des analyses portant sur le taux de dispersion.

II. Le polymorphisme de couleur

Chez cette espèce, le dos est brun-vert avec des dessins dorsaux noirs de forme variable. La couleur du ventre varie selon les âges, les sexes et les individus. Les juvéniles sont entièrement mélaniques, les sub-adultes ont une coloration vert-pâle, et les mâles une coloration orange vif. Chez les femelles, la coloration ventrale est variable et peut se regrouper en trois classes : jaune, orange, et mixte (coloration hétérogène, mélange de jaune et d'orange), qui reflètent des différences spectrophotométriques. Le détail des analyses statistiques décrites dans cette partie est fourni dans l'annexe I.



Les trois morphes de couleur ventrale: (a) jaune, (b) mixte, (c) orange.

1) Caractérisation spectrophotométrique de la couleur ventrale

Pendant de nombreuses années, la couleur ventrale des femelles a été estimée visuellement à l'aide d'un nuancier, et classée en jaune, orange ou mixte. Afin de pouvoir utiliser des données anciennes, nous devions vérifier que cette classification qualitative reflétait bien des différences spectrophotométriques entre individus. En 2004, nous avons mesuré le spectre de réflectance de 246 femelles capturées dans les populations du Mont Lozère (spectromètre Ocean Optics USB2000) et classifié leur couleur visuellement. Des exemples de spectres obtenus pour les différentes classes de couleur sont présentés sur la figure 3.

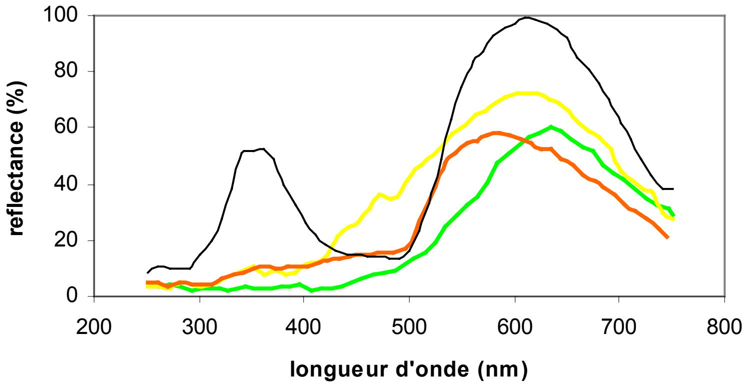


Figure 3: Exemples de spectres de réflectance pour une femelle jaune (en jaune), une femelle mixte (en vert), une femelle orange (en orange) et un mâle (en noir).

Nous avons ensuite cherché si la classification correspondait à des valeurs particulières des différents paramètres du spectre par une analyse discriminante. Nous avons trouvé que la classification des couleurs ventrales reflétait les variations de chroma et de teinte entre les individus (figure 4), et donc était représentative de la variation quantitative de la couleur. Cette analyse nous a donc permis d'utiliser la mesure visuelle de la couleur dans toutes les analyses suivantes.

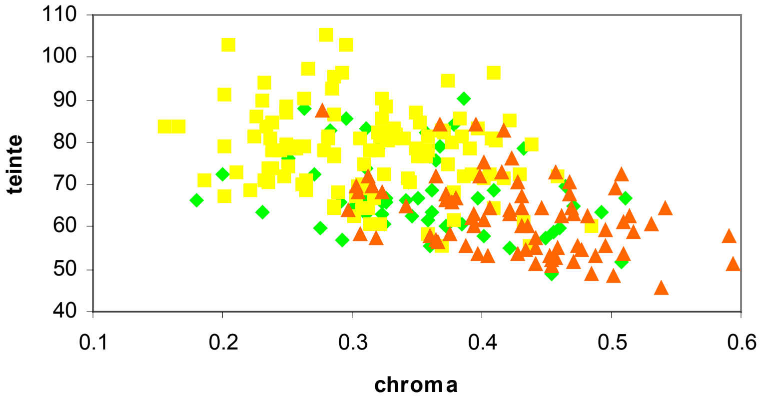


Figure 4: Distribution des femelles jaunes (carrés jaunes), mixtes (losanges verts) et oranges (triangles oranges) en fonction de leurs valeurs de chroma et de teinte.

2) Couleur ventrale et condition-dépendance

La couleur ventrale pourrait être un caractère condition-dépendant, et traduire des différences physiologiques entre femelles. En effet, les couleurs jaune et orange sont probablement déterminées par la présence de caroténoïdes, qui sont également impliqués dans la lutte contre les radicaux libres. La quantité de caroténoïdes disponibles pour l'expression d'une coloration est donc dépendante de la quantité utilisée par les défenses immunitaires, qui varie selon l'état de santé et l'âge des individus. Nous avons testé cette hypothèse en comparant les caractéristiques morphologiques (LMA, poids et condition physique) des femelles de différentes couleurs. Nous n'avons trouvé aucune corrélation entre la couleur ventrale et la morphologie, ce qui ne soutient pas l'hypothèse d'une expression condition-dépendante de la couleur. De plus, une analyse préliminaire des taux de caroténoïdes plasmatiques totaux montre que les femelles de couleur jaune ont davantage de caroténoïdes circulant (13,9 µg/mL ± 1,93) que les femelles oranges (10,9 µg/mL ± 1,38). Il n'y aurait donc pas de carence en caroténoïdes chez les femelles jaunes, mais plutôt une stratégie d'allocation différente entre le signal coloré et les autres fonctions physiologiques.

3) Stabilité et héritabilité de la couleur

La stabilité de la couleur au cours de la vie a été estimée sur un échantillon de 611 femelles recapturées au moins deux fois. Nous avons trouvé que la couleur mesurée à la 2^{de} occasion était fortement corrélée à la couleur mesurée à la $1^{ère}$ occasion, et que cette corrélation n'était pas affectée par des facteurs environnementaux (année, densité, fréquence des morphes, quantité de ressources disponible). Dans un certain nombre de cas cependant, une femelle a changé de classe de couleur au cours de sa vie. Néanmoins, de tels changements ne concernent essentiellement que des transitions entre deux classes de couleur adjacentes (de jaune vers mixte, orange vers mixte, ou inversement), et sont très probablement dus à des erreurs de classification. Par ailleurs, l'analyse de la stabilité des variables spectrophotométriques chez 94 femelles en réponse à une manipulation expérimentale de l'environnement a montré que, si le chroma pouvait varier d'une année à l'autre, la mesure de la teinte restait stable (voir annexe V). Ainsi, au moins une partie du spectre semble invariante au cours du temps et face aux variations d'un facteur de l'environnement.

L'héritabilité de la couleur a été estimée sur un échantillon de 136 couples mère-fille. Nous avons trouvé que la couleur développée par une fille à l'âge adulte était fortement corrélée à la couleur de sa mère, avec une héritabilité maternelle de 0,48. Ici encore, les facteurs environnementaux n'ont pas d'effet sur cette relation. Une telle valeur d'héritabilité est strictement comparable à ce qui est obtenu chez une autre espèce de reptile (*Uta stanburiana*), chez qui le polymorphisme de couleur est sous le contrôle d'un seul locus à trois allèles (locus OBY, Sinervo et Zamudio 2001, Sinervo et al. 2001, 2006).

Les résultats de ces analyses appuient l'hypothèse d'un déterminisme génétique (au moins partiel) de la couleur ventrale. Il est vrai que la variation de couleur pourrait toutefois être un caractère quantitatif, et le regroupement en classes serait alors artificiel. Cependant, si la couleur, même quantitative, est le marqueur de stratégies alternatives, ces stratégies ne sont pas nécessairement corrélées linéairement à la couleur. Autrement dit, la description du phénotype par une variable spectrophotométrique quantitative pourrait masquer une hétérogénéité non-linéaire entre femelles de couleur différente (par exemple si le phénotype des femelles mixtes n'est pas intermédiaire entre les phénotypes des femelles jaunes et oranges). Afin d'éviter ce biais, nous avons donc utilisé la mesure visuelle de la couleur dans toutes les analyses effectuées au cours de cette thèse. Ainsi, nous ne posons pas d'hypothèse a priori sur le sens des relations entre les classes de couleur, ce qui nous permet de déceler à la fois les effets linéaires et non-linéaires de la couleur ventrale (la variation quantitative étant simplement transformée en variable de classes dans le cas d'un effet linéaire).

III. Manipulation expérimentale de la fréquence des morphes jaunes ou orange

A l'origine, les quatre populations expérimentales du Mont Lozère différaient en densité, et en fréquence relative des différents morphes de couleur. Le tableau 2 résume ces différences, telles qu'elles ont été observées en 2004.

Paramètre démographique	Chalet	Bigoudou	Barnassac	Finiels
Densité des femelles adultes	160	140	175	100
Fréquence des femelles oranges	0,42	0,4	0,2	0,21
Fréquence des femelles jaunes	0,36	0,25	0,37	0,42

Tableau 2 : Densité et fréquence des morphes jaunes et oranges dans les 4 populations du Mont Lozère en 2004

Les populations Chalet et Bigoudou étaient donc relativement riches en femelles oranges, tandis que les populations Barnassace et Finiels étaient plus riches en femelles jaunes. Afin d'étudier l'impact de la fréquence locale des différents morphes de couleur sur la fitness des femelles, nous avons expérimentalement augmenté la fréquence des femelles jaunes dans les populations originellement riches en femelles oranges, et inversement, sans altérer la densité locale. Pour cela, nous avons réalisé des transplantations réciproques de femelles avec leurs jeunes entre populations pendant deux années consécutives.

En 2004, 50 femelles de chaque population ont été ramenées au laboratoire et gardées jusqu'à la mise bas. Après la mise bas, 25 femelles oranges de Chalet et leurs jeunes ont été relâchées à l'emplacement d'origine de 25 femelles jaunes de Finiels qui ont, elles, été relâchées dans la population de Chalet. La même manipulation a eu lieu, en échangeant 26 femelles oranges de Bigoudou avec 26 femelles jaunes de Barnassac. En 2005, 60 femelles de chaque population ont été ramenées au laboratoire, et les mêmes échanges ont été réalisés (23 femelles échangées entre Chalet et Finiels, 19 entre Bigoudou et Barnassac). En 2006, 50 femelles de chaque population ont été ramenées au laboratoire, et toutes relâchées à leur point d'origine. Ainsi, l'environnement expérimenté par les femelles en 2004 était leur environnement d'origine, et l'année 2004 sert donc d'année contrôle. En 2005 et 2006, les femelles ont expérimenté un environnement modifié, soit enrichi en femelles jaunes (populations J+), soit enrichi en femelles oranges (populations O+).

Une précédente expérience de transplantation réciproque (Massot et al. 1994) avait montré que les femelles transplantées restaient en majorité proches de leur point de lâcher. Ici, sur les 98 femelles mises en élevage en 2004 et relâchées dans leur population d'origine, 24 ont été recapturées en 2005. Il n'y a donc pas eu de différence de survie apparente entre les femelles transplantées et les autres entre 2004 et 2005. De plus, sur les 102 femelles transplantées en 2004, 22 ont été recapturées en 2005, dont 91% à moins de 20 m de leur point de lâcher et 36% à moins de 10 m. Par conséquent, nous pouvons considérer que la transplantation des femelles a durablement affecté la structure sociale des populations tout en en respectant la structure spatiale. Nous avons donc pu étudier la réponse de la reproduction des femelles, et de la dispersion, de la croissance et de la survie des jaunes à cette manipulation de l'environnement social.

CHAPITRE I : Coloration ventrale et stratégies d'histoire de vie

Au niveau théorique, l'évolution de stratégies alternatives implique l'existence d'une structuration de l'environnement (Heino et al. 1998), et les différentes stratégies vont voir leur fitness respective varier selon un ou plusieurs facteurs de l'environnement. La densité locale affecte la quantité de ressources disponibles pour la réalisation de différentes fonctions, et la présence de congénères a souvent des conséquences majeures sur la fitness des individus (Hassell 1975). Par conséquent, le degré de densité-dépendance est l'un des facteurs principaux affectant la forme des courbes de fitness par des effets négatifs sur la reproduction ou la survie, et les variations spatiales et temporelles de la densité sont souvent à l'origine de l'émergence de stratégies alternatives (Doebeli et Ruxton 1997, Brockmann 2001). De telles stratégies diffèrent dans leur degré de densité-dépendance, c'est-à-dire dans leur sensibilité à la compétition intra-spécifique. Il est donc probable que la fitness des différentes stratégies soit affectée non seulement par la quantité totale de ressources disponibles, mais également par la présence des autres stratégies (au moins pour les stratégies les moins compétitives). Ainsi, on peut prédire que des stratégies alternatives devraient être à la fois densité- et fréquence-dépendantes, l'intensité des relations variant selon les stratégies. Chez le lézard à flancs tachetés *Uta stansburiana*, une des deux stratégies alternatives des femelles est à la fois densité- et fréquence-dépendante (femelles oranges), tandis que l'autre est strictement densité-dépendante (femelles jaunes). Le morphe orange, plus sensible à la compétition, est également plus sensible à l'extinction (voir annexe IX), et est maintenu dans les populations grâce à un taux de dispersion supérieur (Sinervo et Clobert 2003). La coexistence de stratégies alternatives semble donc liée à un équilibre complexe entre leur dynamique (déterminée par le taux de reproduction et la sensibilité à la compétition) et leur taux de dispersion (voir annexe IX). Ainsi, afin de caractériser des stratégies alternatives, il semble nécessaire de commencer par décrire comment leur fitness (reproduction et survie) répond aux variations de densité et de fréquence des autres stratégies, et de rechercher des différences dans les stratégies de dispersion.

Chez le lézard vivipare, les morphes de couleur des femelles semblent impliqués dans la communication sociale et pourraient caractériser des stratégies alternatives. Chez cette espèce, la dynamique des populations est sensible aux effets des variations de la densité (Massot et al. 1992, Lecomte et al. 1994, Clobert et al. 1994), et les différentes stratégies pourraient se distinguer par leur degré de densité- ou de fréquence-dépendance. Les femelles du lézard vivipare ayant un contrôle important de leur allocation de reproduction à la fois par sélection sexuelle (directe : choix du mâle, ou indirecte : choix du sperme) et par de nombreux effets maternels (Massot et al. 2002, Meylan et al. 2002, Belliure et al. 2004), et elles ont donc la possibilité d'adopter différentes stratégies de reproduction en réponse aux variations des facteurs de l'environnement. De même, la dispersion natale étant en partie sous contrôle maternel (Massot et Clobert 2000, de Fraipont et al. 2000, Meylan et al. 2002), les femelles ont aussi la possibilité d'influencer le comportement de leurs jeunes pour définir des stratégies de dispersion alternatives. Cette espèce présente donc des caractéristiques favorables à l'évolution de stratégies d'histoire de vie alternatives, éventuellement signalées par le polymorphisme de couleur ventrale. Afin de tester cette hypothèse, nous avons étudié les différences de reproduction, survie et dispersion natale entre les morphes de couleur en utilisant les données du suivi à long terme, et en particulier les réponses de ces paramètres aux variations de l'environnement externe (densité, fréquence des morphes, qualité de l'habitat, quantité de ressources) et interne des femelles (âge, taille, condition physique).

Coloration ventrale, reproduction et survie[1]

Les femelles de différentes couleurs montrent des différences au niveau des caractéristiques de leur ponte : taille de ponte, succès de ponte, et sexe-ratio, ce qui peut correspondre à des stratégies de reproduction alternatives.

Les femelles jaunes ont une taille de ponte inférieure en moyenne (4,9) à celle des femelles mixtes (5,4) ou oranges (5,6), et les femelles mixtes ont un succès de ponte supérieur en moyenne (0,84) aux femelles jaunes (0,8) et oranges (0,78). Le succès de ponte est également affecté par la fréquence locale des femelles jaunes, la densité de femelles adultes, et l'âge des femelles, ces effets étant dépendants de la couleur individuelle. Ainsi, les femelles jaunes et oranges sont négativement affectées par la fréquence des femelles jaunes, tandis que les femelles mixtes n'y sont pas sensibles (figure 5a). Les femelles oranges sont également affectées fortement par la densité de femelles adultes, tandis que l'effet est plus faible chez les femelles jaunes et mixtes (figure 5b). Enfin, les femelles jaunes subissent une baisse de leur succès de ponte avec l'âge, tandis que les femelles oranges et mixtes subissent une baisse moins sévère (figure 5c).

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[1] Les résultats de ces analyses sont présentés en détail dans l'annexe I : Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara.*

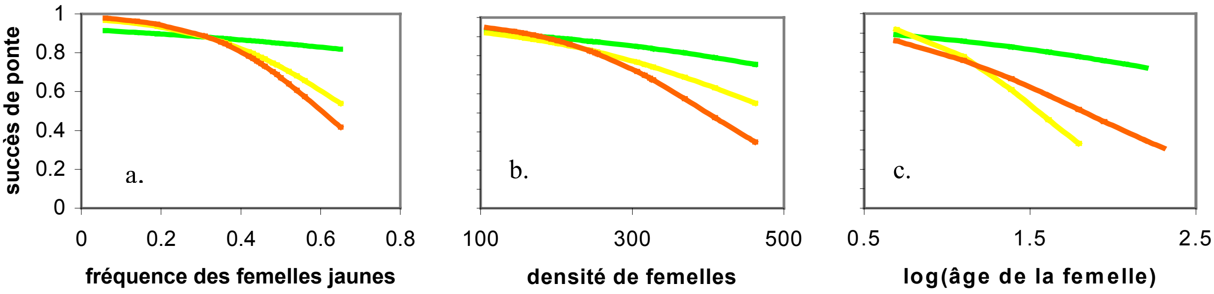

Figure 5 : Effet de différents facteurs sur le succès de ponte des femelles en fonction de leur couleur ventrale (femelles jaunes, en jaune ; femelles mixtes, en vert ; femelles oranges, en orange). (a) Effet de la fréquence des femelles jaunes. (b) Effet de la densité de femelles.
(c) Effet de l'âge de la femelle.

Le sexe-ratio des pontes est dépendant de la condition physique et de la couleur des femelles. Les femelles jaunes en bonne condition produisent relativement plus de descendants femelles, tandis que les femelles oranges en bonne condition produisent relativement plus de mâles (figure 6a). Dans la zone à faible densité, le sexe-ratio de la ponte est aussi affecté par la taille des femelles : les femelles jaunes de grande taille produisent relativement plus de mâles, tandis que les femelles oranges et mixtes de grande taille produisent relativement plus de mâles (figure 6b).

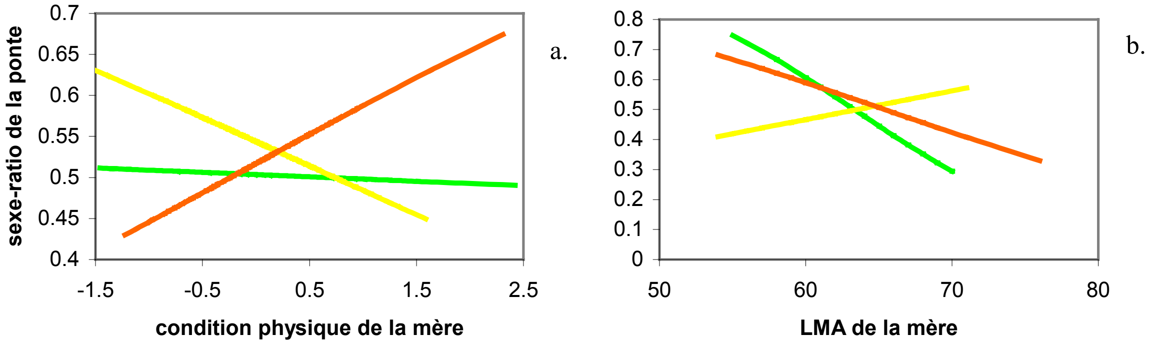

Figure 6: Effet de différents facteurs sur le sexe-ratio de la ponte en fonction de la couleur ventrale de la mère (femelles jaunes, en jaune ; femelles mixtes, en vert ; femelles oranges, en orange). (a) Effet de la condition physique de la mère. (b) Effet de la taille de la mère.

Les femelles de différentes couleurs ne montrent pas de différence de taux de survie. La survie des femelles est variable dans le temps, et positivement corrélée aux variations de la fréquence des femelles jaunes dans la population.

Coloration ventrale et dispersion[2]

Les juvéniles de mère orange ont un taux de dispersion moyen supérieur (0,53) à celui des juvéniles de mère jaune (0,48) ou mixte (0,41). La dispersion des jeunes est également affectée par plusieurs facteurs environnementaux : température au mois de juin, température au mois d'août, et traitement expérimental subi par leur mère durant la gestation (quantité de nourriture fournie). Les juvéniles de mère mixte dispersent moins en réponse à l'augmentation de la température moyenne en Juin (figure 7a), tandis que les juvéniles de mère orange dispersent plus en réponse à l'augmentation de la température en Août (figure 7b). Les juvéniles de mère jaune ne semblent pas répondre aux variations de température.

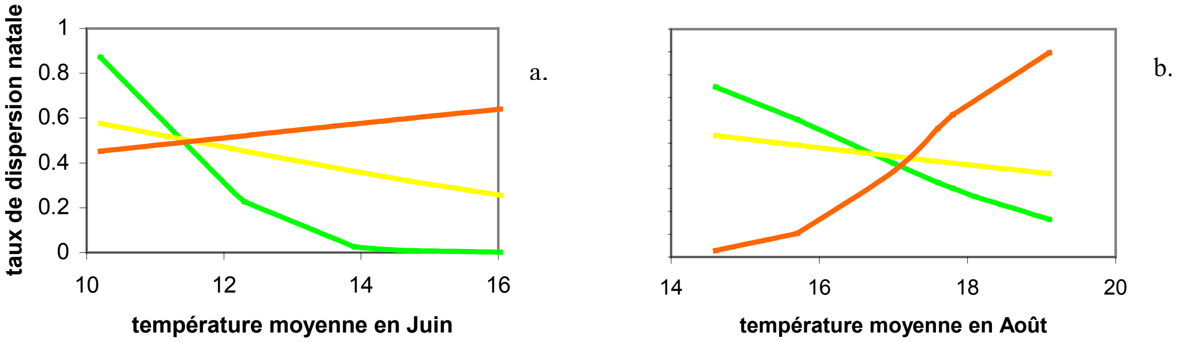

Figure 7 : Effet de la température moyenne en Juin et en Août sur la dispersion natale des jeunes en fonction de la couleur ventrale de leur mère (femelles jaunes, en jaune ; femelles mixtes, en vert ; femelles oranges, en orange). (a) Température en Juin. (b) Température en Août.

Les juvéniles de mère mixte répondent également à la quantité de nourriture reçue par leur mère durant la gestation : leur dispersion augmente en réponse à une restriction alimentaire (figure 8).

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[2] Les résultats de ces analyses sont présentés en détail dans l'annexe II : Female colour morphs in the common lizard display alternative offspring dispersal strategies with respect to climatic change.

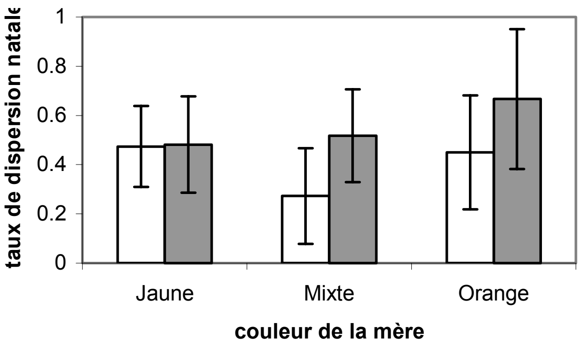

Figure 8 : Taux de dispersion natale des jaunes en fonction de la couleur de leur mère et du traitement de nourrissage subi pendant la gestation (en blanc : « bien nourri » ; en gris : « mal nourri »). Les barres d'erreur correspondent à l'intervalle de confiance à 95% autour de la moyenne.

Peut-on parler de stratégies alternatives?

Ces résultats montrent que les femelles de couleur différente adoptent des stratégies alternatives d'histoire de vie. En effet, bien que la couleur ventrale apparaisse comme un caractère continu, les caractéristiques des femelles de différentes couleurs ne sont pas linéaires. En particulier, le phénotype des femelles mixtes est souvent en opposition par rapport aux deux autres types de femelles et ne représente donc pas un phénotype « intermédiaire ». Par contre, la couleur des femelles mixtes apparaît comme un mélange de jaune et d'orange, et leurs variables spectrophotométriques (chroma et teinte) sont intermédiaires entre celles des femelles jaunes et oranges. Une explication simple de ce phénomène serait que la couleur ventrale soit contrôlée par un locus et deux allèles codominants: jaune (J) et orange (O). Les femelles mixtes seraient alors des hétérozygotes (génotype JO ou OJ), et les femelles jaunes ou oranges des homozygotes (JJ ou OO). Chez le lézard vivipare, les femelles sont le sexe hétérogamétique (Chevalier et al. 1979). Si notre hypothèse concernant le déterminisme de la couleur ventrale est correcte, alors le gène correspondant devrait se trouver sur un autosome, et son expression serait inhibée chez les mâles (presque toujours oranges). Dans ce système, les hétérozygotes femelles détiendraient un avantage sélectif par rapport aux homozygotes (succès de ponte supérieur), et le polymorphisme pourrait être maintenu par overdominance. Néanmoins, il faut admettre que pour l'instant, les mécanismes d'héritabilité de la couleur ventrale ne sont que spéculatifs, et le rôle du génotype paternel n'est pas du tout élucidé. En particulier, l'héritabilité paternelle pourrait affecter fortement le système si les femelles ou les mâles exercent un choix de partenaire dépendant de leur propre couleur ventrale et/ou de celle de leur partenaire. La reproduction sexuée peut ainsi directement affecter le maintien du polymorphisme dans la population, selon que l'appariement est aléatoire, assorti, ou non-assorti.

En dépit des incertitudes restantes sur le déterminisme de la couleur ventrale, il apparaît clairement que les trois classes de femelles présentent des stratégies d'histoire de vie distinctes, qui constituent des phénotypes alternatifs. Ces phénotypes ajustent leur reproduction et la dispersion de leurs jeunes en réponse à différentes pressions de sélection, probablement afin de maximiser leur fitness.

Quelles sont ces stratégies ?

Certains modèles théoriques prédisent que dans un environnement variable spatialement et temporellement, des stratégies alternatives peuvent évoluer, qui diffèrent dans leur degré de densité-dépendance et dans leur taux de dispersion (Johst et al. 1999). Nous retrouvons en partie ces prédictions chez le lézard vivipare, les femelles oranges étant à la fois les plus sensibles à la densité locale et celles montrant le plus fort taux de dispersion chez leurs jeunes. Néanmoins, de nombreux autres facteurs semblent intervenir dans le déterminisme des stratégies de reproduction et de dispersion, ce qui génère des stratégies complexes, sous condition-dépendance multiple.

Les facteurs de l'environnement externe et interne portent des informations quant à l'intensité relative des différentes pressions de sélection susceptibles d'affecter la fitness des individus. Ainsi, la densité de femelles ou la fréquence de femelles jaunes sont probablement corrélées à l'intensité de la compétition intra-spécifique pour les ressources, et à l'intensité de la compétition couleur-spécifique en particulier. En revanche, l'âge de la femelle et sa condition physique sont plutôt à mettre en relation avec le niveau de compétition entre apparentés. Chez cette espèce, la compétition mère-jeunes est une pression de sélection forte agissant notamment au niveau du taux de dispersion des jeunes (Ronce et al. 1998, de Fraipont et al. 2000, Meylan et al. 2002, 2004). L'analyse des stratégies de reproduction des femelles suggère que les femelles oranges sont les plus sensibles à la compétition en général, et à la compétition entre apparentés en particulier, tandis que les femelles mixtes y seraient les moins sensibles. En revanche, les femelles jaunes seraient plus sensibles à la sénescence.

L'analyse des stratégies de reproduction semble indiquer que le morphe orange est le morphe dispersant, et qu'il réagit fortement aux changements des conditions de milieu (réchauffement du climat). La dispersion des jeunes des femelles mixtes semble être plutôt dépendante de la quantité de ressources disponibles : ainsi, les jeunes de mère mixte dispersent davantage lorsque leur mère a subi un nourrissage réduit, et dispersent moins en réponse au réchauffement du climat. En effet, l'augmentation de la température moyenne semble avoir pour l'instant des conséquences positives sur la dynamique des populations des Cévennes (Chamaillé-Jammes et al. 2006), en induisant probablement un enrichissement du milieu. La dispersion des jeunes de mère jaune paraît quant à elle non plastique, ou bien sensible à d'autres facteurs non examinés ici.

Bien que les morphes se distinguent clairement à la fois au niveau de leur reproduction, et de leur dispersion, il est cependant difficile de dégager des caractéristiques définissant leurs stratégies d'un point de vue adaptatif. Les effets significatifs au niveau de la reproduction ne se retrouvent pas au niveau de la dispersion, où d'autres effets apparaissent. Il est possible que les stratégies de reproduction et de dispersion soient affectées de façon indépendante par différents facteurs, et que le phénotype produit résulte d'un équilibre entre les forces agissant sur la reproduction et celles agissant sur la dispersion. En effet, si une femelle module le sexe-ratio de ses pontes en fonction de son âge pour limiter la compétition avec ses filles, il n'est pas forcément nécessaire d'agir également sur le taux de dispersion de ses jeunes, qui peut alors répondre davantage aux facteurs prédisant la quantité de ressources disponible. Ainsi, les effets maternels sur la morphologie et la dispersion des jeunes peuvent se compléter afin de produire des phénotypes adaptatifs au regard de plusieurs facteurs sélectifs (Vercken et al. 2007).

Les stratégies adoptées par les morphes de couleur sont donc probablement multifactorielles : on ne peut pas définir un morphe « sensible à la compétition entre apparentés », et un autre « sensible à la compétition pour les ressources ». Il est en fait probable que tous les individus soient sensibles à ces pressions sélectives, mais à des degrés différents, et avec différentes réponses. Les interactions de compétition semblent en tous cas affecter fortement le succès reproducteur des femelles, et pourraient être à l'origine des différences observées entre les morphes. En effet, si les stratégies se distinguent par leur potentiel compétitif ou la nature des interactions sociales qu'elles réalisent, alors leur sensibilité à la compétition avec les autres stratégies peut varier, et générer des réponses différentes aux variations de l'environnement social décrites par la densité de femelles adultes et la fréquence des femelles jaunes. Afin de tester cette hypothèse, nous avons étudié le comportement de femelles confrontées à d'autres femelles au laboratoire, et vérifié si la couleur des individus en présence affectait le résultat de l'interaction sociale.

CHAPITRE II : Réponses comportementales à la couleur de l'environnement social

Les interactions sociales entre individus sont souvent à l'origine de l'évolution de phénotypes alternatifs complexes (Gross 1996). En particulier, les pressions de sélection générées par les interactions de compétition vont favoriser l'apparition de signaux relatifs au phénotype « social » des individus (potentiel compétitif, Huntingford et al. 2000 ; qualité individuelle, Sheldon 2000 ; statut de dominance, Langmore 2000). Ainsi, l'existence d'une structuration sociale de l'environnement, définie par la répartition spatiale des individus, peut favoriser l'émergence de stratégies alternatives, signalées par un polymorphisme. Si les interactions sociales sont à l'origine de l'évolution de telles stratégies, et d'un signal permettant leur identification, il est probable que les stratégies vont avoir un effet sur la réalisation des interactions sociales, en déterminant des comportements alternatifs en réponse au signal. Ainsi, l'interaction entre deux congénères dépendra, entre autres, de leur stratégie respective, et l'étude des schémas comportementaux associés aux différentes stratégies pourra permettre de comprendre la fonction sociale du polymorphisme de stratégies.

Chez le lézard vivipare, l'habitat est fondamentalement hétérogène, caractérisé par la distribution discrète de certaines ressources (pierres, arbres, buissons). Les individus vont avoir une répartition non aléatoire, agrégée autour de ces ressources. Ainsi, il n'est pas rare d'observer un certain nombre d'individus au même endroit, au même moment. De telles associations spatiales concernent le plus souvent des femelles, les mâles étant plus territoriaux (Massot 1992). Les femelles semblent donc avoir une certaine tolérance sociale, et être régulièrement en contact avec leurs congénères. Ainsi, bien que le lézard vivipare ne soit pas une espèce sociale au sens propre (définie par le partage des soins aux jeunes, Jaisson 1985), les interactions sociales entre individus sont fréquentes, et potentiellement importantes pour l'acquisition d'information concernant l'environnement distant (Cote 2006). De plus, des expériences en populations naturelles suggèrent l'existence d'une forte compétition pour les ressources entre femelles (Massot et al. 1992, Lecomte et al. 1994), et nous avons vu au chapitre I que les femelles de différentes couleurs semblaient avoir des sensibilités différentes à la compétition. La couleur ventrale pourrait donc être un indicateur du potentiel compétitif des femelles, et de leur statut social (dominant ou subordonné). Le polymorphisme de couleur serait alors un marqueur de stratégies complexes, impliquant à la fois les traits d'histoire de vie et le comportement social.

Des comportements couleur-dépendants[3]

Si le polymorphisme de couleur ventrale est impliqué dans les interactions sociales, il est donc probable qu'il joue un rôle dans les interactions de compétition entre femelles, en signalant des différences de potentiel compétitif ou de stratégie comportementale. Sous cette hypothèse, on peut alors prédire que des femelles vont se comporter différemment face à une autre femelle, en fonction de leur propre couleur et de celle de leur congénère, ce qui peut refléter une relation de dominance sociale entre individus.

Afin de tester cette prédiction, nous avons étudié au laboratoire le comportement d'une femelle (femelle focale) mise en présence d'une autre femelle (femelle adverse) de couleur variable et non-familière, dans un espace limité favorisant le contact social, avec une ressource utilisable par une seule femelle (emplacement de thermorégulation). Nous avons suivi différentes variables comportementales de la femelle focale : le temps passé à gratter les parois du terrarium (signe de stress, de Fraipont et al. 2000), le nombre de tentatives de morsure et le nombre de tentatives de fuite (mouvement d'éloignement en réponse au rapprochement de la femelle adverse). Ces expériences ont été réalisées à deux périodes de l'année : au début de la vitellogénèse (mois de mai), et après la mise bas (mois de juillet). Nous avons ensuite regardé si les comportements observés étaient dépendants de la couleur de l'une ou des deux femelles en présence, et si les comportements étaient modifiés selon la période d'activité. Les résultats de ces analyses sont résumés dans le tableau 3.

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[3] Les résultats de ces analyses sont présentés en détail dans l'annexe III : Female colour polymorphism and social dominance in the common lizard (*Lacerta vivipara*)

Variable analysée	Affectée par	Moyennes par couleur		
		Jaune	Mixte	Orange
Temps de grattage (en secondes)	Couleur de la femelle focale	46,2 s	63,9 s	43,8 s
Nombre de tentatives de morsure	Couleur de la femelle focale	0,50	0,64	0,39
	Couleur de la femelle adverse	0,41	0,60	0,50
	Interaction (couleur de la femelle focale)x(couleur de la femelle adverse)	Voir figure 9		
Nombre de tentatives de fuite	Couleur de la femelle adverse	1,3	1,3	0,8

Tableau 3 : Effets significatifs de la couleur de la femelle focale ou adverse sur les variables comportementales, et moyennes de ces variables par couleur (de la femelle focale ou adverse). Exemple : le temps de grattage est affecté par la couleur de la femelle focale. Les femelles mixtes grattent en moyenne pendant 63,9 secondes, tandis que les femelles jaunes grattent 46,2 secondes et les femelles oranges 43,8 secondes.

Le temps passé à gratter dépend de la couleur de la femelle focale : les femelles mixtes grattent davantage que les femelles jaunes ou oranges. Le nombre de tentatives de fuite dépend de la couleur de la femelle adverse : Les femelles focales fuient plus souvent face à une femelle adverse jaune ou mixte que face à une femelle orange.

Le nombre de tentatives de morsure dépend de la couleur de la femelle focale, de celle de la femelle adverse, et de leur interaction : les femelles mixtes attaquent plus souvent leur adversaire que les femelles oranges, et les femelles focales attaquent plus souvent les femelles adverses mixtes que les jaunes. Si on considère l'interaction entre la couleur de la femelle focale et celle de la femelle mixte : les femelles mixtes attaquent les femelles jaunes plus souvent que les femelles mixtes ou oranges, alors que les femelles jaunes ou oranges attaquent moins souvent les femelles jaunes (Figure 9).

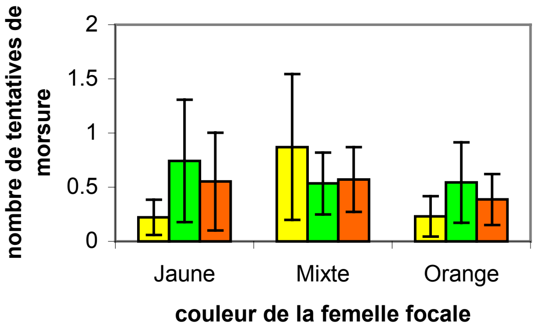

Figure 9 : Nombre de tentatives de morsure en fonction de l'interaction entre la couleur de la femelle focale et la couleur de la femelle adverse (en jaune : femelle adverse jaune, en vert : femelle adverse mixte, en orange : femelle adverse orange). Les barres d'erreur correspondent à l'intervalle de confiance à 95% autour de la moyenne.

Ces résultats démontrent que les femelles de différentes couleurs adoptent des comportements différents, et qu'elles réagissent à la présence d'une autre femelle en fonction de leur propre stratégie et de celle de leur opposant. La couleur ventrale semble donc être un signal utilisé dans les interactions sociales, à la fois pour renseigner sur son propre comportement, et pour acquérir des informations sur le comportement des autres femelles. Cependant, il est possible que d'autres signaux soient également impliqués dans ces interactions sociales, indépendamment ou en complément de la couleur ventrale.

La couleur : un signal social[4]

La couleur ventrale peut être un signal utile lors des interactions sociales, car elle reflète la stratégie d'histoire de vie adoptée par la femelle. Cependant, si la couleur ventrale est le marqueur d'une stratégie génétiquement déterminée, elle ne reflète pas a priori d'autres traits du phénotype également importants lors des interactions sociales (comme l'âge, la condition, la motivation…). Ces traits variables doivent donc être signalés par d'autres composantes du phénotype, capables de porter un signal labile. Les signaux chimiques, comme les odeurs ou les phéromones, peuvent transmettre des informations précises sur les variations de la condition individuelle. Chez les lacertidés, les signaux chimiques ont été impliqués à plusieurs reprises dans la communication intraspécifique (Léna et de Fraipont 1998, Aragon et al. 2001, 2006), et en particulier dans les mécanismes de reconnaissance individuelle (Aragon et al. 2001, Léna et de Fraipont 1998). La signature phéromonale produite par les glandes pré-cloacale et fémorale varie fortement entre les individus (Alberts 1990, 1992), et porte des

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[4] Les résultats de ces analyses sont présentés en détail dans l'annexe IV : Female colour polymorphism in the common lizard (*Lacerta* vivipara) signals for alternative strategies in social encounters

informations potentiellement utiles lors des interactions sociales (Lopez et al. 2003, 2006). Ces signaux chimiques pourraient affecter le comportement social des femelles, en portant un message plus complet que celui de la couleur ventrale, qui serait alors un signal redondant. Ils pourraient également être utilisés en complément du signal visuel afin de décrire plus précisément le phénotype de l'individu adverse.

Afin de vérifier le rôle de la couleur ventrale comme marqueur de stratégie lors des interactions sociales, nous avons répété l'expérience précédente, en masquant avec de la peinture ou non la couleur ventrale de la femelle adverse. Afin d'étudier plus précisément l'‘impact du signal coloré sur le comportement des femelles, nous avons analysé trois variables comportementales supplémentaires : le temps de marche, le temps de thermorégulation, et le nombre de tentatives de rapprochement (lorsqu ‘une femelle se dirige vers l'autre sans comportement agressif). Les résultats de cette expérience sont résumés dans le tableau 4.

Variable analysée	Effet couleur	Effet traitement (peinture)
Temps de marche	Couleur de la femelle adverse	En interaction avec la couleur de la femelle focale
Temps de grattage	-	-
Temps de thermorégulation	-	-
Tentatives de morsure	Couleur de la femelle adverse	Effet simple
Tentatives de fuite	-	-
Tentatives de rapprochement	Couleur de la femelle focale Couleur de la femelle adverse	En interaction avec la couleur de la femelle focale et la couleur de la femelle adverse

Tableau 4 : Effets significatifs de la couleur de la femelle focale ou de celle de la femelle adverse et du traitement expérimental sur les variables comportementales. Exemple : le temps de marche est affecté par la couleur de la femelle adverse, et par l'interaction entre le traitement expérimental et la couleur de la femelle focale.

La visibilité de la couleur ventrale de la femelle adverse affecte le comportement de la femelle focale. Les variables qui ne répondent à la couleur ventrale d'aucune des deux femelles ne sont pas non plus affectées par la visibilité du signal (temps de grattage, temps de thermorégulation et tentatives de fuite). Ainsi, l'effet du traitement n'est significatif que pour les comportements sensibles au signal coloré.

Par contre, la couleur ventrale des femelles et la visibilité de la couleur de la femelle adverse affectent les autres variables (temps de marche, tentatives de morsure et tentatives de rapprochement), indépendamment ou en interaction. Les femelles oranges ont une activité accrue face à une femelle adverse dont la couleur est masquée, alors que les femelles jaunes ou mixtes réduisent leur activité dans le même cas (figure 10).

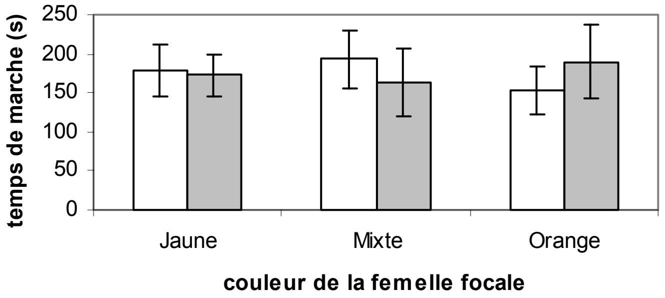

Figure 10 : Temps passé à marcher en fonction de la couleur de la femelle focale lorsque la couleur de la femelle adverse est visible (en blanc) ou masquée (en gris). Les barres d'erreur correspondent à l'intervalle de confiance à 95% autour de la moyenne.

Les femelles focales sont plus agressives envers les femelles adverses oranges (nombre moyen de tentatives de morsures 0,74) qu'envers les femelles jaunes (0,30) ou mixtes (0,15). Les femelles focales sont également plus agressives envers les femelles adverses dont la couleur est visible (0,48) que lorsque leur couleur est masquée (0,25).

Le nombre de tentatives de rapprochement des femelles jaunes est profondément affecté par le traitement, avec des réponses opposées lorsque la couleur de la femelle adverse est visible ou masquée (figure 11). Par contre, la réponse des femelles mixtes ou oranges est similaire dans les deux traitements.

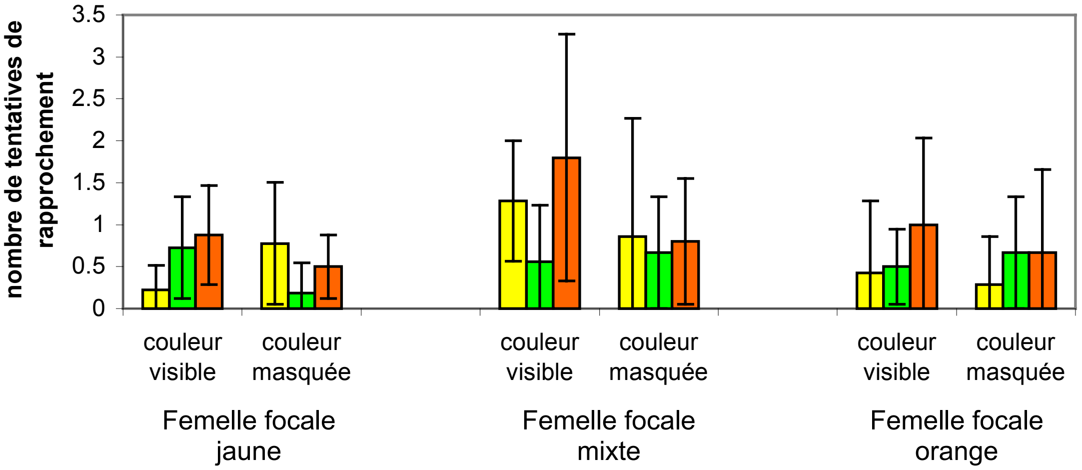

Figure 11 : Nombre de tentatives de rapprochement en fonction de la couleur de la femelle focale et de la couleur de la femelle adverse (femelle jaune : en jaune, femelle mixte : en vert, femelle orange : en orange) lorsque celle-ci est visible ou masquée. Les barres d'erreur correspondent à l'intervalle de confiance à 95% autour de la moyenne.

Nous avons également proposé à des femelles de choisir entre des abris nocturnes portant des signaux chimiques provenant d'une autre femelle, afin de tester si ces signaux chimiques reflétaient la stratégie des femelles et étaient redondants par rapport au signal de la couleur ventrale. Les résultats de cette expérience suggèrent que les femelles n'utilisent pas de signaux chimiques corrélés à la couleur ventrale pour choisir un abri nocturne. D'une part, il est possible que les signaux chimiques produits par les femelles ne soient pas corrélés à la couleur ventrale, c'est pourquoi les femelles ne peuvent pas choisir leur abri en fonction de l'identité de la femelle résidente dans notre expérience (puisque celle-ci n'est pas présente). Une autre explication serait que les femelles identifient correctement le morphe de la femelle résidente grâce aux signaux chimiques qu'elle a laissés, mais qu'elles n'utilisent pas cette information pour choisir un abri (information non pertinente en l'absence de la femelle résidente, ou bien la couleur est utilisée dans d'autres contextes sociaux).

Par contre, la couleur de la femelle adverse a un effet sur certaines variables comportementales de la femelle focale qui répondent alors également à la visibilité de ce signal. Le signal visuel est donc utilisé par la femelle focale pour modifier son propre comportement. Néanmoins, le comportement de la femelle focale n'est pas entièrement dépendant du signal visuel qu'elle perçoit : si c'était le cas, nous devrions observer une réponse différente selon la couleur de la femelle adverse quand celle-ci est visible, et un seul type de réponse quand celle-ci est masquée (réponse à un « nouveau » signal visuel). En particulier, on aurait pu prédire que les femelles seraient plus agressives envers les femelles peintes: en effet, face à un nouveau signal marquant potentiellement une nouvelle stratégie, les femelles auraient eu intérêt à « tester » cette nouvelle stratégie pour éventuellement imposer une dominance. Or la réponse inverse est observée, les femelles peintes subissent moins de tentatives de morsure. Il pourrait donc y avoir un avantage à la nouveauté, et les stratégies inconnues bénéficieraient d'une sorte de « méfiance » initiale des autres femelles. Cependant, cette hypothèse est infirmée par le fait que la peinture ne masque pas entièrement la stratégie de la femelle adverse. En effet, les femelles répondent significativement à la couleur de la femelle adverse même lorsque celle-ci est masquée : il semble donc qu'une partie de l'information concernant la stratégie de la femelle adverse soit tout de même accessible à la femelle focale. D'une part, il est possible que des signaux chimiques corrélés à la couleur ventrale soient utilisés par la femelle focale. D'autre part, étant donné que la couleur de la femelle focale est toujours visible, la femelle adverse adopte un comportement correspondant à celui d'une femelle de cette stratégie en face de la femelle focale. Ce comportement stéréotypé peut donc renseigner la femelle focale sur la stratégie adoptée par la femelle adverse.

Ces résultats démontrent cependant que le signal visuel, même s'il n'est pas forcément unique, est utilisé par les femelles lors des interactions sociales pour adapter leur comportement en fonction de leur propre stratégie. Si ce signal comporte plusieurs composantes qui renseignent sur différents aspects du phénotype de l'individu (stratégie génétiquement déterminée, et variations ponctuelles de l'état physiologique et motivationnel), alors il peut permettre aux femelles de prendre des décisions adaptatives, et de maximiser leur succès en fonction d'un contexte compétitif précis.

Des stratégies sociales alternatives ?

Les femelles de différentes couleurs adoptent des comportements différents, et réagissent spécifiquement à leur environnement social : la couleur ventrale est donc corrélée à des syndromes comportementaux alternatifs qui peuvent affecter les relations de compétition entre femelles. Les différences comportementales observées dans la première expérience peuvent être indicatrices des interactions de compétition entre femelles, et des relations de dominance sociale entre morphes lors d'une compétition pour l'accès à une ressource.

Les femelles jaunes essaient régulièrement de mordre les autres femelles et les font fuir facilement, mais elles sont elles-mêmes en moyenne peu agressées, ce qui serait compatible avec un rang de dominance élevé. En revanche, les femelles oranges sont peu agressives et font rarement fuir les autres femelles, mais sont souvent attaquées, ce qui correspondrait à un statut social inférieur. Le cas des femelles mixtes est plus difficile à interpréter : ces femelles sont relativement agressives, et en particulier envers les femelles jaunes. Ces femelles semblent aussi être les plus stressées, ce qui pourrait être lié à un statut de dominance intermédiaire ou condition-dépendant. Si ces femelles doivent en permanence maintenir leur statut, cela explique qu'elles soient souvent impliquées dans des interactions agonistiques (en particulier avec les femelles jaunes dominantes), ce qui peut générer un stress social important. Les couleurs ventrales pourraient donc être des marqueurs de statut social, correspondant à des stratégies comportementales différentes (dominante, dominée, et challengeur).

Une telle hiérarchie sociale déterminée génétiquement peut en effet être maintenue dans une population, si le bilan des coûts et bénéfices associés à chaque statut est équivalent. Ainsi, un statut dominant est en général associé à des bénéfices importants (exploitation accrue des ressources ou utilisation des ressources de meilleure qualité) et des coûts élevés (coûts métaboliques liés au maintien du statut). L'analyse des stratégies de reproduction des femelles présentée au chapitre I a justement montré que les femelles jaunes (potentiellement dominantes) étaient les plus sensibles à la sénescence. Au contraire, un statut inférieur peut être associé à des bénéfices réduits (exploitation limitée des ressources, ou utilisation de ressources de moindre qualité) et des coûts faibles (peu d'interactions agonistiques et faibles coûts métaboliques). En particulier, l'ajustement du comportement individuel en fonction de cette hiérarchie sociale peut permettre d'optimiser les coûts et bénéfices liés à la compétition sociale pour tous les types d'individus.

Ainsi, dans notre expérience, les femelles de différentes couleurs montrent une variabilité de leur comportement en réponse à la couleur de la femelle adverse : les stratégies sociales des femelles sont donc plastiques, et sensibles à la hiérarchie sociale. De plus, si certaines réponses comportementales sont stables d'une année sur l'autre et peuvent traduire une hiérarchie de dominance fixe entre stratégies, une grande part du comportement apparaît variable dans le temps (effet saisonnier et effet annuel). La « sensibilité sociale » des femelles (relation entre comportement et couleur ventrale) serait donc également plastique, et soumise aux variations des facteurs de l'environnement. Cette plasticité multiple des stratégies sociales peut s'avérer adaptative, si elle permet aux femelles d'adopter un comportement optimal en fonction de l'environnement dans lequel elles se trouvent. Ainsi, une diminution de la quantité de ressources disponibles, ou une modification de l’environnement social (fréquences des différents morphes, apparentement local,…) pourraient modifier les pressions de sélection subies par les femelles, et favoriser certains comportements plutôt que d’autres, en fonction de la couleur (et donc du statut) de l’individu. Ces différentes stratégies sociales pourraient alors être à l’origine de l’évolution et du maintien du polymorphisme de couleur ventrale, si la plasticité du comportement des femelles leur permet d’obtenir des fitness moyennes égales dans les populations. Si les stratégies sont adaptatives, les différents morphes doivent obtenir des fitness moyennes égales dans tous les environnements, ou bien certains morphes sont favorisés dans certains environnements et défavorisés dans d’autres (la variabilité spatiale et/ou temporelle de l’environnement naturel assurant une égalité moyenne des fitness à long terme). Cette hypothèse peut être testée en comparant la fitness des différents morphes de couleur dans différents environnements sociaux : nous avons donc mesuré certaines composantes de la fitness des femelles et de leurs jeunes dans différentes populations où la fréquence locale des femelles jaunes ou oranges a été augmentée.

CHAPITRE III : Variation de l'environnement social et fitness des stratégies

Le polymorphisme de couleur ventrale étant très probablement déterminé génétiquement, il doit être maintenu dans les populations naturelles par un mécanisme sélectif comme l'overdominance, la sélection disruptive, ou la fréquence-dépendance négative (Barton et Turelli 1989). La compétition sociale étant souvent à l'origine de l'évolution de polymorphismes de couleur (West-Eberhard 1983), l'environnement social et ses variations spatiales et/ou temporelles sont donc potentiellement impliqués dans le maintien de stratégies alternatives couleur-dépendantes chez cette espèce. La fréquence des différents morphes en particulier est un bon descripteur de l'environnement social, car la présence et le nombre de femelles de différentes couleurs vont affecter le niveau de compétition locale. En effet, les femelles de différentes couleurs semblent être liées par des relations de dominance sociale, et différeraient dans leur potentiel compétitif et leur stratégie d'exploitation des ressources. La fitness d'un individu pourra donc être affectée par l'intensité de la compétition locale, selon sa propre stratégie et selon les mécanismes sélectifs à l'œuvre dans la population.

L'étude des variations de la fitness des différents morphes dans plusieurs populations où la fréquence des morphes varie peut donc permettre d'identifier le mécanisme sélectif impliqué dans le maintien du polymorphisme (Svensson et al. 2005). Cependant, de telles analyses sont difficiles à effectuer dans le cadre d'une approche corrélative, car de nombreux facteurs confondants (biotiques ou abiotiques) peuvent covarier avec la fréquence des morphes et biaiser les résultats. Afin de limiter l'importance des facteurs confondants, il est donc nécessaire de réaliser des approches expérimentales, où la fréquence des morphes dans les populations est manipulée artificiellement, et de suivre les conséquences de cette manipulation sur la fitness des individus, pour pouvoir identifier les mécanismes sélectifs agissant sur le maintien du polymorphisme. Nous avons donc comparé les réponses des paramètres de reproduction des femelles et de la dispersion, croissance et survie des juvéniles dans des populations où la fréquence des femelles jaunes ou oranges a été augmentée expérimentalement (populations J+ ou O+).

Ainsi, dans le cas d'une overdominance, la fitness des femelles mixtes devrait être supérieure à celle des femelles jaunes ou oranges dans tous les environnements (sous l'hypothèse d'un déterminisme simple de la couleur ventrale). Dans le cas d'une fréquence-dépendance négative, la fitness d'un morphe de couleur doit être supérieure dans les populations où il est rare, et inférieure dans les populations où il est fréquent. Enfin, dans le cas d'une variation de niche, la fitness d'un morphe doit être supérieure dans les environnements où il est naturellement fréquent (par le biais d'une adaptation locale), et ne doit pas augmenter en réponse à la diminution artificielle de la fréquence de ce morphe.

Environnement social et reproduction des femelles[5]

Dans notre expérience, le succès de ponte et la morphologie des juvéniles à la naissance (masse et condition physique) ont été affectés par la modification des fréquences locales des morphes de couleur. Dans les populations O+, les femelles mixtes ont vu leur succès de ponte augmenter en moyenne par rapport à l'année contrôle (figure 12).

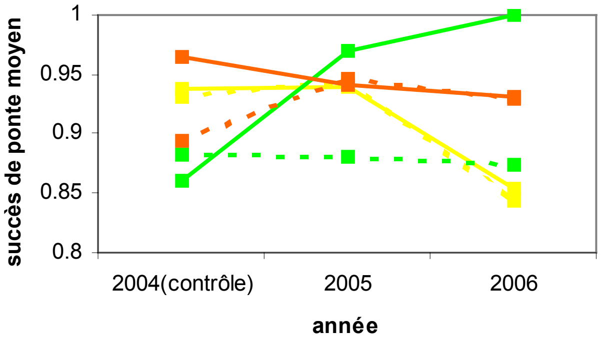

Figure 12 : Succès de ponte moyen pour les femelles jaunes (en jaune), oranges (en orange) ou mixtes (en vert) dans les populations O+ (trait plein) et J+ (trait pointillé) en 2004, 2005 et 2006.

De plus, les juvéniles nés en populations O+ étaient plus lourds que les juvéniles nés en populations contrôle, quelle que soit la couleur de la mère (figure 13a). Dans les populations J+, le succès de ponte des femelles n'a pas été modifié, et la masse des juvéniles a légèrement augmenté. En revanche, la condition physique (résidus de la régression de la masse sur la taille) des juvéniles nés en populations J+ a été fortement diminuée par rapport aux populations contrôle (figure 13b).

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[5] Les résultats de ces analyses sont présentés en détail dans l'annexe V : Female reproductive success is sensitive to the social environment in the common lizard (*Lacerta vivipara*)

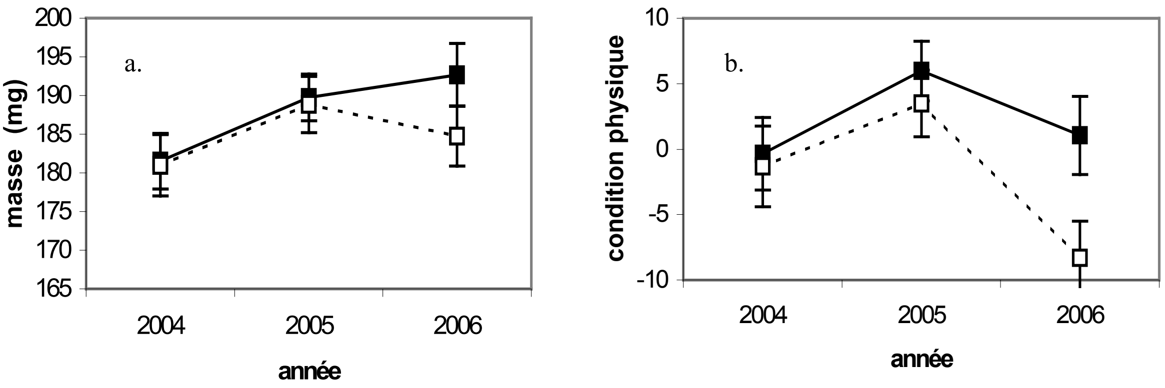

Figure 13 : Masse (a) et condition physique (b) moyennes des juvéniles dans les populations O+ (trait plein) et J+ (trait pointillé) en 2004, 2005 et 2006.

Dans cette expérience, les femelles jaunes ou oranges ne sont jamais affectées différemment par la manipulation de leur propre fréquence, ce qui n'est pas compatible a priori avec les hypothèses de variation de niche ou de fréquence-dépendance négative. En revanche, le succès reproducteur des femelles mixtes est supérieur à celui des autres femelles dans les populations O+. Si ces femelles correspondent à des hétérozygotes, alors il semble qu'un mécanisme d'overdominance permette à ces femelles d'obtenir une fitness supérieure aux homozygotes dans certaines conditions environnementales (ici, dans les populations O+). Les fréquences des morphes variant au cours du temps dans les populations naturelles, il est possible que cet avantage ponctuel confère à long terme un succès reproducteur supérieur aux femelles mixtes. En effet, dans le chapitre I, nous avons vu que les femelles mixtes bénéficiaient d'une taille de ponte et d'un succès de ponte moyen supérieurs aux autres femelles. Une telle overdominance dépendante de l'environnement social pourrait donc permettre le maintien du polymorphisme dans les populations naturelles, si notre hypothèse concernant le déterminisme génétique de la couleur est correcte.

Par ailleurs, la condition physique des jeunes à la naissance est supérieure dans les populations O+ par rapport aux populations Y+. Les populations O+ pourraient donc constituer un environnement plus favorable que les populations Y+. Si les femelles jaunes sont socialement dominantes, agressives et territoriales, alors un environnement social composé d'une majorité de femelles jaunes devrait être caractérisé par une forte compétition sociale, pouvant engendrer un stress important. Au contraire, un environnement social comptant une majorité de femelles oranges devrait être associé à une compétition et un stress social plus réduits. Chez cette espèce, le stress subi pendant la gestation affecte la reproduction des femelles et le phénotype des juvéniles (de Fraipont et al. 2000, Meylan et al.

2004, Belliure et al. 2004), et peut donc engendrer des effets maternels couleur-dépendants comme ceux observés dans notre expérience. De plus, le stress maternel est connu pour avoir des effets importants sur la dispersion des jeunes, qui peuvent être adaptatifs s'ils permettent aux descendants d'éviter des conditions défavorables. Une réponse couleur-dépendante de la dispersion des jeunes à l'environnement social pourrait donc permettre aux femelles de maximiser leur fitness en fonction des variations du niveau de compétition locale.

Environnement social et dispersion [6]

La dispersion natale des juvéniles a été affectée par le traitement expérimental subi par la mère durant la gestation, et par l'interaction entre le traitement et la couleur de la mère. La dispersion globale des jeunes a été fortement réduite quand les mères provenaient de populations J+, alors qu'elle est restée stable quand les mères provenaient de populations O+. Par ailleurs, cette réponse était particulièrement forte pour les jeunes issus de mères mixtes, tandis que les jeunes issus de mères oranges montrent la même tendance, mais atténuée. En revanche, la dispersion des jeunes issus de mères jaunes n'était pas affectée par le traitement expérimental (Figure 14).

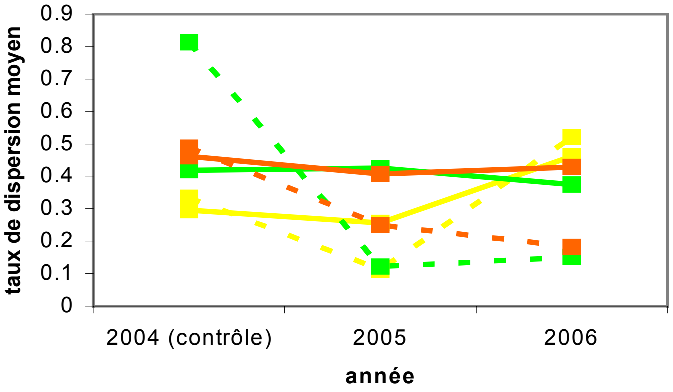

Figure 14 : Taux de dispersion moyen des juvéniles issus de mères jaunes (en jaune), mixtes (en vert) ou oranges (en orange) dans les populations O+ (trait plein) et J+ (trait pointillé) en 2004, 2005 et 2006.

La réponse au traitement expérimental des juvéniles issus de mères mixtes ou oranges peut être liée aux différences de potentiel compétitif et de stratégies sociales entre morphes. En effet, le niveau de compétition locale est supposé être supérieur dans les populations J+, ce qui peut affecter la dispersion des juvéniles de deux façons.

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[6] Les résultats de ces analyses sont présentés en détail dans l'annexe VI : Social environment-dependent dispersal strategies in juvenile common lizards (*Lacerta vivipara*).

Tout d'abord, dans une population où la compétition intraspécifique est forte, les stratégies de coopération pour l'exploitation d'un territoire en commun peuvent être sélectionnées (Jannett 1978, Jones et al. 1988, Lambin et al. 2001). Les bénéfices associés à ces stratégies étant d'autant plus importants que la coopération s'effectue entre apparentés, les individus adoptant ces stratégies devraient être davantage philopatriques (Le Galliard et al. 2003a, 2005a, Matthiopoulos et al. 1998, Lambin et al. 2001). Ainsi, si les femelles mixtes ou oranges développent des stratégies de coopération lorsque les femelles jaunes sont fréquentes, la dispersion de leurs jeunes devrait être réduite dans cet environnement.

Par ailleurs, il est possible que les coûts liés à l'installation dans un nouveau territoire soient plus élevés dans les populations J+. En effet, dans une autre espèce de lézards (*Anolis aeneus*), l'acquisition d'un statut de dominance lors de l'installation sur un nouveau territoire se fait par le biais d'interactions agonistiques (Stamps et Krishnan 1995). La probabilité d'obtenir un statut dominant et un territoire est alors corrélée à l'agressivité déployée par l'individu à cette période (Stamps et Krishnan 1998). Les femelles jaunes semblent les plus agressives, et il est possible que leurs jeunes le soient aussi. Ainsi, dans un environnement où les femelles jaunes sont fréquentes, il peut être très coûteux pour un jeune de disperser et de s'installer sur un nouveau territoire, en particulier pour un jeune non issu de mère jaune. Si le coût de la dispersion devient trop important (et est supérieur au coût de la compétition locale entre apparentés), alors le taux moyen de dispersion devrait diminuer.

Les stratégies de dispersion pourraient également être liées aux variations de qualité de l'habitat. En effet, si les femelles jaunes sont socialement dominantes, elles pourraient se retrouver sur les territoires de meilleure qualité. Ainsi, une forte fréquence locale de femelles jaunes pourrait être un indicateur positif de la qualité du territoire. Les jeunes issus de mères mixtes ou oranges réduiraient alors leur dispersion dans les populations J+ car ils estimeraient que leur territoire de naissance est un environnement favorable.

En ce qui concerne les jeunes issus de mère jaune, leur dispersion ne semble pas (ou peu) être plastique. En effet, aucun des facteurs analysés (environnement physique, chapitre I ; environnement social, ce chapitre) n'affecte la dispersion des jeunes issus de mère jaune. Il est possible que cette stratégie soit moins sensible aux facteurs de l'environnement : si elle est effectivement dominante, son succès doit être moins variable, et les bénéfices liés à une stratégie plastique de dispersion seraient minimes dans ce cas.

Ces résultats montrent que les juvéniles sont sensibles (au moins par le biais d'effets maternels) à la fréquence des morphes, et probablement également au niveau de la compétition locale pour les ressources. Cependant, étant donné que les jeunes adoptent des stratégies de dispersion différentes selon la couleur de leur mère, il est probable qu'ils ne soient pas égaux devant la compétition, et donc que leur fitness soit plus ou moins affectée par le traitement expérimental.

Environnement social et fitness des juvéniles[7]

La croissance des jeunes durant le premier mois a été affectée par le traitement expérimental : la croissance moyenne était supérieure dans les populations J+ (9,96 mm) par rapport aux populations O+ (9,01 mm). La survie des juvéniles avant l'hibernation a été affectée par l'interaction entre l'année et le traitement : en 2004, la survie des juvéniles était égale dans les deux traitements (populations J+ : 0,39 ; populations O+ : 0,41) et en 2005, la survie était supérieure dans les populations J+ (0,55) par rapport aux populations O+ (0,42).

Le taux de dispersion étant plus élevé en populations O+ en 2005, cela pourrait avoir induit une sous-estimation du taux de survie apparente. Dans ce cas, les différences de survie observées entre les populations O+ et J+ ne seraient pas biologiquement significatives. Pourtant, ces différences de survie sont parallèles aux différences de croissance entre les traitements : les jeunes des populations J+ ont à la fois un taux de croissance plus élevé et une meilleure survie, ce qui soutient davantage l'hypothèse d'une réelle différence de fitness pour les jeunes entre les deux environnements.

Une première hypothèse était que la présence de femelles jaunes induisait une forte compétition sociale et un stress important, avec des effets négatifs sur la reproduction des femelles (au moins des femelles mixtes) et sur le phénotype des jeunes à la naissance. Dans ce cas, on pouvait attendre une croissance et une survie réduites dans les populations J+.

Une seconde hypothèse était que les femelles jaunes choisissaient des territoires de bonne qualité, et que leur présence était donc un indicateur de la qualité de l'environnement. Dans ce cas, les femelles investiraient davantage dans leurs jeunes durant la gestation dans les populations O+ afin de les préparer à un environnement peu favorable. Dans notre expérience cependant, la fréquence relative des morphes ayant été manipulée, les populations O+ (où les femelles jaunes étaient fréquentes à l'origine) auraient été en réalité de meilleure qualité que

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[7] Les résultats de ces analyses sont présentés en détail dans l'annexe VII : Juvenile growth and survival in different social environments in the common lizard (*Lacerta vivipara*) : does variation in local competition select for alternative reproductive strategies ?

les populations J+. Dans ce cas, la survie et la croissance auraient également dû être augmentées dans les populations O+.

Or nous avons observé la tendance inverse : les jeunes des populations J+ ont montré une croissance et une survie supérieure aux jeunes des populations O+, et ce quelle que soit la couleur de leur mère. Ce résultat ne soutient donc a priori aucune des deux hypothèses précédentes : l'environnement O+ ne serait donc pas associé à une compétition réduite, ni l'environnement J+ à une plus grande quantité de ressources. Il paraît également peu probable que l'environnement J+ soit directement favorable aux jeunes, étant donné les effets négatifs de cet environnement sur la reproduction des femelles. Par contre, la différence de fitness des jeunes entre les traitements pourrait résulter indirectement des différences de taux de dispersion. En effet, les jeunes des populations O+ ont un taux de dispersion moyen supérieur à ceux des populations J+. De manière générale, la dispersion est considérée comme un trait coûteux, en particulier au cours de la phase de transience (Hamilton et May 1977, Motro 1983), et la survie des dispersants est souvent réduite durant la dispersion et l'installation sur un nouveau territoire (Bélichon et al. 1996). Chez le lézard vivipare cependant, une étude a montré que l'implantation dans un nouveau territoire n'engendrait pas de coûts en survie pour les juvéniles (Massot et al. 1994). Il est néanmoins possible que des différences existent durant la phase de transience. A la naissance, les dispersants sont en moyenne plus actifs (Clobert et al. 1994, de Fraipont et al. 2000), ce qui peut augmenter leur risque de prédation, et donc diminuer leur survie par rapport aux philopatriques. De plus, les dispersants s'alimenteraient moins que les philopatriques (Meylan et al. soumis), ce qui pourrait affecter négativement la croissance et la survie (Le Galliard et al. 2005b). Ainsi, il est possible que les taux de croissance et de survie plus faibles observés dans les populations O+ résultent (au moins en partie) des taux de dispersion plus élevés dans ces populations.

Par ailleurs, la densité des populations O+ a augmenté au cours de l'expérience suite à la fécondité accrue des femelles mixtes. Or la croissance et la survie des juvéniles semblent être sensibles à la densité, car une augmentation de celle-ci avait entraîné une réduction de la fitness des juvéniles lors d'une expérience précédente (Massot et al. 1992). Par conséquent, l'augmentation de la densité locale dans les populations O+, et en particulier de la densité des jeunes, peut avoir causé la réduction de la croissance et de la survie des jeunes observée dans notre expérience, cet effet étant d'autant plus fort en 2005 grâce à l'addition de deux saisons de reproduction. L'environnement où la compétition entre femelles adultes est la moins forte (c'est-à-dire les populations O+) serait alors celui où la compétition entre jeunes est la plus forte, et ce quelle que soit la couleur de leur mère.

Réponse au stress social : contrainte ou adaptation ?

La modification de l'environnement social a affecté la fitness des individus à différents niveaux : la reproduction des femelles, les composantes prénatales et les composantes post-natales du phénotype des jeunes. Les femelles produisent différents types de jeunes dans les populations J+ et O+. Dans les populations O+, les jeunes sont en meilleure condition, dispersent davantage, mais ont un taux de croissance et une survie plus faibles que dans les populations J+. Si l'ensemble de ces effets contribue à la production d'un phénotype optimal dans des conditions environnementales données, alors ces réponses au stress social constitueraient des stratégies adaptatives. Au contraire, certains effets peuvent être des conséquences non adaptatives d'une modification de l'environnement (stress social élevé ou densité accrue).

Dans notre expérience, l'environnement subi par les femelles durant la gestation n'était pas forcément le même que celui subi par leurs jeunes après la naissance. En effet, les jeunes issus de mères oranges capturées dans les populations J+ ont été relâchés dans les populations O+, et inversement pour les jeunes issus de mères jaunes provenant des populations O+. Si les modifications du phénotype des jeunes en réponse aux variations de l'environnement social résultaient d'une stratégie maternelle adaptative, alors on devrait observer un succès supérieur des jeunes relâchés dans le même environnement que celui subi par leur mère durant la gestation (car ces jeunes bénéficieraient d'une pré-adaptation à cet environnement précis). Autrement dit, on devrait observer l'effet de l'interaction entre l'environnement d'origine et l'environnement de lâcher sur la fitness des jeunes, ce qui n'est pas le cas ($p=0,69$). Ainsi, même si les jeunes issus de mères provenant d'environnements différents se distinguent à la naissance par leur morphologie et leur comportement, cette différence initiale ne constitue pas un avantage dans ces environnements particuliers, ce qui s'oppose à l'hypothèse de stratégies adaptatives. Ces résultats recoupent ceux obtenus lors d'une étude préalable des effets post-nataux de la densité (Meylan et al. 2007) : la taille à la naissance n'affecte pas le taux de croissance ni la survie, et les effets post-nataux d'une manipulation de la densité ne semblent pas être adaptatifs. Les effets de la densité ou de l'environnement social sur le développement post-natal des jeunes ne feraient donc pas partie d'une stratégie maternelle adaptative.

Dans notre cas, il est plus probable que les femelles des populations J+ aient produit des pontes réduites (en ce qui concerne les femelles mixtes) ou des jeunes de faible condition à cause des effets néfastes du stress social subi pendant la gestation. La fitness accrue de ces jeunes ne serait alors qu'une conséquence indirecte de la densité réduite dans les populations J+. De même, les femelles des populations O+ produiraient des pontes plus grandes ou des jeunes de meilleure qualité en réponse à des conditions environnementales favorables, mais leurs jeunes subiraient une réduction de leur fitness à cause de l'augmentation de la densité locale. La stratégie des femelles serait donc peut-être davantage liée aux effets maternels sur le comportement de dispersion, qui permettent d'adopter un comportement adaptatif en réponse aux pressions de sélection générées par les variations de l'environnement social.

Perception de l'environnement social : quelle échelle ?

Dans notre expérience, nous avons modifié à la fois le voisinage local des femelles, en remplaçant certaines femelles au niveau même de leur territoire, et nous avons également modifié la population dans son ensemble, en répétant cette manipulation un grand nombre de fois. L'environnement social a donc été affecté à la fois à l'échelle locale et populationnelle, ce qui a eu des conséquences couleur-dépendantes sur les traits d'histoire de vie des femelles et de leurs jeunes, en particulier sur le taux de dispersion.

Le caractère adaptatif de la réponse du taux de dispersion à la modification de l'environnement social est lié à l'échelle à laquelle cet environnement est perçu. Ainsi, sous l'hypothèse d'une dispersion liée à la qualité de l'environnement, la fréquence des femelles jaunes est perçue à l'échelle micro-locale, et est indicatrice d'une bonne qualité du territoire de naissance. Cependant, dans notre expérience, la fréquence des femelles jaunes a été artificiellement augmentée ou réduite et ne reflète donc pas de façon fiable la qualité de l'habitat local. De plus, la dispersion des jeunes est sensible à la fréquence des femelles jaunes dans l'environnement de gestation de la mère, ce qui signifie que le comportement de dispersion est essentiellement déterminé de façon prénatale. Or les femelles ayant vécu plusieurs mois dans l'environnement manipulé, elles ont pu estimer directement la quantité de ressources présente, en contradiction avec la fréquence apparente de femelles jaunes. Dans ce cas, il serait plus probable que la dispersion des jeunes réponde à un signal reflétant directement la qualité de l'habitat (condition physique de la mère, niveau de stress), ou au moins à l'adéquation entre cette information directe et celle indirecte portée par la fréquence des femelles jaunes. En effet, nous avons vu au chapitre I que la dispersion des jeunes issus de mère mixte était augmentée en réponse à une restriction des ressources disponibles durant la gestation. L'hypothèse de l'utilisation de la fréquence des femelles jaunes comme signal indirect de la qualité de l'environnement apparaît donc peu probable.

En revanche, la fréquence des femelles jaunes a pu réellement modifier le niveau de compétition locale, et affecter ainsi la qualité de l'environnement, les populations J+ devenant moins favorables que les populations O+. Dans ce cas, on attendrait une augmentation du taux de dispersion dans les populations J+, en réponse à une augmentation de la compétition au niveau du territoire de naissance. Pourtant, on observe la tendance inverse : la dispersion des jeunes est réduite dans les populations J+, en particulier pour les jeunes issus de mère mixte ou orange, ce qui peut s'expliquer par des coûts d'installation élevés dans les populations J+. Ce scénario impliquerait alors que les femelles puissent estimer le niveau de compétition non seulement dans leur voisinage immédiat, mais également dans les environnements à distance de dispersion. Une telle connaissance des conditions environnementales à large échelle serait possible si les femelles peuvent bénéficier d'une information indirecte (socialement acquise) sur l'état de la population. Un tel mécanisme a déjà été mis en évidence chez cette espèce (Cote 2006) pour la transmission d'information concernant la densité de la population, et il serait donc tout à fait possible qu'une information concernant la nature de l'environnement social puisse également être acquise socialement. Une autre possibilité serait qu'il existe une autocorrélation spatiale de la fréquence des différents morphes dans la population, avec un faible degré d'hétérogénéité spatiale de l'environnement social.

Par ailleurs, les femelles mixtes ont été les plus affectées par la modification de la fréquence des différents morphes dans notre expérience, alors que l'analyse à long terme avait montré qu'elles étaient les moins sensibles aux variations de la fréquence des femelles jaunes (voir chapitre I). Dans cette analyse, la fréquence des femelles jaunes était mesurée à l'échelle de la population, tandis que dans notre expérience, l'environnement social a été modifié au niveau micro-local. S'il existe une forte hétérogénéité spatiale dans la distribution des morphes de couleur, alors il est normal que les variations de fréquence des morphes liées à l'expérience de transplantation réciproque donnent des résultats différents des variations naturelles. En effet, les femelles ayant subi la plus forte altération de leur environnement social étaient les femelles entourées de femelles jaunes dans les populations O+, et les femelles entourées de femelles oranges dans les populations J+. En cas de ségrégation spatiale couleur-dépendante, ces femelles auraient été les moins exposées à une modification naturelle de la fréquence de ces morphes, et les effets que nous avons observés pourraient être compensés en nature par des stratégies adaptatives de distribution spatiale.

L'analyse de la répartition spatiale des individus dans les populations pourrait donc nous renseigner sur la possibilité d'une autocorrélation spatiale de l'environnement social ou bien d'une distribution couleur-dépendante. Dans le premier cas, la fréquence des différents morphes à l'échelle locale serait équivalente à la fréquence globale : les jeunes pourraient donc prendre des décisions de dispersion basées sur la connaissance de l'environnement social à large échelle. Dans le second cas, la distribution non aléatoire des morphes pourrait induire une structuration spatiale de l'environnement, ce qui serait favorable au maintien des stratégies alternatives.

CHAPITRE IV : Compétition sociale et stratégies de distribution spatiale

L'environnement social, déterminé par la présence et la densité des congénères, affecte la fitness des individus à travers différentes pressions de sélection (Formica et al. 2004). Ainsi, la quantité et la qualité des ressources, les prédateurs (Cowlishaw 1999), les parasites (Boulinier et al. 1996), la compétition intraspécifique (Shier et Randall 2004), ou les interactions entre apparentés (Gundersen et Andreassen 1998) peuvent affecter le succès reproducteur des individus. L'intensité de ces différents facteurs varie en fonction de la distribution spatiale des individus, ce qui induit une hétérogénéité spatiale de l'environnement. Selon leur phénotype, différentes classes d'individus vont être particulièrement sensibles à l'un ou l'autre de ces facteurs, et devraient donc opter pour des micro-habitats différents. Ainsi, l'âge (Brotons 2000), le sexe (Luque-Larena et al. 2004) ou le statut de dominance (Wauters et Dhondt 1992) sont des facteurs susceptibles d'affecter la distribution spatiale des individus. De même, les stratégies alternatives devraient être caractérisées par des profils de répartition différents, dépendants de l'environnement social. En effet, les interactions sociales entre congénères sont souvent à l'origine de l'évolution de stratégies alternatives (Gross 1996), et la fitness des différentes stratégies est souvent corrélée à la présence et la fréquence relative des autres stratégies, par le biais de mécanismes fréquence-dépendants (Maynard-Smith 1982).

Les stratégies alternatives associées aux morphes de couleur ventrale chez les femelles du lézard vivipare sont sensibles à la composition de leur environnement social (voir chapitre III), probablement par le biais de différences de potentiel compétitif et de dominance sociale entre morphes (voir chapitre II). Ainsi, l'accès aux ressources des individus, et par conséquent leur fitness, peut dépendre de la présence de compétiteurs supérieurs, c'est-à-dire de l'interaction entre leur propre statut social et celui de leurs voisins les plus proches. Par ailleurs, la compétition entre apparentés représente une forte pression de sélection chez cette espèce (Ronce et al. 1998, de Fraipont et al. 2000, Le Galliard et al. 2003b), et si les morphes de couleur diffèrent dans leur potentiel compétitif, ils devraient alors subir plus ou moins les coûts de la compétition entre apparentés. La fitness des individus devrait donc dépendre de la proximité et du niveau de compétition entre apparentés, cette relation pouvant varier entre les morphes de couleur. Les femelles jaunes sont probablement socialement dominantes : elles devraient donc être les plus territoriales, particulièrement envers les autres femelles dominantes. De plus, les jeunes issus de mères mixtes ou oranges montrent un taux de dispersion réduit dans des conditions de forte compétition, ce qui peut être mis en relation avec une stratégie éventuelle de coopération entre apparentés. Des stratégies alternatives de choix de l'habitat en fonction de la couleur ventrale et du niveau d'apparentement des congénères présents pourraient donc être adaptatives si elles permettent aux différentes stratégies de maximiser leur fitness en limitant les coûts de la compétition pour les ressources.

Afin de tester ces hypothèses, nous avons étudié la distribution spatiale des femelles de la population ROB. Nous avons testé si le nombre de femelles de différentes couleurs ou le nombre de femelles apparentées (de même mère) présentes sur le même territoire qu'une femelle dépendait de ses caractéristiques individuelles (couleur ventrale et taille corporelle) ainsi que des facteurs de l'environnement (zone d'habitat, densité de femelles et fréquence des femelles jaunes).

Distribution spatiale des morphes de couleur[8]

De façon prévisible, le nombre de femelles de chaque couleur présentes dans le voisinage dépend toujours de la zone d'habitat, et de la densité de femelles dans la population, mais aussi de la taille de la femelle considérée. Quelle que soit leur couleur, les femelles ont davantage de voisines dans la zone de forte densité, et lorsque la densité totale est élevée. Par ailleurs, les femelles de grande taille ont en moyenne moins de voisines que les femelles de petite taille.

Par contre, le nombre de femelles présentes sur un même territoire va également dépendre de leurs couleurs respectives :

- Le nombre de femelles jaunes présentes dans le voisinage d'une femelle dépend de sa propre couleur: les femelles jaunes ont en moyenne davantage de femelles jaunes dans leur voisinage (6,6) que les femelles mixtes (5,6) ou oranges (5,6).
- Le nombre de femelles mixtes présentes dans le voisinage d'une femelle dépend de la fréquence des femelles jaunes, en interaction avec sa propre couleur : le nombre de femelles mixtes diminue lorsque la fréquence des femelles jaunes augmente, et cette relation est particulièrement forte pour les femelles mixtes (Figure 15).

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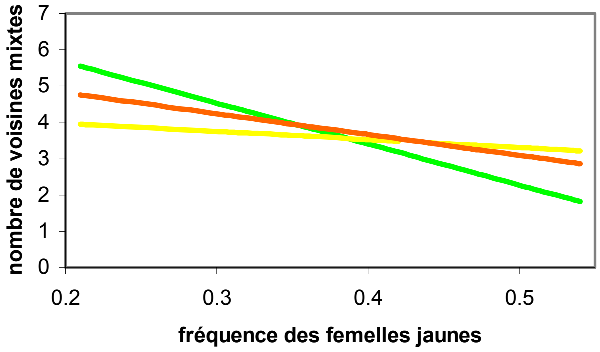
[8] Les résultats de ces analyses sont présentés en détail dans l'annexe VIII : Alternative strategies affect spacing behaviour in female common lizards (*Lacerta vivipara*)

- Le nombre de femelles <u>oranges</u> présentes dans le voisinage d'une femelle ne dépend pas de sa propre couleur, seule ou en interaction avec d'autres facteurs.



<u>Figure 15</u> : Nombre de femelles mixtes présentes dans le voisinage en fonction de la fréquence des femelles jaunes, pour les femelles jaunes (en jaune), mixtes (en vert), ou oranges (en orange).

Le nombre de femelles apparentées présentes dans le voisinage d'une femelle ne dépend pas de sa propre couleur, seule ou en interaction avec d'autres facteurs.

Distribution des femelles jaunes

Les femelles jaunes sont souvent associées spatialement entre elles, ce qui peut résulter d'au moins trois mécanismes différents. Tout d'abord, les femelles jaunes pourraient avoir des exigences écologiques particulières, distinctes des femelles oranges ou mixtes, et donc rechercher le même habitat écologique. Cette hypothèse est néanmoins démentie par le fait que les trois morphes coexistent sur les mêmes territoires, mais en proportion différente. D'autre part, il est possible que les femelles jaunes recherchent le même habitat social, c'est-à-dire qu'elles recherchent le voisinage d'autres femelles jaunes. Une telle hypothèse serait possible si la couleur ventrale est utilisée comme un indicateur de proximité génétique (« barbe verte », Dawkins 1976), permettant la coopération entre apparentés et l'évitement d'individus « tricheurs » (stratégie utilisé par les mâles à gorge bleue chez le lézard à flancs tachetés, Sinervo et Clobert 2003). Ici pourtant, les femelles jaunes ne montrent pas de proximité spatiale particulière entre femelles apparentées, ce qui n'appuie pas cette hypothèse. Enfin, les femelles jaunes peuvent montrer une certaine agrégation spatiale de façon passive, si elles se répartissent aléatoirement mais que les autres femelles évitent préférentiellement les zones où les femelles jaunes sont nombreuses. L'analyse de la distribution spatiale des femelles a également montré que les femelles de grande taille étaient entourées de moins de voisines que les femelles de petite taille. La taille étant également un facteur probablement impliqué dans l'établissement des relations de dominance (lors des expériences de comportement, les femelles sont davantage enclines à prendre la fuite face à une femelle de taille supérieure), ce résultat appuierait l'hypothèse d'une répartition spatiale en fonction du statut de dominance.

Par ailleurs, le nombre de voisines de couleur jaune augmente avec la densité et la fréquence des femelles jaunes, et ce quelle que soit la couleur de la femelle considérée. La fréquence locale des femelles jaunes est donc directement corrélée à la fréquence globale, même s'il existe une variation liée à un certain degré d'agrégation des femelles jaunes entre elles. Les décisions de dispersion basées sur l'environnement social local pourraient donc être adaptatives car elles refléteraient le niveau de compétition à plus large échelle dans la population.

Distribution des femelles mixtes et oranges

Les femelles mixtes et oranges avaient montré une diminution du taux de dispersion de leurs jeunes en réponse à l'augmentation de la fréquence des femelles jaunes. On pouvait donc attendre un effet de la fréquence des femelles jaunes sur le nombre de voisines de même couleur, et sur le nombre de voisines apparentées pour les femelles mixtes et oranges, ce qui n'est pas le cas. Au contraire, le nombre de voisines de couleur mixte diminue lorsque la fréquence des femelles jaunes augmente pour les femelles mixtes. Il est en fait possible que la réduction du taux de dispersion dans les populations à forte fréquence de femelles jaunes soit associée à une diminution de la survie des individus en raison d'une plus forte compétition locale. L'analyse de la distribution spatiale des femelles adultes ne montrerait donc pas d'effet de la fréquence des femelles jaunes sur l'agrégation des femelles mixtes ou oranges, mais un effet négatif global sur la densité de ces femelles, ce que l'on observe effectivement pour les femelles mixtes. Dans ce cas, la stratégie philopatrique des femelles mixtes ou oranges en populations J+ serait une réponse à un environnement très défavorable : les coûts de la compétition locale, même élevés, seraient tout de même inférieurs aux coûts de la dispersion. Tous les morphes seraient donc sensibles à la compétition entre apparentés, mais les différences de potentiel compétitif, et donc des coûts associés à la compétition en général, affecteraient les stratégies de dispersion et de choix de l'habitat. Ce scénario permet d'expliquer la stratégie philopatrique apparemment paradoxale des femelles oranges, qui semblent pourtant les plus sensibles à la compétition intraspécifique, et à la compétition entre apparentés en particulier (voir chapitre I). La fréquence des femelles jaunes affecterait donc les caractéristiques de l'environnement, ce qui pourrait générer des stratégies alternatives de répartition spatiale pour les différents morphes, en réponse à une hétérogénéité des pressions de sélection.

Organisation spatiale des morphes dans un milieu hétérogène

Au sein même des deux zones d'habitat de la population ROB, il existe une hétérogénéité micro-locale de la qualité de l'environnement : certains territoires vont contenir une grande quantité de ressources, et avoir une forte capacité portante, tandis que d'autres vont être de qualité inférieure, et de moindre capacité portante. Les femelles jaunes ont en moyenne plus de voisines, et plus de voisines jaunes en particulier. Ces femelles choisiraient donc préférentiellement les territoires riches, de bonne qualité, et en excluraient partiellement les autres morphes. Ainsi, les femelles mixtes et oranges se distribueraient de façon uniforme dans les territoires de différente qualité, plus fréquentes donc dans les territoires pauvres et moins peuplés, et moins fréquentes dans les territoires riches. Ces stratégies de répartition spatiale des différents morphes pourraient permettre l'égalité à long terme des fitness des femelles jaunes et oranges (voir chapitre I). En effet, une distribution ressource-dépendante des femelles jaunes devrait induire l'homogénéisation des pressions de compétition dans les différents territoires (distribution libre idéale, Fretwell et Lucas 1970). Si les femelles oranges ont des besoins énergétiques inférieurs (par exemple, si la dominance est coûteuse physiologiquement), ou bien une stratégie d'exploitation de l'habitat légèrement différente, alors les femelles jaunes et oranges pourraient obtenir des fitness égales, entre elles et entre les environnements. Par ailleurs, les femelles mixtes ont un succès accru dans des populations où la fréquence des femelles jaunes est réduite (chapitre III). Si une partie des femelles mixtes se distribue dans les zones où les femelles jaunes sont moins fréquentes, elles peuvent alors bénéficier d'un fort avantage sélectif local, ce qui leur assurerait une fitness moyenne supérieure (voir chapitre I). Une telle stratégie de répartition spatiale pourrait donc être adaptative, et induire l'overdominance des femelles mixtes à long terme.

Ce scénario permet d'expliquer le pattern de distribution spatiale des femelles, les stratégies de dispersion des femelles, ainsi que les résultats de l'expérience de manipulation de fréquence des morphes. En effet, dans les populations O+, des femelles jaunes ont été remplacées par des femelles oranges sur des territoires de bonne qualité. Les femelles mixtes étant probablement dominantes sur les femelles oranges, elles ont bénéficié d'un accès important aux ressources, ce qui a augmenté leur succès reproducteur. Au contraire, dans les populations J+, des femelles jaunes ont remplacé des femelles oranges sur des territoires pauvres en ressource, la compétition a donc augmenté sensiblement, ce qui a affecté le phénotype des jeunes produits. Cependant, de nombreux points restent à éclaircir, notamment sur les stratégies d'exploitation de l'habitat par les différents morphes, et davantage de données précises concernant l'étendue et les caractéristiques des territoires des femelles en fonction de leur couleur ventrale seront nécessaires pour confirmer nos hypothèses.

DISCUSSION ET PERSPECTIVES

I. Polymorphisme ou trait continu ? Déterminisme génétique ou condition-dépendance ?

La couleur ventrale peut apparaître comme un trait graduel, avec une augmentation progressive de la teinte depuis le morphe jaune jusqu'au morphe orange, en passant par le morphe mixte. Les morphes de couleur que nous avons décrits seraient alors des classes arbitrairement définies. Dans ce cas, les femelles « jaunes » seraient les femelles dont la couleur est la plus claire, les femelles « oranges », celles dont la couleur est la plus soutenue, et les femelles « mixtes », celles dont la couleur est intermédiaire. Cependant, la couleur « mixte » n'est pas définie simplement par une teinte médiane mais par un mélange de jaune et d'orange, c'est à dire une couleur hétérogène. L'hypothèse d'un déterminisme simple, avec un locus et deux allèles (Jaune et Orange) permet d'expliquer plus facilement le phénotype des femelles mixtes que l'hypothèse d'un trait quantitatif à déterminisme complexe. Par ailleurs, dans la majorité des analyses réalisées, les réponses des femelles mixtes sont supérieures ou inférieures à celles des deux autres morphes, ce qui soutient l'hypothèse d'une troisième classe distincte et non intermédiaire. Il est possible en fait que les femelles mixtes (hétérozygotes) soient intermédiaires dans leur comportement social et leur statut de dominance (plus agressives que les femelles oranges mais moins dominantes que les femelles jaunes), ce qui générerait des effets non-linéaires sur la fitness. Ces femelles seraient donc associées à une stratégie distincte, adaptée à leur statut social particulier.

Par ailleurs, le déterminisme de la couleur ventrale reste encore à établir formellement. Nous avons vu que la classe de couleur était stable et héritable, ce qui soutient l'hypothèse d'un déterminisme génétique. Cependant, l'analyse de la stabilité des composantes du spectre a montré que seule la teinte était stable, tandis que le chroma pouvait varier. En ce qui concerne la brillance, des données expérimentales ont montré son caractère condition-dépendant (Meylan et al. 2007). Il est donc possible que le signal des stratégies alternatives soit la teinte, qui correspondrait à la classe de couleur déterminée génétiquement, tandis que le chroma et la brillance apporteraient des informations quant aux composantes variables du phénotype (stress, état reproducteur, santé…). En effet, la teinte est la composante du spectre la plus affectée par la concentration en pigments caroténoïdes (Andersson 2000), qui varie selon les morphes, mais qui ne paraît pas être un facteur limitant dans l'expression de la couleur (Cote 2003). Les différences de couleur ventrale (teinte) seraient donc causées par des stratégies différentes d'allocation des caroténoïdes circulants, potentiellement sous contrôle génétique (comme c'est le cas chez certaines espèces végétales, Bradshaw et Schemke 2003), et impliquant le système endocrine. Chez d'autres espèces de reptiles, l'expression d'une coloration génétiquement déterminée semble être corrélée à des profils hormonaux différents (Moore 1991, Cooper et Greenberg 1992, Hews et Moore 1995, Sinervo et al. 2000b), et chez le lézard vivipare, une augmentation du taux de corticostérone plasmatique est associée à une teinte plus orangée (Cote 2003). Des différences génétiques dans le taux de corticostérone basal (et/ou de testostérone, voir partie suivante) pourraient donc être à l'origine des différences de teinte entre morphes.

Si la teinte est la composante génétiquement déterminée de la couleur, étant donné que notre classification visuelle reflète à la fois la teinte et le chroma, le signal que nous percevons apparaît brouillé par les variations de chroma (qui serait condition-dépendant), ce qui peut expliquer les erreurs de classification d'une année à l'autre. Des études précises de l'héritabilité des différentes composantes de la couleur permettraient d'affiner notre définition de la couleur, et probablement de mieux comprendre la dynamique des différents morphes. En effet, sous l'hypothèse d'un déterminisme génétique de la couleur, le rôle du génotype mâle dans l'héritabilité de ce caractère reste à éclaircir. En particulier, si le génotype des mâles est accessible aux femelles, alors les femelles pourraient effectuer des choix de partenaire adaptatifs basés à la fois sur leur propre génotype, le génotype du mâle et l'état de l'environnement social, comme c'est le cas chez le lézard à flancs tachetés (Alonzo et Sinervo 2001). Une telle stratégie affecterait probablement la dynamique et la stabilité du polymorphisme, en créant une sélection variable sur les différents allèles du système (Sinervo et Zamudio 2001).

II. Quelle fonction pour le polymorphisme de couleur ?

La couleur ventrale est un trait visible, pouvant jouer le rôle de signal social à destination des congénères. Lors d'une interaction sociale impliquant un signal, l'émetteur et le receveur du signal peuvent avoir des intérêts divergents (Vehrencamp 2000). Ce type de conflit est particulièrement intense lors des interactions agonistiques autour de l'exploitation d'une ressource non divisible. Nous avons vu que la couleur ventrale est utilisée par les femelles comme signal social lors des interactions de compétition, et que cette couleur peut refléter le statut de dominance. Dans notre cas, la femelle aurait toujours intérêt à exagérer le signal de son potentiel compétitif, de manière à acquérir la dominance même en cas d'infériorité. Pour que les signaux sociaux soient fiables, il faut donc qu'ils impliquent un coût ou une contrainte pour l'émetteur qui réduise les bénéfices associés à la tricherie. En particulier, la nature de ces coûts et la forme du signal sont liés à la nature de l'information véhiculée et à la fonction du signal. Ici, le signal ne semble pas être condition-dépendant (il n'y a pas de différences morphologiques entre femelles de différentes couleurs), et il ne paraît pas y avoir de coûts intrinsèques liés à sa production (les femelles jaunes ne montrant pas de carence en caroténoïdes circulant). La couleur ventrale serait donc un signal discret, arbitraire (non déterminé par des coûts physiologiques de production), informant sur le potentiel compétitif des individus (signal « conventionnel », Maynard-Smith et Harper 1988). Un tel signal ne peut être stable que si les coûts et bénéfices des interactions sociales sont dépendants du statut de l'individu (Enquist 1985), c'est-à-dire si les coûts associés à un signal dominant usurpé (par exemple une blessure au cours d'une interaction agonistique avec un vrai dominant) sont trop lourds pour un individu subordonné (Vehrencamp 2000).

Par ailleurs, la stabilité d'un signal honnête du statut de dominance dépend également de l'existence de coûts fixes de la dominance (non dépendants de l'issue des interactions sociales, Johnstone et Norris 1993). Ici, le statut dominant semble être associé à une production accrue d'androgènes, le taux de testostérone plasmatique étant plus élevé chez les femelles jaunes (1.07 ng/mL) que chez les femelles mixtes (0.96 ng/mL) ou oranges (0.85 ng/mL), bien que cette différence ne soit pas statistiquement significative (p=0,43). Les androgènes sont connus pour leurs effets immunosuppresseurs (Grossman 1985, Folstad et Karter 1992), qui induisent un coût physiologique à la dominance. Les femelles jaunes sont peut-être les seules femelles capables de supporter les coûts immunitaires d'un comportement dominant (par le biais de trade-off génétiques), et le signal de la couleur ventrale serait donc honnête (hypothèse du handicap d'immunocompétence, Folstad et Karter 1992). Les caractères génétiquement corrélés à la couleur ventrale affecteraient le système immunitaire et le potentiel compétitif, et les individus adopteraient une stratégie sociale adaptée. Un tel système peut permettre de limiter les coûts des interactions agonistiques chez une espèce où les contacts sociaux entre individus sont probablement fréquents et répétés. Des expériences d'usurpation de signal pourraient permettre de tester l'efficacité de la tricherie, et les coûts éventuels infligés par le récepteur. Par ailleurs, des analyses de l'efficacité du système immunitaire des différentes morphes pourrait préciser la nature des coûts physiologiques éventuels de la dominance.

Par ailleurs, si l'utilité première des signaux conventionnels est liée à la résolution de conflits de compétition intrasexuelle, l'existence de coûts fixes à la dominance permet de relier le signal à la qualité individuelle, et les signaux conventionnels peuvent alors également être utilisés pour sélectionner un partenaire sexuel. La théorie de la sélection sexuelle prédit que seul le sexe qui fournit l'investissement parental le plus élevé (en général les femelles) devrait sélectionner ses partenaires (Trivers 1972). Pourtant, étant donné que les femelles varient à la fois dans leur qualité individuelle et dans leur capacité reproductrice, les bénéfices associés à la sélection de partenaires devraient également être élevés pour les mâles, en particulier lorsque ces derniers sont limités par le nombre d'accouplements qu'ils peuvent obtenir (Cunningham et Birkhead 1998). Chez le lézard vivipare, les accouplements ont lieu immédiatement après l'émergence des femelles, les mâles ayant émergé en premier pour établir leurs territoires (Laloi et al. 2004). Les femelles sont donc disponibles pendant très peu de temps, et lorsqu'un mâle passe du temps à s'accoupler avec une femelle, il renonce potentiellement à d'autres occasions de reproduction. Par conséquent les mâles, et en particulier les mâles dominants (Richard et al. 2005) devraient être sélectifs quant au choix de leurs partenaires (Johnstone et al. 1996). Chez une espèce où des stratégies alternatives de femelles coexistent, l'existence d'un choix actif par les mâles peut affecter profondément la fitness relative des différents morphes de femelles (Henson et Warner 1997). La couleur ventrale étant probablement indicatrice de différences génétiques dans le potentiel compétitif (et peut-être la réponse immunitaire) et dans la stratégie de reproduction, elle pourrait donc être impliquée dans la sélection de partenaires par les mâles, ce qui pourrait là encore affecter la dynamique et le maintien du polymorphisme.

III. Maintien du polymorphisme : overdominance ou fréquence-dépendance ?

Les femelles jaunes, dominantes, produisent probablement les jeunes de meilleure qualité (plus grands, plus gros), et à fort potentiel compétitif. En contrepartie, ces femelles produisent des pontes plus petites, et subissent davantage les effets du vieillissement (sénescence). Les femelles oranges, subordonnées, produisent des jeunes nombreux mais de moindre qualité, et subissent fortement les effets de la compétition intrasexuelle. Il est possible que les femelles oranges obtiennent une fitness moyenne égale à celle des femelles jaunes (équilibre entre les stratégies « r » et « K » comme chez le lézard à flancs tachetés, Sinervo et al. 2000a), ou bien que la stratégie orange soit inférieure. Dans ce cas, le polymorphisme serait maintenu par un mécanisme d'overdominance, sous l'hypothèse que les femelles mixtes sont hétérozygotes. En effet, nous avons vu que les femelles mixtes ont en moyenne un succès reproducteur plus élevé que les autres femelles. Cet avantage pourrait être lié directement à l'hétérozygotie de ces femelles. Si les femelles mixtes possèdent les allèles des deux stratégies, dominante et subordonnée, il est possible qu'elles puissent adopter une stratégie plastique : dominante envers les femelles oranges, et subordonnée envers les femelles jaunes. En effet, en population J+, les femelles mixtes ont une stratégie similaire à celle des femelles oranges en ce qui concerne la dispersion des jeunes. En revanche, les femelles mixtes ont un succès accru en populations O+, où elles bénéficieraient d'un statut dominant. Ce bénéfice serait même supérieur à celui des femelles jaunes, car les femelles mixtes n'auraient pas à subir, ou dans une moindre mesure, les coûts physiologiques de la dominance (taux de testostérone plus faible). Une telle plasticité comportementale des hétérozygotes a déjà été décrite chez le combattant varié (*Philomachus pugnax*), et permet à ceux-ci d'obtenir un avantage sélectif sur les homozygotes à stratégie « fixe » (van Rhijn 1973). De plus, dans notre cas, les femelles mixtes peuvent optimiser leur fitness en fonction de l'hétérogénéité spatiale de l'environnement social, grâce à une dispersion contexte-dépendante et un choix d'habitat adaptatif (évitement des femelles jaunes, et des femelles mixtes dans certaines conditions). La stratégie « optimale » serait alors un mélange de compétitivité (allèle J), qui assure le succès de la stratégie à court terme (avantage sélectif dans certaines conditions), et de potentiel dispersif (allèle O), qui assure la survie de la stratégie à plus long terme, en lui permettant non seulement d'adopter une stratégie de répartition spatiale adaptative, mais aussi de coloniser des territoires vacants, et de survivre aux modifications du milieu.

Si le phénotype hétérozygote est avantagé, et si les femelles sont capables de connaître le génotype des mâles (sous l'hypothèse d'un caractère autosomique dont l'expression est inhibée chez les mâles), alors des stratégies adaptatives de choix de partenaires seraient sélectionnées, favorisant l'hétérozygotie des descendants femelles (Brown 1997). Les femelles pourraient donc sélectionner leurs partenaires mâles sur la base de leur génotype concernant la couleur ventrale, ou pratiquer des stratégies d'accouplements multiples (qui peuvent également augmenter le taux d'hétérozygotie des descendants, Keller 1994, Brown 1997). Chez le lézard vivipare, les stratégies de multi-paternité sont plastiques et variables selon l'âge (Richard et al. 2005). Il est donc possible que ces stratégies diffèrent également entre les morphes de couleur. Les implications des stratégies alternatives sur les mécanismes de sélection sexuelle chez le lézard vivipare pourraient ainsi avoir des conséquences majeures sur les différences de succès reproducteur entre morphes, et donc sur le maintien du polymorphisme. Une analyse détaillée des choix de partenaires par les femelles et les mâles, et de leurs conséquences sur le phénotype des descendants mâles et femelles permettrait de comprendre comment les stratégies alternatives des femelles affectent leur reproduction et leur fitness, et de proposer un scénario complet de la dynamique des morphes de couleur dans les populations de lézard vivipare.

IV. Evolution des stratégies d'histoire de vie alternatives : vers un pattern commun ?

1) Dynamique des stratégies, dispersion, et persistance à long terme

Nous avons vu que les stratégies alternatives différaient souvent dans leur sensibilité à la densité et à la fréquence des autres stratégies, ce qui affecte directement le type de dynamique associée à ces stratégies : ainsi, une stratégie à faible densité-dépendance sera souvent stable (existence d'un équilibre), tandis qu'une stratégie fortement densité-dépendante pourra montrer des régimes dynamiques plus complexes (cycles ou régime chaotique). La coexistence de stratégies à dynamique stable ou complexe nécessite une variabilité spatiale et temporelle de l'environnement, ainsi que des différences dans le taux de dispersion (Johst et al. 1999). Ces caractéristiques se retrouvent chez le lézard à flancs tachetés, où les morphes de couleur des femelles se distinguent à la fois par la complexité de leur dynamique (Sinervo et al. 2000a, annexe IX), et par des différences de taux de dispersion (Sinervo et Clobert 2003, Sinervo et al. 2006). Chez le lézard vivipare, les différences de régime dynamique entre femelles jaunes et femelles oranges (nombre et taille des descendants, sensibilité à la compétition) sont liées à des différences de statut de dominance, mais présentent les caractéristiques prédites par les modèles d'évolution des traits d'histoire de vie. En effet, le morphe jaune est le morphe à dynamique stable, peu sensible à la densité-dépendance, et peu dispersant. Au contraire, le morphe orange présente une dynamique plus complexe, sensible à la densité- et la fréquence-dépendance, ce qui augmente probablement sa probabilité d'extinction locale (de façon similaire au système du lézard à flancs tachetés, voir annexe IX). L'existence d'un taux de dispersion plus élevé, et condition-dépendant pourrait cependant permettre le maintien de ce morphe à l'échelle populationnelle. En particulier, le morphe orange est sensible aux variations de température pour sa dispersion, ce qui peut affecter la survie à long terme de l'espèce : en effet, si ce morphe réagit aux modifications du milieu en augmentant sa dispersion, cela peut lui permettre de résister aux changements climatiques en déplaçant son aire de répartition. Bien que pour l'instant, le réchauffement climatique n'ait pas de conséquences néfastes sur les populations de lézard vivipare (on observe au contraire des effets positifs sur la reproduction et la survie, Chamaillé-Jammes et al. 2006), une modification profonde et rapide de l'environnement pourraitt annoncer une crise écologique importante. Dans ce cas, la stratégie du morphe orange serait adaptative car elle réduirait le risque d'extinction brutale en diversifiant les milieux occupés.

Ce schéma théorique est toutefois complexifié par l'existence d'une troisième stratégie, plastique, qui profite à la fois d'une faible sensibilité à la compétition, d'un taux de reproduction élevé, et d'un taux de dispersion condition-dépendant. Cette stratégie semble réaliser les meilleures performances, et donc être sélectionnée. Cette stratégie étant réalisée par les hétérozygotes, le mécanisme d'overdominance assure le maintien des stratégies « classiques » dans la population. Cette particularité du système du lézard vivipare ne diminue cependant pas la généralité des processus dynamiques observés, caractérisés par la coexistence d'une stratégie stable et peu dispersante et d'une stratégie à dynamique plus complexe (plus sensible à la densité- ou à la fréquence-dépendance), avec un taux de dispersion plus élevé.

2) Stratégies alternatives chez les mâles : variance du succès reproducteur et dispersion

Chez de nombreuses espèces, des stratégies alternatives de reproduction ont été décrites chez les mâles, avec des stratégies de type défensif, où les mâles gardent activement des territoires de petite taille, et des stratégies de type agressif, où les mâles cherchent à obtenir des grands territoires (chez le lézard à flancs tachetés, Sinervo et Lively 1996, chez le bruant à gorge blanche, Tuttle 2003). D'autres stratégies alternatives opposent les comportements des mâles dominants obtenant des accouplements en gagnant des interactions de compétition, et des mâles satellites obtenant des accouplements en déjouant la vigilance des mâles dominants (chez le combattant varié, Widemo 1998 ; chez le lézard arboricole, Thompson et al. 1993). Les prédictions des modèles théoriques sur la dynamique des stratégies alternatives sont applicables également à ce type de système : les mâles défensifs ou satellites auraient une faible variance de leur succès reproducteur (stratégie stable), tandis que les succès des mâles offensifs ou dominants serait beaucoup plus variable (stratégie instable) : dans ce cas, même si la moyenne arithmétique du succès des différentes stratégies est inégale, les moyennes géométriques peuvent être égales et les différentes stratégies coexister dans des populations de taille limitée où la stochasticité démographique agit (Calsbeek et al. 2002). Il serait intéressant de vérifier chez plusieurs espèces si les prédictions quant au taux de dispersion se vérifient également pour les stratégies alternatives adoptées par les mâles (comme c'est le cas chez le lézard à flancs tachetés, Sinervo et Clobert 2003). L'existence de caractéristiques comparables suggère que les mécanismes à l'origine de l'évolution des stratégies alternatives chez les mâles et les femelles sont similaires : l'existence d'une quantité limitée de ressources crée une forte compétition sociale, et donc un conflit entre la réalisation de différentes fonctions (accès aux ressources et maintien de la condition). Une variance importante dans les coûts et bénéfices de la compétition entraînerait donc l'évolution de stratégies d'allocation alternatives, à coûts et bénéfices élevés ou faibles, plus ou moins sensibles aux effets de la densité et à dynamique stable ou complexe.

3) Quelles conditions écologiques pour l'évolution des stratégies alternatives ?

Si l'évolution de stratégies alternatives s'explique par l'existence d'une forte pression de compétition, alors il est possible que des populations différentes, caractérisées par des conditions écologiques distinctes, ne présentent pas toutes les conditions favorables à l'évolution de stratégies alternatives. Ces différences inter-populationelles permettent souvent de connaître la stratégie ancestrale, et de comprendre les facteurs sélectifs favorisant l'évolution de stratégies alternatives chez ces espèces. Chez le lézard vivipare, il existe des populations ovipares (en Italie et dans les Pyrénées), dans lesquelles les mâles sont polymorphes (oranges, jaunes ou blancs) et les femelles monomorphes (de couleur claire, gris-orangé). Le polymorphisme des mâles est probablement l'état ancestral (Sinervo et al. en préparation), et est lié à l'existence d'une forte variance du succès reproducteur chez les mâles, ce qui augmente la compétition intrasexuelle. En effet, dans ces populations, les mâles peuvent contrôler des territoires reproducteurs comptant de nombreuses femelles (car les populations montrent de fortes densités, et l'environnement est spatialement structuré), et les femelles peuvent produire jusqu'à trois pontes par saison. Certains travaux récents ont suggéré que de telles conditions sont favorables à l'évolution d'un polymorphisme de stratégies chez les mâles (Sinervo 2001, Zamudio et Sinervo 2003). Par contre, dans les populations ovovivipares, les contraintes fortes pesant sur les femelles (une seule reproduction par an et un fort investissement durant toute la gestation) les incitent à sélectionner les mâles. Dans ce cas, si le choix de partenaire est basé sur des critères relativement constants, un type de mâle en particulier a pu être sélectionné dans ces populations, induisant la fixation de ce génotype et la disparition du polymorphisme. Dans les populations ovovivipares, seuls les mâles oranges sont présents, qui ont une endurance supérieure aux autres mâles dans les populations ovipares, et ont donc pu être sélectionnés par les femelles sur un critère de qualité individuelle. Si le polymorphisme de stratégies a disparu chez les mâles dans les populations ovovivipares, les femelles ont par contre développé des stratégies alternatives. Il est possible que les coûts de la compétition intrasexuelle soient plus forts pour les femelles des populations ovovivipares, car les interactions de compétition réalisées durant la gestation peuvent affecter non seulement la condition de la femelle mais la qualité de sa ponte. En effet, l'augmentation du taux de corticostérone plasmatique de femelles gestantes (imitant les effets d'un stress) a parfois des effets négatifs sur le succès reproducteur (taille de ponte, succès de ponte, Meylan et al. 2002) et sur le phénotype des juvéniles (condition physique amoindrie, Meylan et al. 2002). Cette vulnérabilité accrue des femelles a pu amplifier le trade-off entre coûts et bénéfices de la compétition, et donc promouvoir l'évolution de stratégies alternatives dans les populations ovovivipares.

Conclusion

Ce travail de thèse a permis de décrire des stratégies alternatives complexes corrélées à la couleur ventrale chez les femelles du lézard vivipare. L'alliance des approches corrélative et expérimentale a permis de cumuler un grand nombre de données afin de caractériser de nombreux aspects du phénotype et de tester des hypothèses sur les processus évolutifs à l'origine du maintien de ce polymorphisme de stratégies dans les populations naturelles. Certaines expériences supplémentaires notamment sur les comportements d'acquisition de territoires et de ressources, ainsi que sur les stratégies d'appariement des femelles et des mâles pourraient permettre de compléter ces résultats et d'esquisser un schéma global plus précis des relations évolutives entre morphes.

Bien que les approches théoriques prédisent que les polymorphismes de stratégies devraient être fréquents chez les femelles, les exemples réels restent rares et ces nouveaux résultats confirment l'importance de la compétition sociale dans l'évolution des stratégies alternatives chez les femelles. En particulier, les résultats de cette étude s'inscrivent en parallèle de ceux observés chez un autre reptile, le lézard à flancs tachetés *Uta stansburiana*. La grande conservation apparente des mécanismes évolutifs en dépit d'une divergence ancienne des lignées, séparées depuis 135 millions d'années, soutient fortement la généralité des processus à l'origine de l'évolution des stratégies alternatives, aussi bien chez les femelles que chez les mâles.

Enfin, cette étude vient s'ajouter à un grand nombre de travaux précédents effectués chez le lézard vivipare. Cette espèce est donc devenue un modèle biologique incontournable, pour lequel la diversité des approches employées et des traits phénotypiques ou génétiques analysés permet de caractériser des processus évolutifs complexes en interaction avec la dynamique des populations.

BIBLIOGRAPHIE

Ahnesjö J, Forsman A. 2003. Correlated evolution of colour pattern and body size in polymorphic pygmy grasshoppers, Tetrix undulata. *Journal of Evolutionary Biology*, 16: 1308-1318.

Alberts AC. 1990. Chemical properties of femoral gland secretions in the desert iguana *Dipsosaurus dorsalis*. *Journal of Chemical Ecology*, 16: 13-25.

Alberts AC. 1992. Pheromone self-recognition in desert iguanas. *Copeia*, 1992:229-232.

Alonzo SH, Sinervo B. 2001. Mate choice games, context-dependent good genes, and genetic cycles in the side-blotched lizard, *Uta stansburiana*. *Behavioral Ecology and Sociobiology*, 49: 176-186.

Amundsen T, Forsgren E, Hansen LTT. 1997. On the function of female ornaments: male bluethroats prefer colorful females. *Proceedings of the Royal Society Biological Sciences Series B*, 264: 1579-1586.

Amundsen T.2000. Why are females birds ornamented? *Trends in Ecology and Evolution*, 15: 149-155.

Andersson S. 2000. Efficacy and Content in Avian Colour Signals. In : *Animal Signals* (Y. Espmark, T. Amundsen, G. Rosenqvist, eds), pp 47-60. Tapir Academic Press, Trondheim.

Aragon P, Lopez P, Martin J. 2001. Chemosensory discrimination of familiar and unfamiliar conspecifics by lizards : implications of field spatial relationships between males. *Behavioral Ecology and Sociobiology*, 50: 128-133.

Aragon P, Massot M, Gasparini J, Clobert J. 2006. Socially acquired information through chemical cues in the common lizard, *Lacerta vivipara*. *Animal Behaviour*, 72: 965-974.

Barton NH, Turelli M. 1989. Evolutionary quantitative genetics : how little do we know. *Annual Review of Genetics*, 23: 337-370.

Beeching SC, Gross SH, Bretz HS, Hariatis E. 1998. Sexual dichromatism in convict cichlids: the ethological significance of female ventral coloration. *Animal Behaviour*, 56: 1021-1026.

Begon M, Harper JL, Townsend CR. 1996. Ecology: Individuals, Populations, and Communities (3rd edition). Blackwell Science, London, 1068 p.

Bélichon S, Clobert J, Massot M. 1996. Are there differences in fitness components between philopatric and dispersing individuals? *Acta Oecologica*, 17: 503-517.

Belliure J, Meylan S, Clobert J. 2004. Prenatal and postnatal effects of corticosterone on behaviour in juveniles of the common lizard *Lacerta vivipara*. *Journal of Experimental Zoology*, 301A: 401-410.

Berglund A, Rosenqvist G. 2001. Male pipefish prefer dominant over attractive females. *Behavioral Ecology*, 12: 402-406.

Boulinier T, Ives AR, Danchin E. 1996. Measuring aggregation of parasites at different host population levels. *Parasitology*, 112: 581-587.

Bradshaw HD, Schemke DW. 2003. Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature*, 426: 176-178.

Brockmann HJ. 2001. The Evolution of Alternative Strategies and Tactics. *Advances in the Study of Behavior*, 30: 1-51.

Brotons L. 2000. Winter spacing and non-breeding social system of the Coal Tit *Parus ater* in a subalpine forest. *Ibis*, 142: 657-667.

Brown JL. 1997. A theory of mate choice based on heterozygosity. *Behavioral Ecology*, 8: 60-65.

Calsbeek R, Alonzo SH, Zamudio K, Sinervo B. 2002. Sexual selection and alternative mating behaviours generate demographic stochasticity in small populations. *Proceedings of the Royal Society Biological Sciences Series B*, 269 : 157-164.

Chamaillé-Jammes S, Massot M, Aragon P, Clobert J. 2006. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology*, 12: 392-402.

Chevalier M, Dufaure JP, Lecher P. 1979. Cytogenetic study of several species of Lacerta (Lacertidae, Reptilia) with particular reference to sex chromosomes. *Genetica*, 50: 11-18.

Clobert J, Massot M, Lecomte J, Sorci G, de Fraipont M, Barbault R. 1994. Determinants of dispersal behavior : the common lizard as a case study. In: *Lizard Ecology : historical and experimental perspectives* (LJ Vitt, ER Pianka, eds), pp183-206. Princeton University Press, Oxford.

Comendant T, Sinervo B, Svensson EI, Wingfield J. 2003. Social competition, Corticosterone and survival in female lizard morphs. *Journal of Evolutionary Biology*, 16: 948-955.

Cooper WE, Greenberg N. 1992. Reptilian coloration and behavior. In: *Biology of the reptilia: hormones, brain, and behavior* (D Crews, C Gans, eds), pp 289-422. Academic Press, New York.

Cote J. 2003. Rôle des caroténoïdes et de la corticostérone dans la relation entre condition et couleur d'un individu chez le lézard vivipare (*Lacerta vivipara*). DEA d'Ecologie – Université Paris VI, Paris XI, INA-PG.

Cote J. 2006. Information socialement acquise chez le lézard vivipare *Lacerta vivipara*. Thèse de Doctorat- Université Paris VI.

Cowlishaw G. 1999. Ecological and social determinants of spacing behaviour in desert baboon groups. *Behavioral Ecology and Sociobiology*, 45: 67-77.

Cunningham EJA, Birkhead TR. 1998. Sex roles and sexual selection. *Animal Behaviour*, 56: 1311-1321.

Dawkins R. 1976. The selfish gene. Oxford University Press, Oxford, 224p.

Dawkins R. 1980. Good strategy or evolutionary stable strategy ? In: *Sociobiology: Beyond Nature/Nurture* (GW Barlow, J Silverberg, eds), pp 331-367. Westview Press.

de Fraipont M, Clobert J, John-Alder H, Meylan S. 2000. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. *Journal of Animal Ecology*, 69: 404-413.

Doebeli M, Ruxton GD. 1997. Evolution of dispersal rates in metapopulation models: Branching and cyclic dynamics in phenotype space. *Evolution*, 51: 1730-1741.

Emlen DJ. 1994. Environmental control of horn length dimorphism in the beetle *Ontophagus acuminatus* (Coleoptera: Scarabaeidae). *Proceedings of the Royal Society Biological Sciences Series B,* 256: 131-136.

Endler JA. 1990. On the measurement and classification of color in studies of animal color patterns. *Biological Journal of the Linnean Society*, 41: 315-352.

Enquist M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour*, 33: 1152-1161.

Fisher RA. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford, 272p.

Folstad I, Karter AJ. 1992. Parasites, bright males, and the immunocompetence handicap. *The American Naturalist*, 139: 603-622.

Formica VA, Gonser RA, Ramsay S, Tuttle EM. 2004. Spatial dynamics of alternative reproductive strategies: The role of neighbors. *Ecology*, 85: 1125-1136.

Fox CW, Roff DA, Fairbairn DJ. 2001. Evolutionary Ecology. Oxford University Press, Oxford, 424p.

Fretwell SD, Lucas HL. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, 19: 16-36.

Galeotti, P., Rubolini, D., Dunn, P.O. & Fasola, M. 2003. Colour polymorphism in birds: causes and functions. *Journal of Evolutionary Biology*, 16: 635-646.

Gross MR. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution*, 11: 92-98.

Grossman CJ. 1985. Interactions between the gonadal steroids and the immune system. *Science*, 227: 257-261.

Gundersen G, Andreassen HP. 1998. Causes and consequences of natal dispersal in root voles, Microtus oeconomus. *Animal Behaviour*, 56: 1355-1366.

Hamilton WD, May RM. 1977. Dispersal in stable habitats. *Nature*, 269 : 578-581.

Hassell MP. 1975. Density-dependence in single-species models. *Journal of Animal Ecology*, 44 : 283-296.

Heino M, Metz JAJ, Kaitala V. 1998. The enigma of frequency-dependent selection. *Trends in Ecology and Evolution*, 13 : 367-370.

Henson SA, Warner RR. 1997. Male and female alternative reproductive behaviors in fishes: a new approach using intersexual dynamics. *Annual Review of Ecology and Systematics*, 28: 571-592.

Hews DK, Moore MC. 1995. Influence of androgens on differentiation of secondary sex characters in tree lizards, *Urosaurus ornatus*. *General and Comparative Endocrinology*, 97: 86-102.

Hughes KA, Du L, Rodd H, Reznick DN. 1999. Familiarity leads to female mate preference for novel males in the guppy, *Poecilia reticulata*. *Animal Behaviour*, 58: 907-916.

Huntingford FA, Taylor AC, Sneddon LU, Neat FC. 2000. Prowess and the resolution of fights. In : *Animal Signals* (Y. Espmark, T. Amundsen, G. Rosenqvist, eds), pp 259-276. Tapir Academic Press, Trondheim.

Jaisson P. 1985. Social behaviour. In: *Comprehensive insect Physiology – Biochemistry and Pharmacology Vol. 9* (GA Kerkut, LI Gilbert, eds), pp 673-394. Pergamon Press, Oxford.

Jannett F. 1978. The density-dependent formation of extended maternal families of the montane vole, *Microtus montanus nanus*. *Behavioral Ecology and Sociobiology*, 3: 245-263.

Johnsen TS, Hengeveld JD, Blank JL, Yasukawa K, Nolan V. 1996. Epaulet brightness and condition in female red-winged blackbirds. *The Auk*, 113: 356-362.

Johnson B. 1965. Wing polymorphism in aphids II. Interaction between aphids. *Entomologia Expermientalis and Applicata,* 8: 49-64.

Johnson K. 1988. Sexual selection in pinion jays II: male choice and female-female competition. *Animal Behaviour*, 36: 1048-1053.

Johnstone RA, Norris K. 1993. Badges of status and the cost of aggression. *Behavioral Ecology and Sociobiology*, 32: 127-134.

Johnstone RA, Reynolds JD, Deutsch JC. 1996. Mutual mate choice and sex differences in choosiness. *Evolution*, 50: 1382-1391.

Johst K, Doebeli M, Brandl R. 1999. Evolution of complex dynamics in spatially structured populations. *Proceedings of the Royal Society Biological Sciences Series B*, 266 : 1147-1154.

Jones W, Waser P, Elliott N, Link N, Bush B. 1988. Philopatry, dispersal, and habitat saturation in the banner-tailed kangaroo rat, *Dipodomys spectabilis*. *Ecology*, 69: 1466-1473.

Keller L. 1994. Rewards of promiscuity. *Nature*, 372: 229-230.

Kettlewell HBD. 1955. Selection experiments on industrial melanism in the Lepidoptera. *Heredity*, 9: 323-342.

Kingston JJ, Rosenthal GG, Ryan MJ. 2003. The role of sexual selection in maintaining a colour polymorphism in the pygmy swordtail, Xiphophorus pygmaeus. *Animal Behaviour*, 65: 735-743.

Krueger O, Lindstrom J, Amos W. 2001. Maladaptive mate choice maintained by heterozygote advantage. *Evolution*, 55: 1207-1214.

Laloi D, Richard M, Lecomte J, Massot M, Clobert J . 2004. Multiple paternity in clutches of common lizard Lacerta vivipara: Data from microsatellite markers. *Molecular Ecology*, 13: 719-723.

Lambin X, Aars J, Piertney SB. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation. In: *Dispersal* (J Clobert, E Danchin, A Dhondt, JD Nichols, eds), pp 110-122. Oxford University Press, Oxford.

Lamotte M. 1959. Polymorphism of natural populations of Cepea nemoralis. *Cold Spring Harbor Symposium on Quantitative Biology,* 24:65-86.

Langmore N. 2000. Why Female Birds Sing. In : *Animal Signals* (Y. Espmark, T. Amundsen, G. Rosenqvist, eds), pp 259-276. Tapir Academic Press, Trondheim.

Le Galliard JF, Ferriere R, Dieckmann U. 2003a. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution*, 57: 1-17.

Le Galliard JF, Ferriere R, Clobert J. 2003b. Mother-offspring interactions affect natal dispersal in a lizard. *Proceedings of the Royal Society Biological Sciences Series B*, 270: 1163-1169.

Le Galliard JF, Ferriere R, Dieckmann U. 2005a. Adaptive evolution of social traits: Origin, trajectories, and correlations of altruism and mobility. *The American Naturalist*, 165: 206-224.

Le Galliard JF, Ferriere R, Clobert J. 2005b. Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos*, 111: 368-376.

LeBas NR, Marshall NJ. 2000. The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. *Proceedings of the Royal Society Biological Sciences Series B*, 267: 445-452.

Lecomte J, Clobert J, Massot M. 1992. Sex identification in juveniles of *Lacerta vivipara*. *Amphibia-Reptilia*, 13: 21-25.

Lecomte J, Clobert J, Massot M, Barbault R. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. *Ecoscience*, 1:300-310

Leimar O. 2005. The evolution of phenotypic polymorphism: Randomized strategies versus evolutionary branching. *The American Naturalist*, 165: 669-681.

Léna JP, de Fraipont M. 1998. Kin recognition in the common lizard. *Behavioral Ecology and Sociobiology*, 42: 341-347.

Léna JP, Clobert J, de Fraipont M, Lecomte J, Guyot G. 1998. The relative influence of density and kinship on dispersal in the common lizard. *Behavioral Ecology*, 9: 500-507.

Lopez P, Aragon P, Martin J. 2003. Responses of female lizards, *Lacerta monticola*, to males' chemical cues reflecting their mating preference for older males. *Behavioral Ecology and Sociobiology*, 55: 73-79.

Lopez P, Amo L, Martin J. 2006. Reliable signaling by chemical cues of male traits and health state in male lizards, Lacerta monticola. *Journal of Chemical Ecology*, 32: 473-488.

Lorenzon P, Clobert J, Massot M. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. *Evolution*, 55: 392-404.

Luque-Larena JJ, Lopez P, Gosalbez J. 2004. Spacing behavior and morphology predict promiscuous mating strategies in the rock-dwelling snow vole, *Chionomys nivalis*. *Canadian Journal of Zoology*, 82: 1051-1060.

Massot M. 1992. Déterminisme de la dispersion chez le lézard vivipare. Thèse de Doctorat, Université Paris XI.

Massot M, Clobert J, Pilorge T, Lecomte J, Barbault R. 1992. Density dependence in the common lizard : demographic consequences of a density manipulation. *Ecology*, 73: 1742-1756.

Massot M, Clobert J, Lecomte J, Barbault R. 1994. Incumbent advantage in common lizards and their colonizing ability. *Journal of Animal Ecology*, 63: 431-440.

Massot M, Clobert J. 2000. Processes at the origin of similarities in dispersal behaviour amog siblings. *Journal of Evolutionary Biology*, 13: 707-719.

Massot M, Clobert J, Lorenzon P, Rossi JM. 2002. Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *Journal of Animal Ecology*, 71: 253-261.

Matthiopoulos J, Moss R, Lambin X. 1998. Models of red grouse cycles. A family affair ? *Oikos*, 82: 574-590.

Maynard-Smith J. 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge. 226p.

Maynard-Smith J, Harper D. 1988. The evolution of aggression: can selection generate variability? *Philosophical Transactions of the Royal Society Series B*, 319: 557-570.

Mazer SJ, Damuth J. 2001. Nature and Causes of Variation. In: *Evolutionary Ecology* (CW Fox, DA Roff, DJ Fairbairn, eds), pp 3-15. Oxford University Press, Oxford.

Mendel G. 1866. Experiments in Plant Hybridization. Document en ligne: http://www.netspace.org/MendelWeb/Mendel.plain.html

Meylan S, Belliure J, Clobert J, de Fraipont M. 2002. Stress and body condition as prenatal and postnatal determinants of dispersal in the common lizard (*Lacerta vivipara*). *Hormones and Behavior*, 42: 319-326.

Meylan S, de Fraipont M, Clobert J. 2004. Maternal size, stress and offspring philopatry: an experimental study in the common lizard (*Lacerta vivipara*). *Ecoscience*, 11: 123-129.

Meylan S, Clobert J, Sinervo B. 2007. Adaptive significance of maternal induced density-dependent phenotype. *Oikos*, sous presse.

Meylan S, de Fraipont M, Aragon P, Vercken E, Clobert J. Are dispersal-dependent personalities produced by phenotypic plasticity ? Soumis à *Behavioral Ecology and Sociobiology*.

Milinski M, Baker TCM. 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature*, 344: 330-333.

Moore MC. 1991. Application of organization-activation theory to alternative male strategies. *Hormones and Behavior*, 25: 154-179.

Morgan TH. 1911. The origin of five mutations in eye color in Drosophila and their mode of inheritance. *Science*, 33: 534.

Motro U. 1983. Optimal rates of dispersal. III. Parent-offspring conflict. *Theoretical Population Biology*, 23: 159-168.

Olendorf R, Rodd FH, Punzalan D, Houde AE, Hurt C, Reznick DN, Hughes KA. 2006. Frequency-dependent survival in natural guppy populations. *Nature*, 441: 633-636.

Pearse DE, Pogson GH. 2000. Parallel evolution of the melanic form of the California legless lizard, Anniella pulchra, inferred from mitochondrial DNA sequence variation. *Evolution*, 54: 1041-1046.

Reusch TBH, Haberll MA, Aeschlimann PB, Milinski M. 2001. Female sticklebacks count alleles in a strategy of sexual selection explaining MHC polymorphism. *Nature*, 414: 300-302.

Richard M, Lecomte J, de Fraipont M, Clobert J. 2005. Age-specific mating strategies and reproductive senescence. *Molecular Ecology*, 14: 3147-3155.

Roff DA, Fairbairn DJ. 2001. The genetic basis of dispersal and migration, and its consequences for the evolution of correlated traits. In: *Dispersal* (J Clobert, E Danchin, AA Dhondt, JD Nichols, eds), pp191-202. Oxford University Press, Oxford.

Rohwer S. 1977. Status signalling in Harris sparrows: some experiments in deception. *Behaviour*, 61: 107-129.

Rohwer S, Ewald PW. 1981. The cost of dominance and advantage of subordinance in a badge signalling system. *Evolution*, 35: 441-454.

Rohwer S, Paulson DR. 1987. The avoidance-image hypothesis and color polymorphism in Butei hawks. *Ornis Scandinavica*, 18: 285-290.

Ronce O, Clobert J, Massot M. 1998. Natal dispersal and senescence. *Proceedings of the National Academy of Science USA*, 95: 600-605.

Roulin A. 2004a. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews of the Cambridge Philosophical Society*, 79: 815-848.

Roulin A. 2004b. Covariation between plumage colour polymorphism and diet in the Barn Owl *Tyto alba*. *Ibis*, 146: 509-517.

Ryan MJ, Pease CM, Morris MR. 1992. A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: testing the prediction of equal fitnesses. *The American Naturalist*, 139: 21-31.

Sheldon BC. 2000. Environmental Dependence of Genetic Indicator Mechanisms. In: *Animal Signals* (Y. Espmark, T. Amundsen, G. Rosenqvist, eds), pp 195-207. Tapir Academic Press, Trondheim.

Shier DM, Randall JA. 2004. Spacing as a predictor of social organization in kangaroo rats (*Dipodomys heermanni arenae*). *Journal of Mammology*, 85: 1002-1008.

Sinervo B, Lively CM. 1996. The rock-paper-scissors game and the evolution of alternative male reproductive strategies. *Nature*, 380: 240-243.

Sinervo B, Svensson E, Comendant T. 2000a. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature*, 406:985-988.

Sinervo B, Miles DB, Frankino WA, Klukowski M, DeNardo DF. 2000b. Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behaviour*, 38: 222-233.

Sinervo B. 2001. Runaway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. *Genetica*, 112-113: 417-434.

Sinervo B, Zamudio K. 2001. The evolution of alternative reproductive strategies : fitness differential, heritability, and genetic correlation between the sexes. *The Journal of Heredity*, 92: 198-205.

Sinervo B, Bleay C, Adamopoulou C. 2001. Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. *Evolution*, 55: 2040-2052.

Sinervo B, Clobert J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science*, 300: 1949-1951.

Sinervo B, Calsbeek R, Comendant T, Both C, Adamopoulou C, Clobert J. 2006. Genetic and maternal determinants of effective dispersal: the effect of sire genotype and size at birth in side-blotched lizards. *The American Naturalist*, 168: 88-99.

Sinervo B, Heulin B, Surget-Groba Y, Clobert J, Miles DB. A new rock-paper-scissors mating system in the European common lizard: evidence from performance traits, payoff matrices, and frequency cycles. Manuscrit en preparation.

Stamps JA, Krishnan VV. 1995. Territory acquisition in lizards: III. Competing for space. *Animal Behaviour*, 49: 679-693.

Stamps JA, Krishnan VV. 1998. Territory acquisition in lizards: IV. Obtaining high status and exclusive home ranges. *Animal Behaviour*, 55: 461-472.

Stearns SC. 1992. The evolution of life histories, Oxford University Press, Oxford, 264 p.

Svensson E, Abbott J, Hardling R. 2005. Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. *The American Naturalist*, 165: 567-576.

Thompson CW, Moore IT, Moore MC. 1993. Social, environmental and genetic factors in the ontogeny of phenotypic differentiation in a lizard with alternative male reproductive strategies. *Behavioral Ecology and Sociobiology*, 33: 137-146.

Trivers RL. 1972. Parental investment and sexual selection. In: *Sexual selection and the Descent of Man , 1871-1971* (B Campbell, ed), pp. 136-179. Aldine-Atherton, Chicago.

Tuttle EM. 2003. Alternative reproductive strategies in the white-throated sparrow: Behavioral and genetic evidence. *Behavioral Ecology*, 14: 425-432.

van Rhijn JG. 1973. Behavioural dimorphism in male ruffs *Philomachus mugnax*. *Behaviour*, 47: 153-228.

Vehrencamp SL. 2000. Handicap, Index, and Conventional Signal Elements of Bird Song. In: *Animal Signals* (Y. Espmark, T. Amundsen, G. Rosenqvist, eds), pp 277-300. Tapir Academic Press, Trondheim.

Vercken E, de Fraipont M, Dufty AM, Clobert J. 2007. Mother's timing and duration of corticosterone exposure modulate offspring size and natal dispersal in the common lizard (*Lacerta vivipara*). *Hormones and Behavior*, sous presse.

Wauters L, Dhondt AA. 1992. Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. *Animal Behaviour*, 43: 297-311.

Weiss SL. 2006. Female-specific color is a signal of quality in the striped plateau lizard (*Sceloporus virgatus*). *Behavioral Ecology*, 17: 726-732.

West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, 58: 155-183.

Widemo F. 1998. Alternative reproductive strategies in the ruff, *Philomachus pugnax*: a mixed ESS? *Animal Behaviour*, 56: 329-336.

Woltereck R. 1909. Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphniden. *Versuche Deutsche Zoologische Gesellschaft*, 19: 110-172.

Zamudio KR, Sinervo B. 2003. Ecological and social contexts for the evolution of alternative reproductive mating strategies. In: *Lizard Social Behavior* (SF Fox, TA Baird, JK McCoy, eds), pp 83-106. John Hopkins University Press, Baltimore.

ANNNEXE I: Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*

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Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*

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Running title: Colour and reproductive strategies in lizards

Summary

Within-sex colour variation is a widespread phenomenon in animals that often plays a role in social selection. In males, colour variation is typically associated to the existence of alternative reproductive strategies. Despite ecological conditions theoretically favourable to the emergence of such alternative strategies in females, the social significance of colour variation in females has less commonly been addressed, relative to the attention given to male strategies. In a population of the common lizard, females display three classes of ventral colouration: pale yellow, orange and mixed. These ventral colours are stable through individual's life and maternally heritable. Females of different ventral colourations displayed different responses of clutch size, clutch hatching success and clutch sex-ratio to several individual and environmental parameters. Such reaction patterns might reflect alternative reproductive strategies in females. Spatial heterogeneity and presence of density- and frequency-dependent feedbacks in the environment could allow for the emergence of such alternative strategies in this population and the maintenance of colour variation in females.

Keywords: *colour variation, females, alternative reproductive strategies*

INTRODUCTION

Variation in colour is an intriguing phenomenon found in a widespread number of animal taxa, particularly vertebrates (Galeotti et al. 2003). Animal colour patterns are potentially used in intraspecific communication, thermoregulation, and predation avoidance (Endler 1990, Forsman & Shine 1995). For these last two functions, variation in colouration is essentially found at large geographical scale in response to variations in climate, habitat and predators (Galeotti et al. 2003). Syntopic variation in colouration occurs much less frequently (Thompson & Moore 1991), and is more likely to convey socially important information regarding sex (Cooper & Burns 1987, Andrés et al. 2002), reproductive condition (Weiss 2002), social status (Dawkins & Krebs 1978, Thompson & Moore 1991) and in some cases competitive ability (Cooper & Burns 1987). Syntopic variation can arise from between-sex, or within-sex differences, or both. If sexual dimorphism is related to mate choice (Mazer & Damuth 2001), within-sex polymorphism is expected to be more related to social interactions than to ecological functions such as climate, habitat or anti-predator strategies (Forsman & Shine 1995, Gross 1996), and within-sex polymorphism is often associated with alternative reproductive strategies (in birds, Tuttle 2003; in fishes, Hutchings & Myers 1994; in insects, Ahnesjö & Forsman 2003; in reptiles, Rand 1988).

The determinism of a colour variation can be genetically based (true polymorphism) or condition- dependent (Gross 1996). In the latter case, the phenotype that develops depends on the individual's condition (like the reproductive state, Weiss 2002), or on an environmental factor (like population density, Eadie & Fryxell 1992). Colour signals are assumed to be costly (e.g. carotenoid-based colouration, Olson & Owens 1998), and thus are expected to be displayed by the most physiological vigorous individuals who would also adopt the a high performance reproductive strategy. In the case of a genetic polymorphism, allelic variation can be maintained if the alternative strategies achieve equal mean fitness (Ryan et al. 1992, Calsbeek et al. 2001). Variation can also be maintained if the environment is heterogeneous (different phenotypes have unequal fitness under different environmental conditions, but the environment is variable enough spatially or temporally for all alternative phenotypes to persist, Mazer & Damuth 2001), or if there is negative frequency-dependent selection (the rare phenotype gains a fitness advantage over the common phenotype, Gross 1996). Finally, variation might also be maintained by overdominance of heterozygous genotypes relative to homozygous genotypes, or through an interaction between overdominance and frequency-dependent selection (Sinervo & Zamudio 2001).

In reptiles, variation in colour pattern is common (Cooper & Burns 1987, Rand 1988, Thompson, Moore & Moore 1993, Forsman & Shine 1995, Sinervo & Lively 1996, Weiss 2002) and in several cases this variation is genetically based (Thompson et al. 1993, Sinervo & Zamudio 2001, Sinervo et al. 2001). Such colour polymorphism is often associated to the existence of alternative behavioural strategies (Rand 1988, Thompson et al. 1993, Sinervo & Lively 1996) but only in males for most cases, whereas female colour pattern polymorphism is usually related to thermoregulation or predation avoidance (Forsman & Shine 1995). However, increasing awareness of an active female mating choice (Olsson et al. 2003, Richard et al. 2005) suggests that intrasexual competition and therefore alternative tactics should be common in females (Gross 1996). As colour variation often reflects alternative tactics in males, we expect the same pattern to be found in females. In *Uta stansburiana*, female colour morphs actually display alternative reproductive strategies (Sinervo et al. 2000), associated with complex behavioural and physiological syndromes (Sinervo et al. 2001, Svensson et al. 2001). But apart from this example (and a few in insects, see Sirot et al. 2003, Svensson et al. 2005), there seems to be a striking lack of information on such alternative female strategies and the genetic or environmental causes of such variation.

The common lizard (*Lacerta vivipara*) is a well-documented species, as many aspects of its demography (Massot et al. 1992), ecology (Lorenzon et al. 2001), behaviour (Léna et al. 2000), and life-history (Pilorge et al. 1987) have been extensively studied. However, colour variation in this species has not yet been considered, even though females display conspicuous ventral colourations ranging from pale yellow to bright orange. As this colour pattern is ventral, we do not expect it to play any role in thermoregulation (even a minor role in thigmothermy, see Belliure & Carrascal 2002) or in predation avoidance, and therefore it is more likely to act as a social cue. As females have strong control over reproductive decisions by mate choice (direct or indirect) and through various maternal effects (Massot et al. 2002, Meylan et al. 2002, Belliure et al. 2004), they have the opportunity to adopt different reproductive strategies. In addition, males could select their mates upon their ventral colour depending on their own individual strategy.

Populations of this species are subject to strong density feedback effects (Massot et al. 1992, Lecomte et al. 1994, Clobert et al. 1994, Aragon et al. in press), a situation that may open the field for alternative demographic strategies to evolve (Heino et al. 1997). The first objective of this study was to describe female colour variation and to characterize alternative phenotypes using visual classification and spectrophotometry measures. We then examined stability of colour throughout life as well as its heritability. The second objective was to look for life-history differences between colour variants, which can reveal alternative strategies. The morphology, reproduction and survival were compared between colour phenotypes, in particular the interactions with time, density and space. These analyses might help to answer questions about the nature of the maintenance of a colour variation in this species of lizard.

METHODS

The Species

Lacerta vivipara is a small (adult snout-vent length from 50 to 70 mm) live bearing lacertid lizard, which is found throughout Europe and Asia. The population we studied is located on Mont Lozère (Southern France, altitude 1420 m), and is divided into two contiguous zones that differ in structural diversity of the microhabitat (Clobert et al. 1994): a zone with high structural diversity and high lizard densities (high quality zone), and a zone with low structural diversity and lower lizard densities (low quality zone). In this population, adult males emerge from hibernation in mid-April, followed by yearlings, and adult females in mid-May. Mating occurs at female emergence, and gestation lasts for two months. Parturition starts in mid-July and lasts for two or three weeks. Females lay an average clutch of 5 soft-shelled eggs (range 1-12). Offspring hatch within one or two hours after laying and are immediately independent of their mother. The activity season ends in late September and juveniles are the last to enter hibernation. A more detailed description of life history can be found in Massot et al. (1992). In this population, adult females display a ventral colouration varying from pale yellow to bright orange, whereas adult males are almost always orange. Juveniles start by being melanic, and slowly turn to a pale green ventral colouration when yearlings. Stability of ventral colour arises with sexual maturity (usually at two years in the Mont Lozère population).

Data set

From 1989 to 2002, 1009 females were temporarily removed from the population. Each year, from the beginning of July, females were kept in the laboratory until parturition. At capture, females were measured (snout-vent length or SVL) and weighted. Corpulence was calculated as the residual from the relationship between body mass and SVL. Females were housed in plastic terraria with damp soil, a shelter and water *ad libitum*. Two feeding treatments were applied: females on “full rations” were offered one larva of P*yralis farinalis* every week, and females on “half-rations” one every two weeks. They were exposed to natural daylight and were heated 6 h per day with an electric bulb. Female ventral colouration was estimated visually using a colour references, and fell into three distinct classes: pale yellow, bright orange and mixed colouration (intense yellow or mixture of yellow and orange).

At birth, offspring were individually marked by toe-clipping and sexed by counting ventral scales (Lecomte et al. 1992). Offspring and their mother were measured and weighed. They were then released at the mother’s last capture point.

Spectrophotometry measures

In 2004, 246 adult females were captured at other study sites on the Mont Lozère and their ventral colouration has been both estimated visually and measured with a spectrophotometer (Ocean Optics USB2000). Data analysis was handled with the aid of the Color Project 1 software, developed by Jean-Marc Rossi (Laboratoire d’Ecologie, Université Pierre et Marie Curie, Paris). The software allowed us to calculate several parameters quantifying colour: i) the hue, which is the everyday meaning of ‘colour’ (e.g. blue, green, yellow, red, purple, etc…) and which is correlated with the wavelength of the maximum slope of the colour spectrum; ii) the chroma, which is a measure of the saturation of a colour and a function of how rapidly intensity changes with wavelength; iii) the classification segments LM and MS described by Endler (1990) which are the differences in brightness between binned segments of the spectral range; and iv) the wavelength for which the reflectance is the highest (peak wavelength).

Density and Survival Analysis

Annual densities were estimated by mark-recapture methods, using the software Capture in the computer program MARK (White 1998). To estimate density, several capture sessions were organized within each year. The capture sessions were concentrated in time such that we could assume no mortality, emigration or immigration between sessions (closed populations). Colour morph frequencies in the population were estimated from the sub-sample of females captured in summer and brought to the laboratory (more than half of the adult female population). We verified (see survival analyses) that the capture probability was not colour morph-dependent.

Females were captured annually in spring, so we had a data set of 867 capture histories constituted of 14 capture occasions. The females apparent survival rate (including mortality and emigration) was estimated using the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) extended to group effects (Clobert et al. 1988, Lebreton et al. 1992). As migration rate is low in this population (Massot *et al.* 1992), we considered the apparent survival rate as representative of the actual survival rate. The computer program MARK (White 1998) was used to fit models. Models were compared by Akaike Information Criterion (AIC) and we retained the most parsimonious of them (lowest AIC, Anderson et al. 1994). We tested the effects of colour and year and their interactions independently on survival and capture probabilities. We also replaced the year effect on survival by an effect of female density, male density, yellow females frequency, orange females frequency and the various interactions between density and frequency. These variables can be considered as statistically independent since the total density, the female morphs frequency and the survival probability have been estimated on different data set.

Statistical Analysis

To verify that our visual classification was relevant, we conducted a discriminant analysis on the variables from an analysis of the spectrum. We used the DISCRIM procedure of the statistical package of SAS Institute (SAS, 1992) to calculate the discriminant power of variables, a canonical discriminant function, and a discriminant score by re-classifying individuals of known visual colour with the discriminant function. To avoid a bias in the reclassification process, we used the cross-validate option of the DISCRIM procedure, which allowed us to classify each individual using a discriminant function calculated from all others. We selected the combination of variables that led to a minimum of errors in the re-classification process.

For the analysis of morphology (SVL or corpulence, corpulence being calculated as the residual from the relationship between body mass and SVL) and reproduction, we only retained one year of data for the females that had been recaptured several times in order to avoid individual effects (we chose one year randomly in order to have a sample representative of all age classes). 730 females were used for the analysis of morphology. For the analysis of reproduction, many females had missing values for at least one of the variables, and were thus excluded from the analyses. 409 females were retained for the analysis of reproduction.

We analysed continuous variables (morphological variables and clutch size) with general linear models (GLM procedure, SAS Institute). For variables that constituted proportions (clutch hatching success, sex-ratio), we used logistic-linear regression analyses (GENMOD procedure, SAS Institute). Log-likelihood ratio tests (χ^2 values) were used to assess significance of effects. Type III sum of squares was used in all cases. We started with a general model including all the potential effects and their interactions (up to three-ways interactions with habitat zone and ventral colour): year (or annual female density), habitat zone, annual orange female frequency, annual yellow female frequency, ventral colour, SVL, age (logarithm and squared logarithm), corpulence, feeding treatment. We then dropped the non-significant effects (backward selection), starting with the most complex interaction terms. Only the results of the final model are reported. Colour effects were interpreted by comparing alternately the three different colour pairs. In that case, we used a Bonferroni correction to assess significance of effects (the significance threshold for the critic probability being lowered to 0.017). Colour effects were graphically represented with conditional plots: only the effect of one covariate on the response variable is represented, all other covariates being replaced by their mean values in the multivariate model.

The stability of ventral colour at the individual level was estimated on 611 females by a general linear model (GLM procedure, SAS Institute) testing for the effect of the ventral colour in the first capture occasion on the ventral colour in the second capture occasion, with ventral colours being additively scored as 0 = yellow, 1 = mixed and 2 = orange (following Sinervo et al. 2001). We tested for the effects of several environmental variables: year effect, annual density, orange and yellow females frequencies, and feeding treatment. Heritability of ventral colour was estimated by a general linear model testing for the additive effects of maternal ventral colour on daughter ventral colour (when recaptured as adult) on 136 mother-daughter pairs, and we tested for the environmental effects noted above to estimate the potential source of maternal effect variation.

RESULTS

Spectrophotometrical characterization of colour morphs

Individuals of different colour classes display different reflectance spectra (Fig. 1a). Yellow females are characterized by a large peak between 400 and 750 nm, the climax being around 620 nm, with a small bump around 480 nm. Orange females display a steeper slope leading to a narrower peak between 500 and 750 nm, the climax being around 590 nm. Mixed females have a spectrum with characteristics from both the yellow and the orange spectra, but sometimes arranged in different ways depending on the individual: on average, the peak starts around 400 but with a low slope at first, the slope increasing around 500 nm, and a slight change of inclination around 550 nm. For males, the spectrum is composed of a major peak similar to the orange females peak, and a smaller peak between 300 and 400 nm, corresponding to the ultra-violet A wavelength. From the discriminant analysis, we retained only the chroma and the hue among the various coefficients describing the reflectance spectrum, because this combination led to a minimum of errors in the re-classification process. These two variables have a very strong discriminant power ($F_{2,243}$ equal to 63.16 and 63.84 respectively, both probabilities being less than 0.0001) and allow us to separate well all three of the colour classes (the squared Mahalanobis distance between groups is different from 0, all probabilities being inferior to 0.0001 and Fig. 1b). Although the mixed colouration category appeared as a bit less well discriminated, the hit score (which is the proportion of correctly classified individuals) nevertheless reaches 0.67 with a net gain of 0.81 yielding to a highly significant discrimination of the mixed class from the yellow and orange classes ($p<0.0001$).

The different colour morphs are actually better characterized by the global shape of the reflectance spectrum than by the wavelengths, as the chroma and the hue are the most discriminating variables. With that criterion, orange and yellow spectra are always distinguishable, but the mixed spectrum can sometimes be confused with an orange or a yellow one even if the visual inspection clearly classified these individuals in the mixed-coloured category.

Stability and Heritability of colour

Individual colour was stable through life ($F_{1,478}$=923.55, p<0.0001, n=611). Only for 25% of cases the colour changed in the course of an individual life, and in most cases that change occurred between two nearby colour classes. Transitions from pale yellow to bright orange or vice-versa concerned less than 2% of individuals (8 cases), and are likely to be mistakes in recording the colour pattern. No effect of year ($F_{8,470}$=0.33, p=0.96), density($F_{1,421}$=0.05, p=0.82), morph frequencies ($F_{1,465}$=0.02, p=0.89 for yellow female frequency, and $F_{1,465}$=0.1, p=0.75 for orange female frequency) or feeding treatment ($F_{1,477}$=1.46, p=0.23) was found on the stability of colour.

The regression between mother's and daughter's ventral colour was significant ($F_{1,134}$=8.17, p=0.005, n=136), with a regression coefficient of 0.24, leading to an estimation of heritability equal to 0.48. Again no environmental effect could be found on the heritability of colour (for year $F_{5,129}$=0.71, p=0.62; for density $F_{1,106}$=0.81, p=0.37; for yellow female frequency $F_{1,123}$=0, p=0.99; for orange female frequency $F_{1,123}$=0.43, p=0.51; for feeding treatment $F_{1,133}$=0.61, p=0.43). If heritability of colour is calculated on yellow or orange individuals only, maternal heritability increases slightly up to 0.62 ($F_{1,72}$=7.9, p=0.006, n=74). Mixed-coloured individuals are not altering significantly the heritability score, which strongly suggest that they are not a simple alteration of pale yellow or orange colour but rather a true category, intermediate in colour spectrum.

Morphology

Morphological characters were always affected by year (for SVL $F_{12,714}$=19.88, p<0.0001, n=730; for weight $F_{12,710}$=4.56, p<0.0001, n=727; for corpulence before treatment $F_{12,710}$=7.12, p<0.0001, n=727), but only SVL was also affected by female age ($F_{1,714}$=197.36, p<0.0001, n=730). We did not find any significant relationships between colour and morphological characters once the effects of year and age had been removed (for SVL $F_{2,714}$=0.12, p=0.89, n=730; for weight $F_{1,710}$=0.45, p=0.63, n=727; for corpulence before treatment $F_{1,710}$=0.45, p=0.64, n=727). There was an effect of food treatment on corpulence after treatment (full-ration females being more corpulent than half-ration females $F_{1,455}$=20.74, p<0.0001, n=469), but no interaction between colour and food treatment ($F_{2,455}$=0.16, p=0.85, n=469).

Reproduction

Clutch size (number of juveniles, living or dead, and of aborted eggs) was affected by female SVL ($F_{1,397}$=352.88, p<0.0001, n=409), corpulence before treatment ($F_{1,397}$=115.5, p<0.0001) female density ($F_{1,397}$=115.5, p<0.0001), feeding treatment ($F_{1,397}$=6.73, p=0.006), and by the interactions of ventral colour with habitat zone ($F_{2,397}$=3.92, p=0.021), and of yellow female frequency with habitat zone ($F_{1,397}$=13.19, p=0.0003). Large or corpulent females laid larger clutches than small or thin females, and females exposed to the “half-ration” treatment laid larger clutches than females exposed to the “full-ration” treatment. Female density had a negative effect on clutch size, but yellow female frequency had a positive effect, especially in the low-density zone ($F_{1,110}$=10.38, p=0.0017, n=118). Moreover, yellow females laid smaller clutches (mean 4.9) than orange (mean 5.6) or mixed (mean 5.4) females, especially in the low-density zone ($F_{2,110}$=2.86, p=0.061, n=118 in the low-density zone; $F_{2,283}$=1.19, p=0.31, n=291 in the high-density zone).

Clutch hatching success (number of living juveniles on the total number of eggs laid) was affected by female SVL (χ^2_1=34.8, p<0.0001, n=409) and age (χ^2_1=61.54, p<0.0001), feeding treatment (χ^2_1=11.75, p=0.0005), female ventral colour (χ^2_2=15.38, p=0.0005), female density (χ^2_1=79.62, p<0.0001), yellow female frequency (χ^2_1=47.79, p<0.0001) and by the interaction of several variables (female age, female density and yellow female frequency) with ventral colour (see Table 1 for probabilities). Large females had a higher clutch hatching success than small females, and so did full-ration females in comparison with half-ration females. Mixed females had a higher clutch hatching success (mean=0.84) than yellow (mean=0.8) and orange (mean=0.78) females. Orange and yellow females' clutch hatching success was negatively affected by yellow female frequency, whereas this was not the case for mixed females (see Table 1 for probabilities, and Fig. 3a). Female density had a strong negative effect on orange females' clutch hatching success, but a weaker effect for yellow and mixed females (Table 1, Fig. 3b). Finally, clutch-hatching success of yellow females was negatively affected by female age, whereas the trend was less significant for orange and mixed females (Table 1, Fig. 3c).

Clutch sex-ratio was significantly affected by the interactions between ventral colour and female corpulence (χ^2_2=7.01, p=0.03, n=407), and between habitat zone, female SVL and ventral colour (χ^2_2=14.98, p=0.0018). Yellow corpulent females produced clutches with a higher proportion of females (lower sex-ratio), whereas the opposite was true for orange females (Table 1 and Fig. 4a). The interaction between female SVL and ventral colour was significant in the low-density zone only (χ^2_2=7.851, p=0.02, n=110). In the low-density zone, larger yellow females laid clutches with a higher proportion of males, whereas the opposite was true for orange and mixed females (Table1 and Fig. 4b)

Apparent survival rates

Female survival probability was affected by yellow female frequency only (see Table 2 for models results). Female survival probability was positively correlated to yellow females frequency (r=0.99).

DISCUSSION

Significant variation in ventral colouration of the female common lizard is associated with patterns of reproduction and sex allocation. Colour variants are stable through individual's life, heritable between mothers and daughters, and characterized by differences in reproductive output and different sensitivity to the environment. The ground is open for the existence of alternative reproductive strategies in females of this species.

Heritability and stability of colour

From field measurements, ventral colouration appeared in three distinctive colour classes: yellow, orange, and mixed. However, the distribution of spectrophotometric variables seems to be continuous among and within the colour classes (Fig. 1b). Ventral colour may thus be a continuous trait, or a threshold trait, which appears as a discrete polyphenism to the human eye. Nevertheless, discriminant analysis of colour spectra allowed to efficiently separate these three colour classes on the basis of chroma and hue, which means that the ranking of colour into visual colour classes is representative of the continuous variation in colour spectrum.

Although stability and maternal heritability of colour were both statistically significant, they appeared lower than what could be expected under the hypothesis of pure genetic polymorphism, especially when we consider that the heritability calculated on mother-daughter regression is likely to be overestimated by the presence of maternal effects. The determinism of ventral colour may be condition-dependent with respect to individual condition (yellow or orange colouration is most probably carotenoid-based, Gray 1996, Bartolotti et al. 2000), but we did not find any morphological difference between females of different colours, weakening the support for condition-dependence. Colour determinism could also include a part of phenotypic plasticity, or other non-genetic or peri-genetic mechanisms. As the stability through life and the heritability have not been affected by the environmental factors that were found in previous studies to affect many aspects of this species' life, environmental effects do not seem to influence the development of ventral colouration. This strongly suggests the existence of a genetic determinism to ventral colouration, which might be associated with phenotypic plasticity or epistatic interactions with other genetic factors. As mixed colour females display a distinct reproductive strategy from yellow or orange individuals, which is clearly not intermediate to the strategies of these extreme phenotypes, the hypothesis of the continuity of colour variation is poorly supported. A discrete polymorphism seems more likely, and mixed colour individuals could be heterozygotes expressing more or less of the yellow and orange alleles depending on their own environment: internal (genetic and physiological), or external (biotic and abiotic).

Comparison of the heritability of colour in the common lizard ($h^2=0.48$) is salient with early estimates of the heritability of colour in the side-blotched lizard ($h^2=0.48$, Sinervo et al. 2000). Since these early estimates, heritability estimates based on sire-progeny regression from controlled laboratory crosses in the side-blotched lizard indicate colour has a heritability approaching 1.0 ($h^2 = 0.96$, Sinervo et al. 2001). Heritability estimates from mother-progeny correlations are always significantly lower, presumably due to very strong maternal effects associated with the reproductive traits that interact with measured biases in colour transmission arising from natural selection, which cull progeny before maturity owing to strong frequency-dependent selection (see Appendix in Sinervo et al. 2001). Genetic mapping studies of free-ranging lizards indicate that colour in the side-blotched lizard maps to a single major genetic factor. As controlled crosses become available in the common lizard it thus seems likely that these initial impressions will be revised by incorporating, models of more complex maternal-effects and the distorting effects of selection on heritable variation.

Zone effect

In the study population the habitat is heterogeneous, with a zone of high structural diversity and high lizard densities (high quality zone), and a zone of low structural diversity, and of poor habitat quality (low-density zone, Clobert et al. 1994). This population thus displays a coupling between habitat structure and processes of density-dependent regulation (Massot et al. 1992, Lecomte et al. 1994, Clobert et al. 1994), which are known to increase the dimensionality of the environment (Heino et al. 1998). In this system, the environment is likely to be at least two-dimensional, which allows for the evolution and maintenance of a stable polymorphism (Heino et al. 1997). In two of our analyses, we found colour effects to be significant only in a specific area of the population, the low-density zone. It is possible that these effects of colour are essentially relevant at a very local scale (in the case of interactions between close neighbours for example, as found in the side-blotched lizard, see Sinervo et al. 2000), and thus are more obvious in the low-density zone. This would mean that these effects are present in the high-density zone, but not visible at the spatial scale of our study. Alternatively, selective pressures could be different between zones (level of intraspecific competition and relatedness) and therefore adaptive responses to these pressures would also differ.

Alternative strategies

There was no simple colour-dependent difference in morphological characters, but we found differences in clutch size and clutch hatching success. Yellow females lay smaller clutches than mixed and orange females, whereas mixed females have the highest clutch hatching success. These differences in mean reproductive value of females of different colours are balanced by other interactions between colour classes and individual or environmental variables on reproductive parameters, which are characteristics of a variation in phenotypic plasticity between colour variants. Such a variation in reaction norms could result from different constraints or of different strategies, depending on the adaptive value of that response.

We found colour effects on the response of clutch hatching success to various environmental parameters. Orange and yellow females tended to lay smaller clutches when yellow females were frequent in the population. Orange females also laid smaller clutches when female density was high. Orange females thus seem sensitive to intraspecific competition, and more specifically to colour-specific competition, which has likewise been observed in the side-blotched lizard for reproduction (Sinervo et al. 2000) immune function (Svensson et al. 2001, 2002) and corticosterone secretion (Comendant et al. 2003). Orange females reduced their clutch when density was high, or when surrounded by many yellow competitors. This could be compatible with a specific strategy of energy saving for survival and future reproduction events, which is indicative of a cost of reproduction, or a strategy of energy allocation by redistributing energy among the surviving juveniles, which is indicative of a potential trade-off between progeny size and number and the survival costs of reproduction (reviewed in Sinervo 1998). Juveniles from small clutches tend to be larger ($F_{1,502}=15.66$, $p<0.0001$, $n=504$), so if the female reduces her clutch, it will affect the corpulence of juveniles at birth and therefore their future survival in a context of high competition.

Yellow females had a lower clutch hatching success when aging. This effect is likely to be a physiological constraint because if a small clutch was beneficial for an old female, it would be less costly to adjust initial clutch size directly, as female age is a parameter already assessable at the beginning of gestation. Yellow females may thus be more physiologically sensitive to aging and senescence than orange and mixed females. Moreover, yellow female frequency correlates with a higher female survival, and a larger clutch size in the low-density zone. It is possible that yellow females are more sensitive to environmental conditions, and that their abundance is strongly influenced by environment quality. Therefore, yellow females would be more frequent in good years, where survival is high and reproduction relatively easy.

Reproduction of mixed-coloured females was the least sensitive to female density and female age, and not affected at all by yellow female frequency. Mixed females are thus clearly different from yellow and orange females, and their reproduction seems to be little sensitive to female competition and colour-specific competition. Under a simple genetic model where the intermediate females possess copies of yellow and orange alleles, one might expect that these females can adopt the best responses of either the orange or yellow, a form of overdominance (discussed in greater detail below).

Clutch sex-ratio was affected by maternal corpulence and snout-vent length. Clutch sex-ratio is known to respond to different internal (female age, hormonal level) and external (population density) factors in order to maximize the fitness of offspring (Ronce et al. 1998, Le Galliard et al. 2003). Corpulence may be an indicator of female body condition or health, and thus be related to the female's probability of survival. On the other hand, snout-vent length is thought to correlate with female age in this species and could also be a predictor of females' survival prospects (Meylan et al. 2002, 2004). Orange females in poor condition, with a low probability of survival, produced more daughters. Mother-daughter competition is a strong evolutionary force in the common lizard (Léna et al. 1998, Ronce et al. 1998, Le Galliard et al. 2003), and this competition is expected to decrease with the probability of survival of the mother. In that case, we expect an increase in the production of daughters when the female prospects of survival are low, because kin competition is reduced and female offspring may benefit from the territory of their mother. Large orange females also produced more daughters, which supports the hypothesis of kin competition avoidance. Mixed females also produced more daughters when getting larger, and could thus be sensitive to kin competition too, though in a lesser extent.

On the other hand, yellow females produced more sons when in poor condition or old, which is not expected under the hypothesis of kin competition avoidance. In the common lizard, juveniles born from older females are larger at the age of two years than juveniles born to younger females. This size advantage is likely to affect mostly male reproductive success, because if almost all females reproduce at the age of two years, only the largest males can do so (Leturque 2002). Differences in social behaviours or life-history strategies between colour variants might modulate the benefits from an early reproduction, so that male offspring of yellow females would take more advantage of a size advantage than those of other females. Yellow females may thus benefit more than other females from producing male offspring that will reproduce earlier, supporting the hypothesis of an intrasexual competition for access to reproduction.

We proposed here several hypotheses explaining the differences in sex allocation strategy between female morphs, but there could be others. Clutch sex-ratio is known to affect natal dispersal (Massot & Clobert 2000), which is also under maternal control (Meylan et al. 2002). Females could thus act at different levels (clutch size, sex-ratio, dispersal and even differential energy allocation) and integrate various internal and external factors, in order to produce a specific type of offspring whose fitness should be maximized considering their mother's phenotype.

Maintenance of colour variation

If colour variation in these populations of common lizard is at least partly genetically determined, then this variation must be maintained by natural selection.

We showed that the reproduction of females of the different colours was affected differently by several environmental factors (density, yellow female frequency, habitat structure). As these environmental factors vary temporally and spatially in this population, all three of the colour variants might achieve equal geometric mean fitness, which would allow for the persistence of colour variation (Calsbeek et al. 2001, Mazer & Damuth 2001). Moreover, we showed that mixed females had a higher mean clutch size than yellow females, and a higher mean clutch hatching success than both yellow and orange females. Under the hypothesis of a discrete polymorphism, mixed females would be heterozygotes, and the observed differences in mean reproductive parameters could be indicative of the overdominance of heterozygous genotypes relative to homozygous genotypes, which is known to maintain polymorphisms in nature. On the other hand, we found frequency-dependent effects on clutch hatching success of yellow and orange females. Yellow female frequency had a negative impact on clutch hatching success of both female types. Yellow females could thus be subject to negative frequency-dependent selection, and orange females to frequency-dependent competition. If orange females have a competitive disadvantage towards yellow females, which are more aggressive and territorial (E. Vercken and J. Clobert unpublished data), then their higher clutch size could balance this disadvantage and allow for the persistence of colour variants in this population. Finally, all these mechanisms are likely to interact in nature to maintain colour variation, and might also be complemented by other colour-specific effects on fitness (differences in dispersal, mating strategies, behaviour, and physiology). This would also be the case, even if the heritability of colour were due to a polygenic form of inheritance.

Comparison to the side-blotched lizard system

The existence of colour variants in females associated to differences in reproductive strategies in the common lizard are extremely similar to those observed in the side-blotched lizard system (*Uta stansburiana*). In that North American species, a colour polymorphism supported by a single locus with three alleles (the OBY locus, Sinervo and Zamudio 2001, Sinervo et al. 2001, 2006a,b) is associated with a rock-paper-scissors game in males (with three colour morphs, Sinervo and Lively 1996), and with r and K reproductive strategies in females (with two colour morphs, Sinervo et al. 2000). The patterns of density-dependent and frequency-dependent progeny allocation in colour variants of the common lizard we described here are remarkably analogous to those observed in the side-blotched lizard (clutch and egg size, Sinervo et al. 2001, costs of reproduction, Svensson et al. 2001, 2002). There also appears to be a common mechanism of overdominance in fitness traits associated with heterozygous genotypes (Sinervo and Calsbeek unpublished data) and striking parallels in progeny dispersal (E. Vercken, M. Massot, B. Sinervo and J. Clobert, unpublished data*,* Sinervo *et al.* in press). Intriguingly, the colours are also conserved in the form of orange and yellow female morphs in the side-blotched lizard.

However, several specific features demarcate the two systems. Indeed, in the side-blotched lizard, colour variation is expressed as a true discrete polymorphism, also present in males, which makes the heritability of colour much higher (0.96 in sire-offspring regression, Sinervo et al. 2001, and 0.48 in dam-offspring regression, Sinervo et al. 2000). In the common lizard, phenotypic plasticity and epigenetic mechanisms are likely to play a stronger role in colour determinism. Moreover, female strategies in the common lizard differ less in their mean values of reproductive parameters than in their reaction norms to several environmental and internal factors.

The common lizard and the side-blotched lizard, although they display some specific characteristics, nevertheless possess similar density-dependent life history syndromes. Given that *Uta* and *Lacerta* are phylogenetically divergent, having last shared a common ancestor 175 million years ago (Estes 1983), either the OBY locus is extremely conserved phylogenetically and is homologous in the common lizard, or such colour-related life history polymorphisms evolved independently in a highly coordinated and replicated fashion. Either of these possibilities is of considerable interest for general life history theory and mating system theory. Future comparisons of these two social systems with respect to density regulation (Sinervo and Calsbeek, unpublished data), dispersal (Sinervo et al. in press), and kin competition (Sinervo and Clobert 2003) will be most informative for general theory on the evolution of alternative life-history strategies, and the genetic causes of density regulation.

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REFERENCES

Ahnesjö, J. & Forsman, A. 2003. Correlated evolution of colour pattern and body size in polymorphic pygmy grasshoppers, Tetrix undulata. J. Evol. Biol. 16: 1308-1318.

Anderson, D.R., Burnham, K.P. & White, G.C. 1994. AIC model selection in overdispersed capture-recapture data. Ecology 75: 1780-1793.

Andrés, J.A., Sanchez-Guillén, R.A. & Cordero Rivera, A. 2002. Evolution of female colour polymorphism in damselflies : testing the hypotheses. Anim. Behav. 63: 677-685.

Aragon, P., Massot, M., Gasparini, J. & Clobert, J. Socially acquired information through chemical cues in the common lizard, Lacerta vivipara. Anim. Behav, in press.

Belliure, J. & Carrascal, L.M. 2002. Influence of heat transmission mode on heating rates and on the selection of patches for heating in a Mediterranean lizard. Physiol. Biochem. Zool. 75: 369-376.

Belliure, J., Meylan, S. & Clobert, J. 2004. Prenatal and postnatal effects of corticosterone on behaviour in juveniles of the common lizard *Lacerta vivipara*. J. Exp. Zool. 301A: 401-410.

Bartolotti, G.R., Tella, J.L., Forero, M.G., Dawson, R.D. & Negro, J.J. 2000. Genetics, local environment and health as factors influencing plasma carotenoids in wild American kestrels (*Falco sparverius*). P. Roy. Soc. B-Biol. Sci. 267: 1433-1438.

Calsbeek, R., Alonzo, S.H., Zamudio, K. & Sinervo, B. 2001. Sexual selection and alternative mating behaviours generate demographic stochasticity in small populations. P. Roy. Soc. B-Biol. Sci. 269: 157-164.

Clobert, J., Perrins, C.M., McCleery, R.H. & Gosler, A.G. 1988. Survival rate in the great tit *Parus major* in relation to sex, age and immigration status. J. Anim. Ecol. 57: 287-306.

Clobert, J., Massot, M., Lecomte, J., Sorci, G., de Fraipont, M. & Barbault, R. 1994. Determinants of dispersal behavior : the common lizard as a case study. In: Lizard

Ecology : historical and experimental perspectives (L.J. Vitt & E.R. Pianka eds), pp183-206. Princeton University Press, Oxford.

Comendant, T., Sinervo, B., Svensson, E. & Wingfield, J. C. 2003. Social competition, corticosterone, and survival in female lizard morphs. J. Evol. Biol. 16: 948-955.

Cooper, W.E. Jr & Burns, N. 1987. Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. Anim. Behav. 35: 526-532.

Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. Biometrika. 51: 429-438.

Dawkins, R. & Krebs, J.R. 1978. Animal signals: information or manipulation. In: Behavioral Ecology (J.R.Krebs & N.B.Davies eds), pp282-309. Sinauer Associates.

Eadie, J.M. & Fryxell, J.M. 1992. Density dependence, frequency dependence, and alternative nesting strategies in Goldeneyes. Am. Nat. 140: 621-641.

Endler, J.A. 1990. On the measurement and classification of color in studies of animal color patterns. Biol. J. Linn. Soc. 41: 315-352.

Estes, R. 1983. The fossil record and early distribution of lizards. In: Advances in herpetology and evolutionary biology (G.J Rhodin & K. Miyata eds), pp365-398. Museum of Comparative Zoology, Cambridge.

Forsman, A. & Shine, R. 1995. The adaptive significance of colour pattern polymorphism in the Australian scincid lizard *Lampropholis delicata*. Biol. J. Linn. Soc. 55: 273-291.

Galeotti, P., Rubolini, D., Dunn, P.O. & Fasola, M. 2003. Colour polymorphism in birds: causes and functions. J. Evol. Biol. 16: 635-646.

Gray, D.A. 1996. Carotenoids and sexual dichromatism in north American passerine birds. Am. Nat. 148: 453-480.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol. Evol. 11: 92-98.

Heino, M., Metz, J.A.J. & Kaitala, V. 1997. Evolution of mixed maturation strategies in semelparous life histories: The crucial role of dimensionality of feedback environment. Philos. T. Roy. Soc. B 352: 1647-1655.

Heino, M., Metz, J.A.J. & Kaitala, V. 1998. The enigma of frequency-dependent selection. Trends Ecol. Evol. 13: 367-370.

Hutchings, J.A. & Myers, R.A. 1994. The evolution of alternative mating strategies in variable environments. Evol. Ecol. 8: 256-268.

Jolly, G.M. 1965 Explicit estimates from capture-recapture data with both dead and immigration-stochastic models. Biometrika 52: 225-247.

Le Galliard, J.F., Ferriere, R. & Clobert, J. 2003. Mother-offspring interactions affect natal dispersal in a lizard. P. Roy. Soc. B-Biol. Sci. 270: 1163-1169.

Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992 Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62: 67-118.

Lecomte, J., Clobert, J. & Massot, M. 1992. Sex identification in juveniles of *Lacerta vivipara*. Amphibia-Reptilia 13: 21-25.

Lecomte, J., Clobert, J., Massot, M. & Barbault, R. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. Ecoscience 1: 300-310.

Léna, J.P., Clobert, J., de Fraipont, M. , Lecomte, J. & Guyot, G. 1998. The relative influence of density and kinship on dispersal in the common lizard. Behav. Ecol. 9: 500-507.

Léna, J.P., de Fraipont, M. & Clobert, J. 2000. Affinity towards maternal odour and offspring dispersal in the common lizard. Ecol. Lett. 3: 300-308.

Leturque H. 2002. Evolution du sexe-ratio et de la dispersion en populations structurées. Phd Thesis, Biologie de l'Evolution et Ecologie, Université Montpellier II.

Lorenzon, P., Clobert, J. & Massot, M. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. Evolution 55: 392-404.

Massot, M., Clobert, J., Pilorge, T., Lecomte, J. & Barbault, R. 1992. Density dependence in the common lizard : demographic consequences of a density manipulation. Ecology 73: 1742-1756.

Massot, M. & Clobert, J. 2000. Processes at the origin of similarities in dispersal behaviour amog siblings. J. Evol. Biol. 13: 707-719.

Massot, M., Clobert, J., Lorenzon, P. & Rossi, J.-M. 2002. Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. J. Anim. Ecol. 71: 253-261.

Mazer, S.J. & Damuth, J. 2001. Nature and Causes of Variation. In: Evolutionary Ecology : concepts and case studies (C.W. Fox, D.A. Roff & D.J. Fairbairn eds), pp3-15. Oxford University Press, Oxford.

Meylan, S., Belliure, J., Clobert, J. & de Fraipont, M. 2002. Stress and body condition as prenatal and postnatal determinants of dispersal in the common lizard (*Lacerta vivipara*). Horm. Behav. 42: 319-326.

Meylan, S., de Fraipont, M. & Clobert, J. 2004. Maternal size, stress and offspring philopatry : an experimental study in the common lizard (*Lacerta vivipara*). Ecoscience 11: 123-129.

Olson, V.A. & Owens, I.P.F. 1998. Costly sexual signals : are carotenoids rare, risky or required ? Trends Ecol. Evol. 13: 510-514.

Olsson, M., Madsen, T., Nordby, J., Wapstra, E., Ujvari, B. & Wittsell, H. 2003. Major histocompatibility complex and mate choice in sand lizards. P. Roy. Soc. B-Biol. Sci. 270: S254-S256.

Pilorge, T. 1987. Density, size structure, and reproductive characteristics of three populations of *Lacerta vivipara* (Sauria : Lacertidae). Herpetologica 43: 345-356.

Rand, M.S. 1988. Courtship and aggressive behavior in male lizards exhibiting two different sexual colorations. Am. Zool. 28: 153A.

Richard, M., Lecomte, J., de Fraipont, M. & Clobert, J. 2005. Age-specific mating strategies and reproductive senescence. Mol. Ecol. 14: 3147-3155.

Ronce, O., Clobert, J. & Massot, M. 1998. Natal dispersal and senescence. P. Natl. Acad. Sci. USA 95: 600-605.

Ryan, M.J., Pease, C.M. & Morris, M.R. 1992. A genetic polymorphism in the swordtail *Xiphiphorus nigrensis* : testing the prediction of equal fitnesses. Am. Nat. 139: 21-31.

SAS 1992. SAS User's Guide: Statistics. SAS Institute.

Seber, G.A.F. 1965. A note on the multiple-recapture census. Biometrika 52: 249-259.

Sinervo, B. & Lively, C.M. 1996. The rock-paper-scissors game and the evolution of alternative male reproductive strategies. Nature 380: 240-243.

Sinervo, B. & Svensson, E. 1998. Mechanistic and selective causes of life history trade-offs and plasticity. Oikos 83: 432-442.

Sinervo, B. & Zamudio, K. 2001. Genetic correlations between the sexes, fitness differentials, and the evolution of alternative reproductive strategies. J. Hered. 98: 198-212.

Sinervo, B., Svensson, E. & Comendant, T. 2000. Density cycles and an offspring quality and quantity game driven by natural selection. Nature 406: 985-988.

Sinervo, B., Bleay, C. & Adamopoulou, C. 2001. Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. Evolution 55: 2040-2052.

Sinervo, B. & Clobert, J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. Science: 1949-1951.

Sinervo, B., Calsbeek, R., Comendant, T., Both, C., Adamopoulou, C. & Clobert, J. 2006a. Genetic and maternal determinants of effective dispersal: the effect of sire genotype and size at birth in side-blotched lizards. Am. Nat. in press.

Sinervo, B., Chaine, A., Clobert, J., Calsbeek, R. G., McAdam, A., Hazard, H., Lancaster, L., Alonzo, S., Corrigan, G., and M. Hochberg. 2006b. Self-recognition, color signals and greenbeard cycles of altruism and mutualism. Proc. Natl. Acad. Sci. (U.S.A.) 102: 7372-7377.

Sirot, L.K., Brockmann, H.J., Marinis, C. & Muschett, G. 2003. Maintenance of a female-limited polymorphism in *Ischnura ramburi* (Zygoptera : Coenagrionidae). Anim. Behav. 66: 763-775.

Svensson, E., Sinervo, B. & Comendant, T. 2001. Condition, genotype-by-environment interaction and correlational selection in lizard life-history morphs. Evolution 55: 2053-2069.

Svensson E.I., Sinervo B. & Comendant, T. 2002. Mechanistic and experimental analysis of condition and reproduction in a polymorphic lizard. J. Evol. Biol. 15: 1034-1047.

Svensson, E., Abbott, J. & Hardling, R. 2005. Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. Am. Nat. 165: 567-576.

Thompson, C.W. & Moore, M.C. 1991. Syntopic occurrence of multiple dewlap color morphs in male tree lizards, *Urosaurus ornatus*. Copeia 2: 493-503.

Thompson, C.W., Moore, I.T. & Moore, M.C. 1993. Social, environmental and genetic factors in the ontogeny of phenotypic differentiation in a lizard with alternative male reproductive strategies. Behav. Ecol. Sociobiol. 33: 137-146.

Tuttle, E.M. 2003. Alternative reproductive strategies in the white-throated sparrow: Behavioral and genetic evidence. Behav. Ecol. 14: 425-432.

Weiss, S.L. 2002. Reproductive signals of female lizards: Pattern of trait expression and male response. Ethology 108: 793-813.

White, G. 1998. Mark and recapture survival rate estimation.

http://www.cnr.colostate.edu/~gwhite/mark/mark.htm

Table 1 : Results of likelihood-ratio tests for colour effects on different variables.

Effect	Difference between yellow and mixed females	Difference between yellow and orange females	Difference between orange and mixed females
Female density on clutch success	$\chi^2_1=2.44$ p=0.12 n=290	$\chi^2_1=5.29$ **p=0.021** (marginal) n=294	$\chi^2_1=10.68$ **p=0.001** n=234
Yellow female frequency on clutch success	$\chi^2_1=5.77$ **p=0.016**	$\chi^2_1=0.63$ p=0.43	$\chi^2_1=11.74$ **p=0.0006**
Female age on clutch success	$\chi^2_1=17.45$ **p<0.0001**	$\chi^2_1=6.89$ **p=0.0087**	$\chi^2_1=2.6$ p=0.107
Female corpulence on clutch sex-ratio	$\chi^2_1=1.21$ p=0.27	$\chi^2_1=6.98$ **p=0.0082**	$\chi^2_1=2.26$ p=0.13
Female SVL on clutch sex-ratio in the low-density zone	$\chi^2_1=7.76$ **p=0. 0053** n=45	$\chi^2_1=2.62$ p=0.106 n=34	$\chi^2_1=0.96$ p=0.327 n=31

Table 2 : Results of model selection for survival and capture rate, AIC (number of estimable parameters). Fdens: female density. Fo: orange females frequency. Fy: yellow females frequency.

Capture rate (P) / Survival rate (Φ)	P fixed	P(time)	P(colour)
Φ fixed	2443.06 (2)	2445.39 (14)	2445.88 (4)
Φ(time)	2449.45 (14)	2446.26 (25)	2452.45 (16)
Φ(colour)	2446.49 (4)	2448.97 (16)	2449.52 (6)
Φ(fdens)	4255.43 (3)	3732.33 (15)	4258.84 (5)
Φ(fo)	2444.47 (3)	2447.24 (15)	2447.33 (5)
Φ(fy)	**2436.66** (3)	2439.72 (15)	2439.53 (5)
Φ(time+colour)	2452.96 (16)	2449.97 (27)	2456.13 (18)
Φ(time*colour)	2476.68 (40)	2474.75 (51)	2480.18 (42)
Φ(fdens+colour)	4259.46 (5)	3736.42 (17)	4262.88 (7)
Φ(fdens*colour)	4141.91 (7)	4129.78 (19)	2881.29 (9)
Φ(fo+colour)	2447.91 (5)	2450.64 (17)	2450.98 (7)
Φ (fo*colour)	2449.37 (7)	2451.89 (19)	2452.55 (9)
Φ(fy+colour)	2440.14 (5)	2443.34 (17)	2443.163 (7)
Φ(fy*colour)	2440.36 (7)	2444.26 (19)	2443.49 (9)

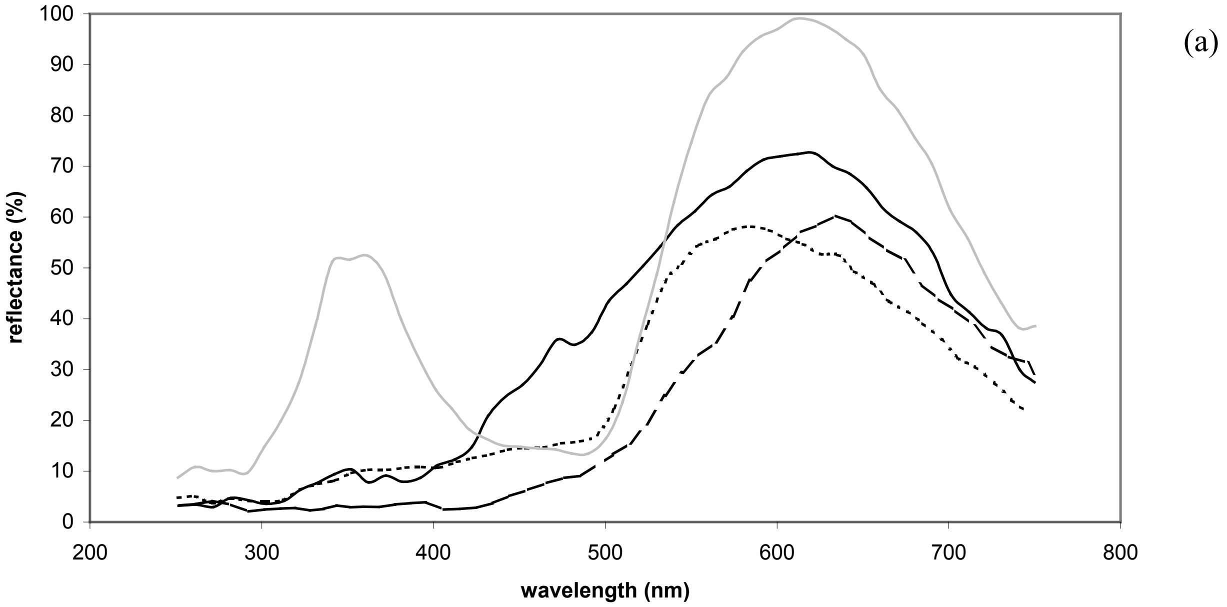
Figure legends

Figure 1: (a) Examples of reflectance spectra: for yellow females (black solid line), for orange females (short-dashed line), for mixed females (long-dashed line) and for males (grey solid line). (b) Discriminant analysis of colour parameters. Distribution of yellow (white squares), orange (grey triangles) and mixed-coloured (black circles) females in function of their values of chroma and hue multiplicated by the discriminant coefficients.

Figure 2: Effect of various explanatory variables on clutch hatching success for yellow (solid line), orange (short-dashed line) and mixed-coloured (long-dashed line) females. (a) Effect of female density. (b) Effect of yellow females frequency. (c) Effect of female age.

Figure 3: Effect of maternal morphological traits on clutch sex-ratio for yellow (solid line), orange (short-dashed line) and mixed-coloured (long-dashed line) females. (a) Effect of female corpulence. (b) Effect of female SVL in the low-density zone.

Figure 1


100
90
80
70
60
50
40
30
20
10
0
reflectance (%)
200
300
400
500
600
700
800
wavelength (nm)
(a)

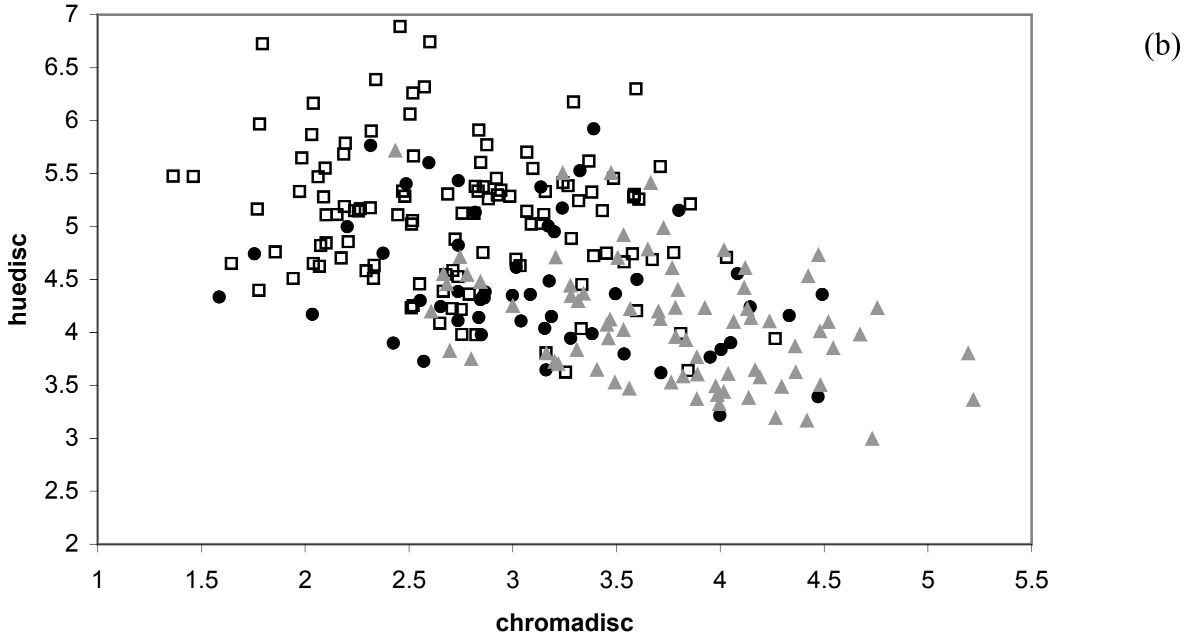

7
6.5
6
5.5
5
4.5
4
3.5
3
2.5
2
huedisc
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
chromadisc
(b)

Figure 2

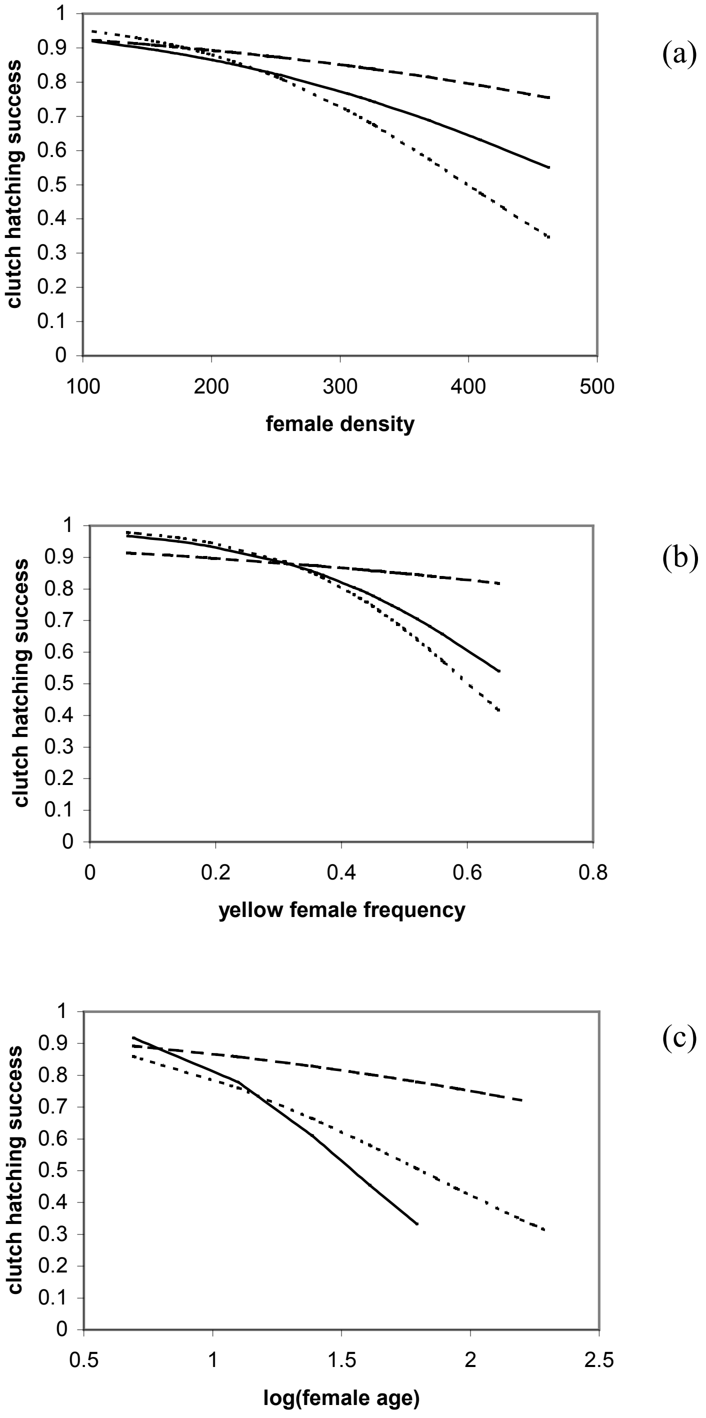
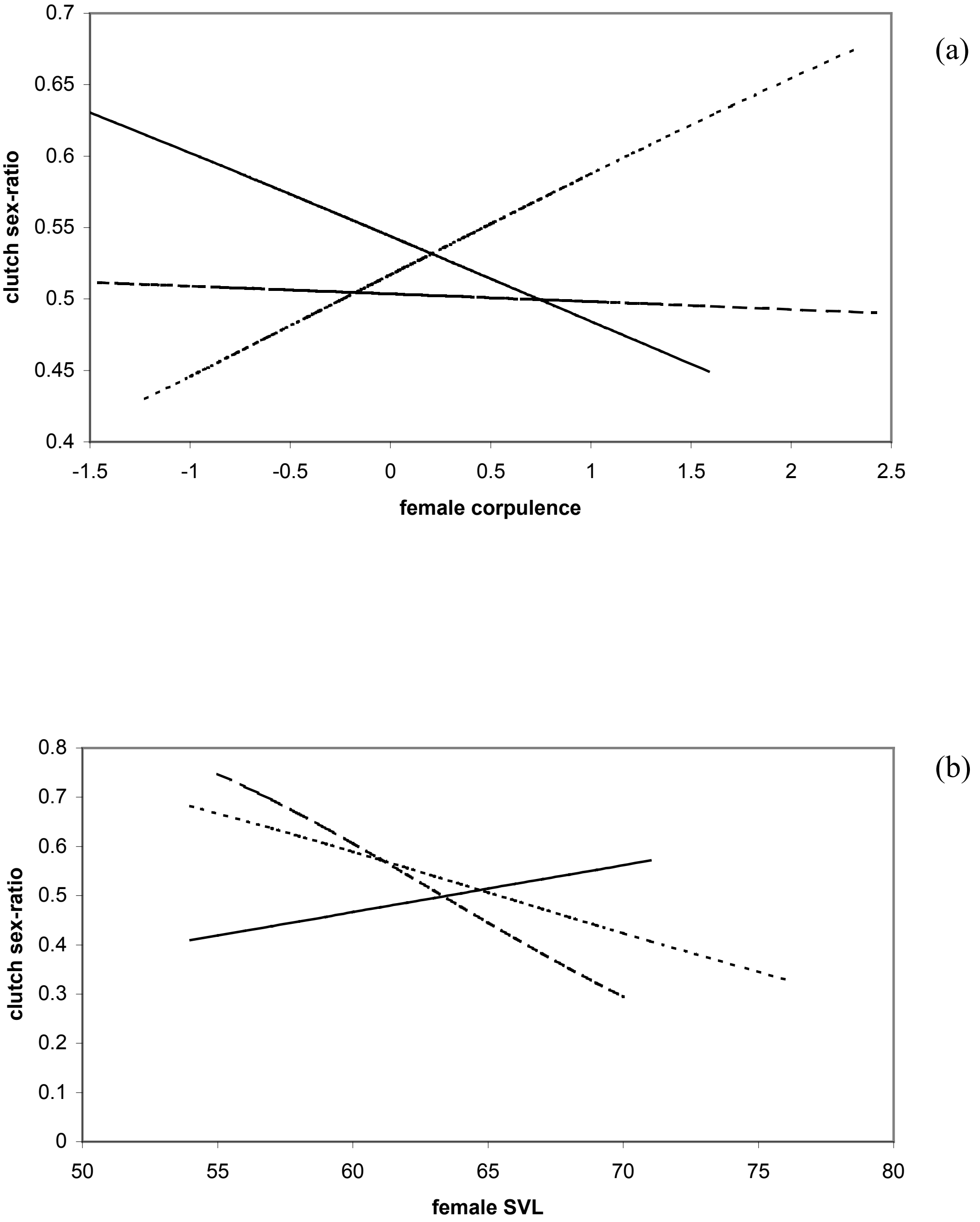

(a)
clutch hatching success
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
100
200
300
400
500
female density
(b)
clutch hatching success
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.2
0.4
0.6
0.8
yellow female frequency
(c)
clutch hatching success
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.5
1
1.5
2
2.5
log(female age)

Figure 3


(a)
clutch sex-ratio
0.7
0.65
0.6
0.55
0.5
0.45
0.4
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
female corpulence
(b)
clutch sex-ratio
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
50
55
60
65
70
75
80
female SVL

ANNNEXE II: Female colour morphs in the common lizard display alternative offspring dispersal strategies with respect to climatic change

Article soumis

Female colour morphs in the common lizard display alternative offspring dispersal strategies with respect to climatic change

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Running title: Alternative dispersal strategies in lizards

Abstract

Within-sex colour variation is a widespread phenomenon in animals that often plays a role in social selection. Colour variants are often associated with alternative strategies that are sensitive to their social environment. As dispersal affects the spatial structure of the environment, it should have a direct effect on the success of alternative strategies, and thus dispersal is expected to differ between colour morphs. In a population of the common lizard, females display three classes of ventral colouration (yellow, orange and mixed) that have been shown to reflect alternative reproductive strategies. As natal dispersal is highly plastic in this species, and is known to respond to many environmental factors through maternal effects, we predicted that offspring dispersal strategies should differ between female colour variants. We found that offspring from females of different ventral colour did not respond to the same dispersal cues. Offspring from yellow females seemed to have a condition-independent dispersal. Offspring from orange females increased their dispersal in response to climate warming, whereas offspring from mixed females decreased their dispersal in response to the same cues. In addition, offspring from mixed females increased their dispersal in response to resource limitation. The implications of these strategies for species persistence in the long-term are discussed.

Introduction

Colour polymorphism within populations, and in particular within-sex colour polymorphism, is a determinant of social interactions and reproductive investment in many species (Andrés *et al.* 2002, Cooper and Burns 1987, Weiss 2002, Thompson and Moore 1991, Forsman and Shine 1995). In particular, colour variation is often a signal of alternative reproductive strategies in a population (in birds, Tuttle 2003 ; in fishes, Hutchings *et al.* 1994; in insects, Ahnesjö and Forsman 2003 ; in reptiles, Rand 1988). Such alternative reproductive strategies are usually characterised by elaborate differences in many phenotypic traits (Gross 1996), and individuals pursuing different strategies typically differ in morphology, physiology, behaviour and in particular dispersal (Thompson *et al.* 1993, Sinervo and Lively 1996, Sinervo *et al.* 2000, Svensson *et al.* 2001, Sinervo and Clobert 2003, Sinervo *et al.* 2006a, 2006b). Dispersal is usually thought to have evolved as a response to habitat variability, intraspecific competition (for mates or resources), or kin interactions (Johnson and Gaines 1990, Clobert *et al.* 2004). The same evolutionary forces are typically implicated in the maintenance of phenotypic variants and alternative strategies (Mazer and Damuth 2001, West-Eberhard 1983, Sinervo and Clobert 2003). Dispersal appears therefore to be a common solution to many different evolutionary problems (Clobert *et al.* 2001), and the effective dispersal pattern is likely to result from a complex interaction between several opposing selective forces (Gandon and Michalakis 2001) or results from correlated selection with other traits, such as life-history traits, which define particular strategies (Ronce *et al.* 2001, Ronce and Olivieri 2004). Dispersal is thus expected to differ between alternative reproductive strategies (Sinervo and Clobert 2003, Sinervo *et al.* 2006a, 2006b). Indeed, by their action on local density and relatedness, dispersal or philopatry of alternative reproductive strategies will affect the social environment of individuals, which is known to have a feedback effect on the selective pressures acting on the evolution of dispersal (Clobert *et al.* 2001). Thus, the success of alternative reproductive strategies should depend on the social composition of the local environment. Therefore individuals playing alternative strategies may benefit differently from dispersal as a function of this local environment. Different individuals in the same population may thus react differently to the same dispersal cues, depending on their social status, quality, sex, or life-history strategy (Ims and Hjermann 2001, Clobert *et al.* 2004, Sinervo *et al.* 2006a, 2006b). Moreover, in most cases dispersal propensity is correlated with many other behavioural, morphological and/or physiological traits (Swingland 1983, Fairbairn and Roff 1990, Clobert *et al.* 1994, de Fraipont *et al.* 2000), and thus dispersal is likely to take part in the constitution of adaptive syndromes, as has been found in the side blotched lizard (*Uta stansburiana*, Sinervo and Clobert 2003, Sinervo *et al.* 2006a, 2006b).

To study the link between dispersal and alternative reproductive strategies we selected the common lizard as our model system. Dispersal in *Lacerta vivipara* has been extensively studied (Massot and Clobert 2000, Massot *et al.* 2002, Dufty *et al.* 2002). The social context (relatedness and density competition) has been demonstrated to have a major impact on offspring dispersal (Massot *et al.* 1992, Clobert *et al.* 1994, Léna *et al.* 1998, Ronce *et al.* 1998, de Fraipont *et al.* 2000, Meylan *et al.* 2002, Le Galliard *et al.* 2003). In this species, there is also strong maternal control on offspring dispersal through maternal effects (maternal age, Ronce *et al.* 1998; maternal parasitic load, Sorci *et al.* 1994 ; local relatedness, Le Galliard *et al.* 2003 ; maternal stress, de Fraipont *et al.* 2000; multiple factors Massot and Clobert 2000, Massot *et al.* 2002). Environmental effects, both pre- and post-natal, have also been shown to affect offspring dispersal (pre-natal effects: food availability Massot and Clobert 2000; post-natal effects: local density Léna *et al.* 1998, Le Galliard *et al.* 2003, habitat structure Massot and Clobert 2000; both pre- and post-natal effects: humidity Massot *et al.* 2002, temperature Massot *et al.* in prep).

Female common lizards display variation in ventral colour correlated with differences in the plasticity of reproduction (Vercken *et al.* 2007). In particular, females of different colours seem to adopt different allocation strategies considering offspring sex and number in response to several environmental variables (female density and colour variant frequencies). As natal dispersal in this species is highly sensitive to maternal effects, and as dispersal pattern is likely to covary with alternative reproductive strategies, we predict that dispersal pattern will differ between colour variants. In particular, offspring dispersal response to maternal characteristics and environmental factors (in particular climatic change, Massot *et al.* in prep) is likely to be modulated by maternal ventral colour. To challenge this hypothesis, we analysed offspring dispersal for females with different ventral colour. We tried to test for multiple environmental and individual effects in order to characterise colour-specific dispersal cues and strategies.

Methods

The Species

Lacerta vivipara is a small (adult snout-vent length from 50 to 70 mm), live bearing lacertid lizard, inhabiting peatbogs and heathland throughout Europe and Asia. The population we studied is located on Mont Lozère (in southern France, altitude 1420 m), and is divided into two contiguous zones that differ in structural diversity of the microhabitat (Clobert *et al.* 1994): a zone with high structural diversity and high lizard densities (high quality zone), and a zone with low structural diversity and lower lizard densities (low quality zone). In this population, males emerge from hibernation in mid-April, followed by yearlings and adult females in mid-May. Mating occurs at female emergence, and gestation lasts for two months. Parturition starts in mid-July and lasts for 2-3 weeks. Females lay an average clutch of 5 soft-shelled eggs (range 1-12). Offspring hatch within one or two hours after laying and are immediately independent of their mother. Juvenile dispersal takes place within the first 10 days of life (Léna *et al.* 1998). The activity season ends in late September and juveniles are the last to enter hibernation. A more detailed description of life history can be found in Massot *et al.* (1992).

Data set

Lizards in this population have been individually marked by toe-clipping and followed by capture-recapture from 1989 till 2002. To study reproduction, 1009 females have been temporarily removed from the population over this period. Each year, from the beginning of July, females were kept in the laboratory until parturition. Females were housed in plastic terraria with damp soil, a shelter and water *ad libitum*. Two feeding treatments were applied: females on "full rations" were offered one larva of P*yralis farinalis* every week, and females on "half-rations" one every two weeks (see Massot and Clobert 1995, for further details on food treatments). They were exposed to natural daylight and were heated 6 h per day with an electric bulb. Female ventral coloration was estimated visually and classified as yellow, orange, or mixed (with both yellow and orange ventral scales), which has been shown to reflect spectrophotometrical differences (Vercken *et al.* 2007).

At birth, offspring were individually marked by toe-clipping and sexed by counting ventral scales (Lecomte *et al.* 1992). Toe-clipping is known to have no influence on probability of recapture (Massot *et al.* 1992), and maximal sprint speed in the common lizard (G. Sorci, personal communication). Offspring and their mother were measured and weighed. They were then released at the mother's last capture point. Recapture sessions in fall and spring allowed us to map the location of juveniles after dispersal. Dispersers were defined as individuals for which the distance moved between the release point and the last recapture point was greater than 30 m (upper 95% confidence limit of the home range diameter). Philopatric individuals were defined as individuals that had moved less than 20 m (average home range diameter) (Clobert *et al.* 1994, Massot and Clobert 2000). Individuals moving more than 30 meters were never found to return to their natal territory. Juveniles that had moved between 20 and 30 m were not assigned any dispersal status, and were excluded from the analysis. We obtained dispersal status for 289 offspring.

Statistical Analysis

Dispersal status was considered as a binomial variable (0 : philopatric offspring; 1 : disperser), and therefore was analysed using logistic-linear regression analysis (GENMOD procedure, SAS Institute). Log-likelihood ratio tests (χ^2 values) were used to assess significance of effects. The analysis of dispersal often raises a statistical issue due to overdispersion of data (Massot *et al.* 1994), induced by the non-independence among siblings (Massot and Clobert 1995, 2000). The DSCALE option of the GENMOD procedure allowed us to correct for overdispersion (Clobert *et al.* 1993, Massot *et al.* 2002). Individual characteristics were described by body size (snout-vent length or SVL), body condition (residual from the relationship between body mass and SVL) and sex; maternal characteristics by SVL, age (logarithm and squared logarithm) and ventral colour of the mother; environmental parameters by maternal feeding treatment, habitat zone, adult density, yellow and orange female frequencies, and mean temperatures in June and August. We started with a general model including all the potential explanatory variables and their interactions, up to three-factors interactions. We then dropped the non-significant effects (backward selection), starting with the most complex interaction terms. Only the results of the final model are reported. Because of missing values, some data could not be used in all models, and the sample size used in the final model is 148 individuals.

Colour effects were interpreted by comparing alternately the three different colour pairs. In this case, we used a Bonferroni correction to assess significance of effects (the significance threshold for the critic probability being lowered to 0.017.

Results

Juvenile dispersal was affected by juvenile characteristics, maternal characteristics, temperature, and several interactions. A sex bias in dispersal was found, with female offspring dispersing less than males (female dispersal rate=0.36, male dispersal rate=0.56, χ^2_1= 7.98, p=0.005). Juvenile dispersal decreased when mean temperature in June increased (χ^2_1= 8.26, p=0.004) or when the mother was old (χ^2_1= 5.94, p=0.015). Maternal feeding treatment affected offspring dispersal: on the whole, juveniles tended to disperse less when their mother had received a full-ration (dispersal rate in the "full-ration" group=0.41, dispersal rate in the "half-ration" group=0.53, χ^2_1= 6.67, p=0.01), but feeding treatment also interacted with mean temperatures in June (χ^2_1= 4.17, p=0.041) and August (χ^2_1= 3.94, p=0.047), and with maternal age (χ^2_1=6.64, p=0.01). Offspring from females exposed to the "full-rations" treatment responded more strongly to the temperature, with a negative effect of the temperature in June, and a positive effect of the temperature in August on juvenile dispersal. Offspring from females exposed to the "half-rations" treatment reacted more strongly to maternal age, with a decrease in dispersal rate for offspring from aged mothers.

Maternal ventral colour also affected offspring dispersal, alone or in interaction with other variables. Juveniles from orange mothers tended to disperse more (dispersal rate=0.53) than juveniles from yellow (dispersal rate=0.48) or mixed females (dispersal rate=0.41, χ^2_2=6.63, p=0.036). Maternal colour interacted with mean temperatures in June (χ^2_2=8.15, p=0.017) and August (χ^2_2=6.05, p=0.048), and with maternal feeding treatment (χ^2_2= 11.63, p=0.003). The mean temperature in June had a negative effect on the dispersal of offspring from mixed females, and no effect on the dispersal of offspring from yellow or orange females (see table 1 for probabilities, and figure 1). The mean temperature in August had a marginal positive effect on the dispersal of offspring from orange females, and no effect on the dispersal of offspring from yellow or mixed females (see table 1 for probabilities, and figure 2). Maternal feeding treatment affected the dispersal of offspring from mixed females: offspring from mixed females that had received “full-rations” dispersed significantly less than offspring from mixed females that had received “half-rations”, whereas no such trend was found for offspring from yellow or orange females (see table 1 for probabilities, and figure 3).

Discussion

All effects on natal dispersal in our study, except the colour effects, had previously been described (individual sex and feeding treatment, Massot and Clobert 2000; maternal age, Ronce *et al.* 1998; temperatures, Massot *et al.* in prep), which confirms the high consistency of such analyses over the years. In addition to these already documented effects, ventral colour of the mother was found for the first time to influence offspring dispersal in the common lizard, in interaction with the external environment. Although kin competition has been shown to be a major force driving dispersal in this species (Ronce *et al.* 1998, Le Galliard *et al.* 2003, Meylan *et al.* 2004), and although it has previously been found to affect differently colour-specific reproductive strategies (Vercken *et al.* 2007), it does not seem to play any role in colour-specific dispersal strategies. In opposition, environment quality and the quantity of resources strongly interact with maternal colour to build different dispersal strategies.

Dispersal of offspring from yellow females did not respond to any of the variables tested in this study. Yellow females may respond to another variable (parasitic load, maternal stress, or local relatedness) or play a fixed or condition-independent dispersal strategy.

Offspring from orange females displayed the highest mean dispersal rate. Thus the orange colour might be associated with higher dispersal ability, and orange individuals could play a “colonizing” strategy in the populations. In another species of lizard with very similar colour syndromes, *Uta stansburiana*, colour morphs also differ in dispersal ranges, and the orange morph appears to be the dispersing morph (Sinervo *et al.* 2006a, 2006b). In addition, in our population of common lizard, offspring from orange females reacted to climate warming (increase of the mean temperature in August) by increasing their dispersal. At the study site, temperatures in May, June and August have increased significantly for 30 years (Chamaillé *et al.* 2006, Massot *et al.* in prep). Therefore, in response to global warming, offspring of orange females tended to increase their dispersal and thus are more likely to be able to shift their geographic location in order to follow their optimal climatic range (e.g., up the altitudinal gradient). This behaviour seems adaptive, and may allow the species to resist climatic change. On the other hand, even if climate warming is not detrimental to the common lizard (it appears on the contrary beneficial to reproduction and survival, Chamaillé-Jammes *et al.* 2006), it might be a sign of a future instability (and unsuitability) of the environment. Orange females might thus play a diversified bet-hedging dispersal strategy (Philippi and Seger 1989), intensified by the climate warming. Such a strategy would allow their offspring to survive in case of a major landscape perturbation, allowing the population to escape extinction.

Dispersal of offspring from mixed females reacted to two factors: the mean temperature in June and maternal feeding treatment.

Reaction to maternal feeding treatment can be interpreted in two ways: food shortage may reflect a deterioration of the environment and thus enhance offspring dispersal, or it may be a sign of low maternal survival prospects and thus promote philopatry in the context of mother-offspring competition avoidance (de Fraipont *et al.* 2000). Mixed females were previously shown to be relatively insensitive to female competition in their reproductive parameters (e.g., clutch size), but they did adjust their clutch sex-ratio in response to kin competition (Vercken *et al.* 2007). However, we found that offspring from mixed females dispersed more when their mother had received the “half-rations” treatment, which is not expected under the hypothesis of kin competition avoidance, but is more likely to be an adaptive response to the limitation of environmental resources. The dispersal pattern of progeny from mixed females appears to be consistent with their reproductive strategy, which is quite tolerant of female competition at high density. As long as conditions are good, progeny from mixed females should be more philopatric. Mixed females may use a cue of reduced food availability as a sign that the environment is deteriorating and induce dispersal in their progeny. Clutch adjustment (energy and sex allocations) and control of natal dispersal rate thus allow mixed females to act on different levels of their offspring's phenotype at different development times. They may integrate many sources of information about their global and local environment, and modify their offspring's phenotype in response to several and sometimes opposing selective forces, in order to increase their offspring's fitness.

However, offspring from mixed females tended to disperse less when the temperature in June increased. Therefore, offspring from mixed females tend to reduce their dispersal in response to climatic change, and thus are likely to enter a "spatial evolutionary trap" (Massot *et al.* in prep). As they lose their ability to disperse and as environmental conditions continue to deteriorate, the population becomes less likely to disperse. The population we studied is situated on the upper altitudinal and southern latitudinal limit of the species range, and currently benefits from its high altitude position (scattered populations are found at elevations down to 1000 m, and robust populations are generally restricted to 1300-1500 m, B. Sinervo and J. Clobert, personal observations). If the mean temperatures keep increasing, local ecological conditions for the maintenance of common lizard populations may not persist in the long term. However, as dispersal of mixed individuals also responded to environmental resources, we cannot predict how the interaction between all environmental cues will affect dispersal if the climate warming makes the environment unsuitable for the species. This critically will depend on how climate deterioration impacts the local food availability, which seems to be a key parameter used in adjusting offspring dispersal.

Conclusion

This study described the differences in dispersal strategy between colour variants in the common lizard. These differences may have major consequences on social interactions through their influence on the spatial distribution of individuals, and they may be determinants in the long-term persistence of populations in the context of global warming. Population dynamics and the evolutionary stability of colour variants are also expected to depend on the game played out between colour-specific alternative strategies and various environmental factors. In order to fully understand this evolutionary game, and the adaptive syndromes associated with each strategy, more information is needed on the level and type of intraspecific competition that individuals experience in the population. Studies to come should focus in particular on colour-specific social environment with behavioural, spatial and genetic data, in order to estimate the relative roles of competition and cooperation in the evolution of social interactions in this species (Sinervo and Clobert 2003, Sinervo *et al.* 2006a, 2006b) and the effect of climatic change on this game.

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REFERENCES

Ahnesjö J, Forsman A (2003) Correlated evolution of colour pattern and body size in polymorphic pygmy grasshoppers, Tetrix undulata. *Journal of Evolutionary Biology*, **16**, 1308-1318.

Andrés JA., Sanchez-Guillén RA, Cordero Rivera A (2002) Evolution of female colour polymorphism in damselflies : testing the hypotheses. *Animal Behaviour*, **63**, 677-685.

Chamaillé-Jammes S, Massot M, Aragon P, Clobert J (2006) Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology*, **12**, 392-402.

Clobert J, Danchin E, Nichols JD, Dhondt AA (2001) *Dispersal*. Oxford University Press, Oxford, 452 pp.

Clobert J, Ims RA, Rousset F (2004) Causes, mechanisms and consequences of dispersal. In: *Ecology, Genetics and Evolution of Metapopulations* (eds Hanski I, Gaggiotti OE), pp. 307-335. Academic Press, San Diego.

Clobert J, Julliard R, McCleery RH (1993) The components of local recruitment. In : *The study of bird population dynamics using marked individuals* (eds Lebreton JD, North P), pp. 281-294. Birkauser Verlag, Basel.

Clobert J, Massot M, Lecomte J, Sorci G, de Fraipont M, Barbault R (1994) Determinants of dispersal behavior : the common lizard as a case study. In: *Lizard Ecology : Historical and Experimental Perspectives* (eds Vitt L, Pianka R), pp. 183-206. Princeton University Press, Princeton.

Cooper WE Jr, Burns N (1987) Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. *Animal Behaviour*, **35**, 526-532.

de Fraipont M, Clobert J, John-Alder H, Meylan S (2000) Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. *Journal of Animal Ecology*, **69**, 404-413.

Dufty AM, Clobert J, Moller AP (2002) Hormones, developmental plasticity and adaptation. *Trends in Ecology and Evolution*, **17**, 190-196.

Fairbairn DJ, Roff DA (1990) Genetic correlations among traits determining migratory tendency in the sand cricket *Gryllus firmus*. *Evolution*, **44**, 1787-1795.

Forsman A, Shine R (1995) The adaptive significance of colour pattern polymorphism in the Australian scincid lizard *Lampropholis delicata*. *Biological Journal of the Linnean Society*, **55**, 273-291.

Gandon S, Michalakis Y (2001) Multiple causes of the evolution of dispersal. In: *Dispersal* (eds Clobert J, Danchin E, Dhondt AA, Nichols JD), pp. 155-167. Oxford University Press, Oxford.

Gross MR (1996) Alternative reproductive strategies and tactics : diversity within sexes. *Trends in Ecology and Evolution*, **11**, 92-98.

Hamilton WD, May RM (1977) Dispersal in stable habitats. *Nature*, **269**, 578-581.

Heino M, Metz JAJ, Kaitala V (1998) The enigma of frequency-dependent selection. *Trends in Ecology and Evolution*, **13**, 67-370.

Hutchings JA, Myers RA (1994) The evolution of alternative mating strategies in variable environments. *Evolutionary Ecology*, **8**, 256-268.

Ims RA, Hjermann DO (2001) Condition-dependent dispersal. In: *Dispersal* (eds Clobert J, Danchin E, Dhondt AA, Nichols JD), pp. 203-216. Oxford University Press, Oxford.

Johnson ML, Gaines MS (1990) Evolution of Dispersal : Theoretical Models and Empirical Tests Using Birds and Mammals. *Annual Review of Ecology and Systematics*, **21**, 449-480.

Le Galliard JF, Ferriere R, Clobert J (2003) Mother-offspring interactions affect natal dispersal in a lizard. *Proceeding of the Royal Society Biological Sciences Series B*, **270**, 1163-1169.

Lecomte J, Clobert J, Massot M (1992) Sex identification in juveniles of *Lacerta vivipara*. *Amphibia-Reptilia*, **13**, 21-25.

Léna JP, Clobert J, de Fraipont M, Lecomte J, Guyot G (1998) The relative influence of density and kinship on dispersal in the common lizard. *Behavioral Ecology*, **9**, 500-507.

Massot M, Clobert J, Chambon A, Michalakis Y (1994) Vertebrate natal dispersal: the problem of non-independence of siblings. *Oikos*, **70**, 172-176.

Massot M, Clobert J, Pilorge T, Lecomte J, Barbault R (1992) Density dependence in the common lizard : demographic consequences of a density manipulation. *Ecology*, **73**, 1742-1756.

Massot M, Clobert J (1995) Influence of maternal food availability on offspring dispersal. *Behavioral Ecology and Sociobiology*, **37**, 413-418.

Massot M, Clobert J (2000) Processes at the origin of similarities in dispersal behaviour among siblings. *Journal of Evolutionary Biology*, **13**, 707-719.

Massot M, Clobert J, Lorenzon P, Rossi JM (2002) Condition-dependent dispersal and ontogeny of the dispersal behaviour : an experimental approach. *Journal of Animal Ecology*, **71**, 253-261.

Massot M, Clobert J, Ferrière R. Dispersal plasticity constrains species range adjustment to climate warming. In preparation.

Mazer SJ, Damuth J (2001) Nature and Causes of Variation. In: *Evolutionary Ecology : concepts and case studies* (eds Fox CW, Roff DA, Fairbairn DJ), pp.3-15. Oxford University Press, Oxford.

Meylan S, Belliure J, Clobert J, de Fraipont M (2002) Stress and body condition as prenatal and postnatal determinants of dispersal in the common lizard (*Lacerta vivipara*). *Hormones and Behavior*, **42**, 319-326.

Meylan S, de Fraipont M, Clobert J (2004) Maternal size, stress and offspring philopatry : an experimental study in the common lizard (*Lacerta vivipara*). *Ecoscience*, **11**, 123-129.

Philippi T, Seger J (1989) Hedging One's Evolutionary Bets, Revisited. *Trends in Ecology and Evolution*, **4**, 41-44.

Rand MS (1988) Courtship and aggressive behavior in male lizards exhibiting two different sexual colorations. *American Zoologist*, **28**, 153A.

Ronce O, Clobert J, Massot M (1998) Natal dispersal and senescence. *Proceedings of the National Academy of Sciences, U.S.A.,* **95**, 600-605.

Ronce O, Olivieri I, Clobert J, Danchin E (2001) Perspectives on the study of dispersal evolution. In *Dispersal* (eds Clobert J, Danchin E, Dhondt AA, Nichols JD), pp. 341-357. Oxford University Press, Oxford.

Ronce O, Olivieri I (2004) Life history evolution in Metapopulations. In: *Ecology, Genetics, and Evolution of Metapopulations* (eds I. Hanski and O.E. Gaggiotti), pp 227-258. Academic Press, San Diego.

SAS (1992). *SAS User's Guide : Statistics.* SAS Institute, Cary.

Sorci G, Massot M, Clobert J (1994) Maternal parasite load increases sprint speed and philopatry in female offspring of the common lizard. *The American Naturalist*, **144**, 153-164.

Sinervo B, Lively CM (1996) The rock-paper-scissors game and the evolution of alternative male reproductive strategies. *Nature*, **380**, 240-243.

Sinervo B, Miles DB, Frankino WA, Klukowski M, DeNardo DF (2000) Testosterone, endurance, and Darwinian fitness : natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior*, **38**, 222-233.

Sinervo B, Clobert J (2003) Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science*, **300**, 1949-1951.

Sinervo B, Chaine A, Clobert J, Calsbeek R, McAdam A, Hazard L, Lancaster L, Alonzo SH, Corrigan G, Hochberg M (2006a) Self-recognition, color signals and cycles of greenbeard mutualism and transient altruism. *Proceedings of the National Academy of Sciences, U.S.A.,* **102**, 7372-7377.

Sinervo B, Calsbeek R, Comendant T, Both C, Adamopoulou C, Clobert J (2006b). Genetic and maternal determinants of effective dispersal: the effect of sire genotype and size at birth in side-blotched lizards. *The American Naturalist*, **168**, 88-99.

Svensson E, Sinervo B, Comendant T (2001) Condition, genotype-by-environment interaction and correlational selection in lizard life-history morphs. *Evolution*, **55**, 2053-2069.

Swingland IR (1983) Intraspecific differences in movement. In: *The Ecology of Animal Movement* (eds Swingland IR, Greenwood PJ), pp. 102-115. Clarendon Press, Oxford.

Thompson CW, Moore MC (1991) Syntopic occurrence of multiple dewlap color morphs in male tree lizards, *Urosaurus ornatus*. *Copeia* , **2**, 493-503.

Thompson CW, Moore IT, Moore MC (1993) Social, environmental and genetic factors in the ontogeny of phenotypic differentiation in a lizard with alternative male reproductive strategies. *Behavioral Ecology and Sociobiology*, **33**, 137-146.

Tuttle EM (2003) Alternative reproductive strategies in the white-throated sparrow: Behavioral and genetic evidence. *Behavioral Ecology*, **14**, 425-432.

Vercken E, Massot M, Sinervo B, Clobert J (2007) Colour polymorphism in females and alternative reproductive strategies in the common lizard *Lacerta vivipara*. *Journal of Evolutionary Biology*, **20**, 221-232.

Weiss SL (2002) Reproductive signals of female lizards: Pattern of trait expression and male response. *Ethology*, **108**, 793-813.

West-Eberhard MJ (1983) Sexual selection, social competition, and speciation. *Quarterly Review of* Biology, **58**, 155-183.

Variable in interaction with maternal ventral colour	Yellow vs Mixed (n=116)	Yellow vs Orange (n=97)	Orange vs Mixed (n=83)
Mean temperature in June	$\chi^2_1 = 5.68$ **p=0.017**	$\chi^2_1 = 0.57$ p=0.45	$\chi^2_1 = 6.28$ **p=0.012**
Mean temperature in August	$\chi^2_1 = 0.24$ p=0.62	$\chi^2_1 = 5.04$ **p=0.025** (marginal)	$\chi^2_1 = 2.65$ p=0.1
Maternal feeding treatment	$\chi^2_1 = 6.66$ **p=0.01**	$\chi^2_1 = 0.22$ p=0.64	$\chi^2_1 = 6.58$ **p=0.01**

Table 1: Results of likelihood-ratio tests for the colour interactions in the three different colour pairs. The significance threshold for critic probabilities is equal to 0.017 (Bonferroni correction). Significant p-values are in bold.

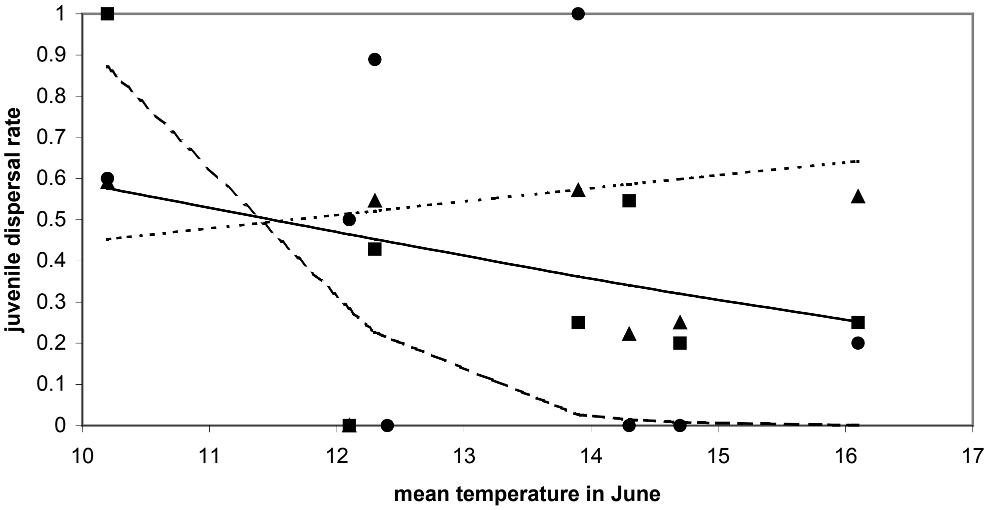
Figure legends

Figure 1: Mean values and model fit for the effect of the temperature in June on juvenile dispersal. Offspring from mixed mothers (squares, long-dashed line) are more sensitive to the mean temperature in June than offspring from yellow (triangles, solid line,) or orange females (dots, short-dashed line).

Figure 2: Mean values and model fit for the effect of the temperature in August on juvenile dispersal in interaction with maternal ventral colour. Offspring from orange mothers (dots, short-dashed line) are more sensitive to the mean temperature in August than offspring from yellow (triangles, solid line) or mixed females (squares, long-dashed line).

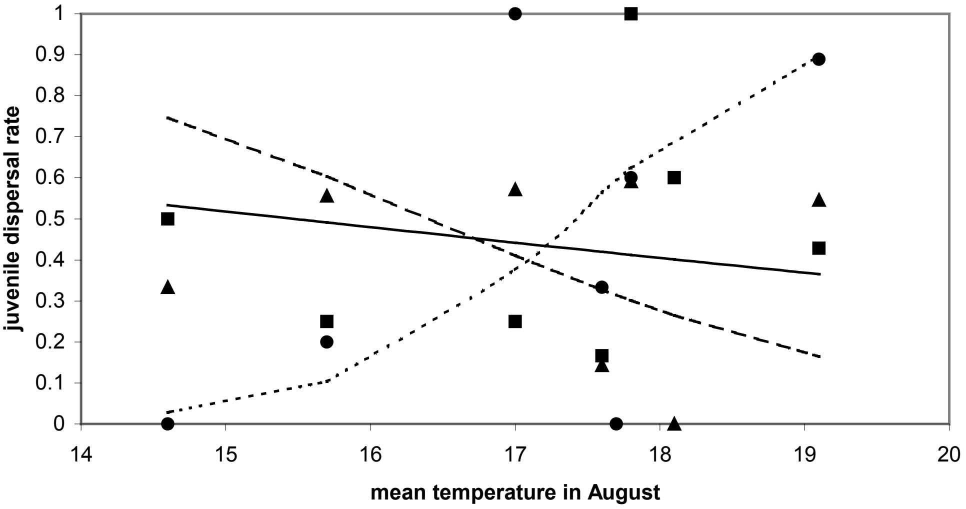
Figure 3: Effect of maternal feeding treatment (white: full-rations, grey: half-rations) on juvenile dispersal in interaction with maternal ventral colour. Error bars are 95% confidence intervals (+/- 2 s.e.).

Figure 1



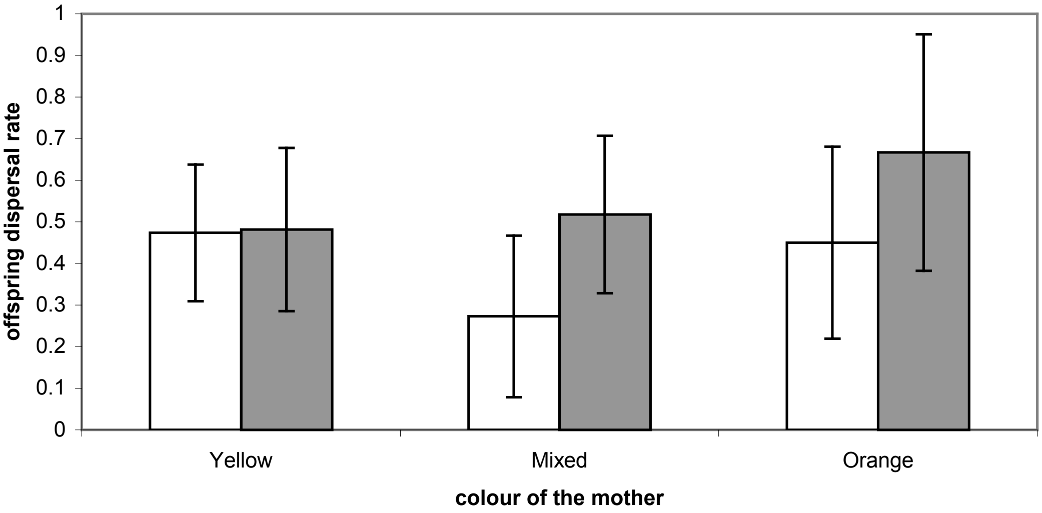
juvenile dispersal rate
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
10
11
12
13
14
15
16
17
mean temperature in June

Figure 2



juvenile dispersal rate
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
14
15
16
17
18
19
20
mean temperature in August

Figure 3


1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
offspring dispersal rate
Yellow
Mixed
Orange
colour of the mother

ANNNEXE III: Female colour polymorphism and social dominance in the common lizard *Lacerta vivipara*

Article soumis

Female colour polymorphism and social dominance in the common lizard (*Lacerta vivipara*)

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Abstract

Social competition is known to promote the evolution of conspicuous traits in both sexes, and female ornamentation can often be related to intrasexual competition for mates or resources. In the common lizard, female competition for resources is thought to be a strong selective pressure, yet females do not defend exclusive territories. The existence of a stable social hierarchy could explain the cohabitation of many females in limited areas, if the rapid assessment of resource holding potential can limit the cost of unbalanced agonistic interactions. Female common lizards display a polymorphism in ventral colour, correlated with differences in reproduction, dispersal strategies, and susceptibility to resource competition. We tested the hypothesis that this polymorphism is used as a badge of status in female competition and signals social dominance. We studied the agonistic behaviour and social stress of females of different colours during laboratory staged encounters. We found that the behaviour of females was affected by their own colour and the colour of their social environment. One colour morph was the least likely to aggress and the most likely to flee, and thus was considered as subordinate. Another morph was rarely aggressed and often made its opponent flee, and thus was considered as dominant. The third morph was aggressive, especially towards the dominant morph, but was also often attacked, which could be characteristic of an intermediate or condition-dependent dominance status.

Keywords: *colour polymorphism; females; resource holding potential; social dominance.*

Although female ornamentation has often been considered as a non-functional by-product of sexual selection on males caused by genetic correlation between the sexes (Lande 1980), recent evidence from comparative studies have challenged this view and suggested that selection has also acted directly on females to favour increased showiness (Rowland et al. 1991, Irwin 1994, Bleiweiss 1997, Burns 1998, Ord & Stuart-Fox 2006). Indeed, social competition is known to promote the evolution of conspicuous traits in both sexes (West-Eberhard 1983), and might be at the origin of female extravagant traits in many species (Amundsen 2000). In particular, female contest competition can promote the evolution of signals related to female competitive ability (Langmore 2000). Female showiness can also be selected by male mate choice, and conspicuous characters can be used as badges of status in mating competition (in pinyon jays, Johnson 1988) or as indicators of female quality (in bluethroats, Amundsen et al. 1997; in striped plateau lizards, Weiss 2006). Social competition can thus lead to variations in social signalling between females, setting the ground for the evolution of complex phenotypic alternatives characterized by differences in behaviour (aggressiveness, Johnson 1988, Trail 1990), physiology (sexual receptivity, Rowland et al. 1991, LeBas & Marshall 2000; hormonal levels, Sinervo et al. 2000a), and/or life-history traits (offspring size and number, Sinervo et al. 2000b).

In the common lizard, *Lacerta vivipara*, both correlative and experimental data suggest that female contest competition is a strong selective pressure, at least at high densities (Massot et al. 1992, Lecomte et al. 1994), and affects female reproductive success (Vercken et al. 2007). Recent evidence support the hypothesis that female common lizards are involved in active mate choice (Laloi et al. 2004, Richard et al. 2005), and female mating competition is likely to take place since males are a limiting resource in this species (Richard et al. 2005, Fitze et al. 2005). However, mating competition should affect females only during the mating season, which is notably short in this species (a few days, Laloi et al. 2004, Massot et al.

1992, Richard et al. 2005). Competition for resources is therefore more likely to generate a prolonged social stress during gestation, as demonstrated by its consequences on clutch size, offspring size and survival (Massot et al. 1992, Meylan et al. 2007, Vercken et al. 2007).

However, if competition for resources between females was strong, we would expect females to adopt a spacing behaviour limiting their social interactions, which is not what is observed in nature. On the contrary, females do not appear strictly territorial, and aggregate around discrete resources, like rocks, trees, or streams (Massot 1992, E. Vercken, pers. obs.). Such spatial association is possible only if some degree of social organization limits the costs of competition, by reducing the necessity of agonistic interactions. In many species, the home ranges of dominant individuals are mutually exclusive, but dominant individuals tolerate the presence of subordinate individuals on their territory (Wauters & Dhondt 1992, Luque-Larena et al. 2004, Shier & Randall 2004). Individual differences in resource holding potential can thus lead to stable social dominance that allows the cohabitation of dominant and subordinate individuals in a context of strong competition for resources.

Female common lizards display a polymorphism in ventral coloration (yellow, orange, or mixed) that is associated with alternative strategies in reproduction (Vercken et al. 2007) and offspring dispersal (Vercken et al. submitted). Females of different colours seemed to differ in their sensitivity to intrasexual competition, and to colour morph-specific competition (Vercken et al. 2007). Such differences in the fitness costs of competition might results from colour-related differences in resource holding potential and dominance status. Indeed, individual differences in competitive ability are expected to be signalled by conspicuous traits, such as ventral colour. Competitive ability and social behaviour would thus be part of larger phenotypic syndromes including differences in reproduction and dispersal.

To test for the existence of colour-dependent female behavioural, we studied the agonistic behaviour and social stress of females during laboratory staged encounters at different periods of the activity season. We tested for the effect of the colour and the morphology of both females interacting in order to identify conspicuous correlates of social dominance in female common lizards.

Methods

The species

Lacerta vivipara is a small (adult snout-vent length from 50 to 70 mm), live bearing lacertid lizard, which is found throughout Europe and Asia. The four study populations are located on Mont Lozère (in southern France, altitude 1455 m). In these populations, males emerge from hibernation in mid-April, followed by yearlings, and females in mid-May. Mating occurs at female emergence, and up to five different males can sire one same clutch (Richard et al. 2005). Gestation lasts for two months, and parturition starts in July and lasts for two to three weeks. Females lay a clutch of, on average, five soft-shelled eggs (range 1-12). Offspring hatch within two hours after laying and are immediately independent of their mother. A more detailed description of life history can be found in Clobert et al. (1994). In these populations, adult females display a ventral colouration varying from pale yellow to bright orange, whereas adult males are almost always orange. Juveniles start by being melanic, and slowly turn to a pale green ventral colouration when yearlings. Stability of ventral colour arises with sexual maturity (around two years), and no further modifications of the colour signal (hue and chroma) was found to be age-dependent thereafter (Vercken et al. 2007). In addition, the heritability of the ventral colouration was found to be high (0.48 for maternal heritability), with no effect of the pre- and post-natal environments (Vercken et al. 2007).

Data set

Because social interactions might be of different nature and strength in the course of the season, females were captured in spring (early gestation period, n=424) or in summer (late gestation period, n=264) from 4 different populations and brought to the laboratory. At each capture, females were measured (snout vent-length or SVL) and weighed. Ventral colouration was assessed visually by comparison to a home-made colour reference at the initiation of a long term study in 1988.. Female ventral colour fell into one of three categories: pale yellow, bright orange or mixed colouration (mixture of yellow and orange). This classification was proved to reflect differences in chroma and hue, and alternative strategies in reproduction (Vercken et al. 2007) and offspring dispersal (Vercken et al. submitted). The apparent continuity of colour variation was contested by the non-linearity of the responses of mixed females' reproductive parameters and offspring dispersal to the variations in environmental factors. Therefore, the three colour classes were assumed to represent three distinct colour morphs, correlated with discrete alternative strategies.

Females were housed in plastic terraria with damp soil, a shelter and water *ad libitum*. They were exposed to natural daylight and heated by electric bulbs from 9h to 12h and from 14h to 17h. Females captured in spring were challenged the day after capture, then fed and released on their capture point. Females captured in summer were kept in the laboratory until parturition. They were challenged the day after parturition, then fed and released with their offspring at the mother's capture point. Females were challenged after parturition to avoid perturbation during gestation, and because females slow down their activity when approaching parturition (Bauwens & Thoen 1981, Lecomte et al. 1993).

Laboratory staged encounters

Experiments were conducted during the heating hours in order to match the natural activity pattern of the species. A female common lizard (focal female) was introduced in a plastic terrarium (25 x 15 x 15 cm) containing a small heating wire (allowing basking for one female only) and left for 10 minutes, so that it could explore the terrarium and find the heating source (the competing resource). Then another female was introduced in the opposite side of the terrarium (opponent female) and the behaviour of both females was monitored for 10 minutes.

Several components of the behaviour were analysed: time spent scratching the terrarium walls (considered as a sign of stress, de Fraipont et al. 2000), number of biting attempts and number of escape attempts (when a female moved away in reaction to the other female's approach). The two females were always unfamiliar, either because from different populations, or because of non-overlapping home ranges in the same population. Even though the experimental enclosure is smaller than a female home range (30m in diameter on average, Massot 1992), females are likely to interact at close range when competing for the access to discrete resources in nature, and the behaviours displayed in this setting should be representative of real-life competitive interactions. This kind of experimental design has been used successfully for this species in other contexts and the observed behaviours were found to relate to specific differences in behavioural decisions or life history traits in the field (de Fraipont et al. 2000, Léna et al. 2000, Belliure et al. 2004, Aragon et al. 2006a, Cote & Clobert 2007). The analysis of colour-specific behavioural patterns is thus likely to give reliable information about the social relationships that connect the different colour morphs.

Statistical Analysis

For each trial, we analysed only the behaviour of the focal female, whereas the behaviour of the opponent female was disregarded because it could not be considered as independent. To analyse the time spent scratching, we used a general linear model (GLM procedure, SAS Institute). Variables that followed a Poisson distribution (number of biting or escape attempts), were analysed using log-linear regressions (GENMOD procedure, SAS Institute). F statistics and likelihood ratio tests (χ^2 values) were used to assess significance of effects. Type III sum of squares was used in all cases. We started with a general model including all the potential effects and their interactions (up to three-ways interactions): season, focal female colour, focal female size, opponent female colour, opponent female size, and the size difference between focal female and opponent female. We then dropped the non-significant effects (backward selection), starting with the most complex interaction terms. Only the results of the final model are reported.

Colour effects were interpreted by comparing alternately the three different colour pairs. In this case, we used a Bonferroni correction to assess significance of effects (the significance threshold for the critic probability being lowered to 0.017).

Results

Scratching time was found to depend on season ($F_{1,349}=24.43$, $p<0.0001$) and focal female colour ($F_{2,349}=4.61$, $p=0.01$). Females tended to scratch longer in summer (mean scratching time=71s) than in spring (38.6s), and mixed females tended to scratch longer than yellow or orange females (see table 1 for probabilities and Fig.1).

The number of biting attempts depended on focal female colour ($\chi^2_2=9.01$, $p=0.011$, $n=354$), opponent female colour ($\chi^2_2=7.25$, $p=0.027$) and their interaction ($\chi^2_4=15.05$, $p=0.005$). Mixed females attempted to bite their opponent more often than orange females (see table 1 for probabilities and Fig.2a). Focal females attempted to bite more often a mixed opponent than a yellow opponent (see table 1 for probabilities and Fig.2b). Mixed focal females attempted to bite more often yellow opponents than mixed or orange opponents, whereas the opposite trend was found for yellow and orange focal females (see table 1 for probabilities, and Fig.2c)

The number of contact avoidance depended on season ($\chi^2_1=16.08$, $p<0.0001$, $n=347$), size difference between focal female and opponent ($\chi^2_1=24.98$, $p<0.0001$), and opponent colour ($\chi^2_2=29.17$, $p<0.0001$). Focal females tended to flee more often when facing an opponent larger than themselves, and more often in spring (mean number of flight attempts=1.24) than in summer (0.93). Focal females also tended to flee more often when facing a yellow or a mixed opponent than an orange opponent (see table 1 for probabilities and Fig. 3)

Discussion

In our experiment, females differed in their stress level and in their agonistic behaviour when facing other females, depending on their own colour, or the colour of their opponent, or both. The population of origin never influenced female behaviour, which supports the generality and reliability of ventral colour as a signal in social interactions. As female ventral colour appears to be strongly correlated with individual behaviour and to influence the outcome of social interactions, it could thus act as a badge of status signalling social dominance.

Relevance of the experimental design

We allowed the focal female to explore the terrarium alone, before the introduction of the opponent female, which might generate an asymmetry in the competitive encounter. However, the time the focal female spent alone in the terrarium (10 minutes) is probably too short to allow the focal female to establish residency, and thus to gain a competitive advantage over the opponent female. The purpose of this design was to allow at least one female to find the heating source, so that she could reveal its presence to the other female by basking. However, even if the 10 minutes of exploration were enough for the female to acquire a resident status, this competitive asymmetry should not have affected our results, because we only analysed the behaviour of the focal female. Therefore, we would have analysed the colour differences in territorial behaviour and dominance over intruders, instead of simple social dominance. In all cases, this should not restrict the range of our conclusions concerning colour-related differences in social behaviour.

Another intriguing issue comes from the fact that females common lizard do not perform conspicuous displays of their ventral colour. However, ventral coloration extends up to the throat where the signal can easily be seen whenever an individual is raising its head. Ventral colouration can also be visible in many other occasions of the every day females' life, for instance when a female is walking in or climbing over the substrate. Furthermore, as ventral colour is correlated with many aspects of the phenotype (Vercken et al. 2007, Vercken et al. submitted), it could also correlate with chemosensory signals that females would assess at close range (Alberts 1990, 1992). However, recent experimental results suggest that, although females behaviour might be influenced by other signals, such as chemical signals or behavioural displays (Aragon et al. 2006b), they use the ventral colour of their opponent directly as a signal to adjust their own behaviour (E. Vercken and J. Clobert, unpublished data). Ventral colour is therefore likely to be an ecologically relevant signal of both the owner's individual phenotype (Vercken et al. 2007) and its social behaviour.

Seasonal effect

In our experiment, two out of the three behavioural variables were found to depend significantly on season, which could result from seasonal variations in the levels of hormones implicated in behaviour (Dauphin-Villemant et al. 1990, Woodley & Moore 1999), as well as from behavioural responses to the time spent in captivity. However, seasonal effects never interacted with colour effects, which means that although the season (or the time spent in captivity) affects the global pattern of activity, it does not modify the nature of social interactions. This result suggests that the selective pressures acting on female social behaviour do not change during the whole reproductive season, i.e. that competition for resources is far more likely to shape females social relationships than mating competition, and that female ventral colour might signal for stable individual differences in resource holding potential.

Dominance status and social function of colour

Orange females were the least aggressive, and tended to avoid agonistic interactions more often than other females. This behaviour could be compatible with a subordinate status, or a submissive strategy. On the other hand, yellow females tended to make their opponents flee, and were rarely aggressed. This pattern is rather characteristic of dominant individuals, with high resource holding potential. Mixed females showed a more original behavioural pattern: although these females seemed aggressive, they were often challenged by other females, and they spent more time scratching the terrarium walls, thus showing a higher stress level than other females. This could be related to an intermediate or condition-dependent dominance status. These females were indeed especially aggressive towards yellow (potentially dominant) females, and might play the role of social challengers. Mixed females would thus have to enter regularly agonistic interactions to maintain their social status, in particular towards yellow females.

Such differences in dominance status would no be related to female condition since there is no difference in morphology between colour morphs (Vercken et al. 2007), and in our experiment, morphological variables never interacted with colour effects. The observed behavioural patterns would rather result from genetically-based differences in resource holding potential, leading to differences in social dominance. Indeed, preliminary results tend to show a higher testosterone concentration in plasma for yellow females (1.07 ng/mL) than for mixed (0.96 ng/mL) and orange females (0.85 ng/mL), although these differences are non-significant ($p=0.43$). In addition, in a previous study, yellow females appeared also more senescent (Vercken et al. 2007), which can result from the immunosuppressive effects of an elevated testosterone level often associated with social dominance (immunocompetence handicap hypothesis, Folstad & Karter 1992). Ventral colour could thus act as a badge of status in social interactions, and limit the costs of agonistic interactions between females of unequal resource holding potential. Indeed, as adult common lizards are sedentary (Massot et al. 1992, Clobert et al. 1994), the groups of individuals that are spatially associated are likely to be temporally stable. A stable social organization based on honest (genetic) signalling could thus replace the costly assessment of the competitive ability of neighbouring individuals.

In addition, females that are spatially associated in nature might not be random individuals. In this study, we showed that the outcome of social interactions was colour-dependent, and could affect female fitness. Settlement decisions are thus likely to be based on the colour of the social environment, alone or in interaction with local relatedness. We chose to confront unfamiliar and most probably unrelated females to avoid kin interaction effects and to isolate the sole part of ventral colour in shaping behavioural pattern. However, spatial studies on the distribution of females with regard to relatedness and ventral colour would help further clarifying how the social landscape affects female spacing behaviour and fitness. In particular, adaptive spacing strategies could allow the maintenance of several phenotypic alternatives associated with unequal competitive abilities.

Conclusion

Female colour polymorphism in the common lizard was found to reflect individual differences in behavioural patterns that are likely to correlate with different dominance status. Such differences in social dominance could define alternative social strategies, that would be part of larger adaptive syndromes including various life-history traits, such as reproductive or dispersal strategies as already found in another lizard species (Sinervo et al. 2000b, Sinervo & Clobert 2003, Sinervo et al. 2006). However, to understand better the role of ventral colouration in competitive interactions and in the establishment of social dominance, experimental studies of territory settlement and resource exploitation would be necessary.

Studies of the spatial organization of females in nature are also needed to understand how the colour environment affects a female's life history choices.

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REFERENCES

Alberts, A.C. 1990. Chemical properties of femoral gland secretions in the desert iguana *Dipsosaurus dorsalis*. *Journal of Chemical Ecology*, 16, 13-25.

Alberts, A.C. 1992. Pheromone self-recognition in desert iguanas. *Copeia*, 1992, 229-232.

Amundsen, T., Forsgren, E. & Hansen, L.T.T. 1997. On the function of female ornaments: male bluethroats prefer colorful females. *Proceedings of the Royal Society Biological Sciences Series B*, 264, 1579-1586.

Amundsen, T. 2000. Why are females birds ornamented? *Trends in Ecology and Evolution*, 15, 149-155.

Aragon, P., Meylan, S. & Clobert, J. 2006a. Dispersal status-dependent response to the social environment in the common lizard, *Lacerta vivipara*. *Functional Ecology*, 20, 900-907.

Aragon, P., Massot, M., Gasparini, J. & Clobert, J. 2006b. Socially acquired information through chemical cues in the common lizard, Lacerta vivipara. *Animal Behaviour*, 72, 965-974.

Bauwens, D. & Thoen, C. 1981. Escape tactics and vulnerability to predation associated with the reproducrtion in the lizard Lacerta vivipara. *Journal of Animal Ecology*, 50, 733-743.

Belliure, J., Meylan, S. & Clobert, J. 2004. Prenatal and postnatal effects of corticosterone on behaviour in juveniles of the common lizard *Lacerta vivipara*. *Journal of Experimental Zoology*, 301A, 401-410.

Bleiweiss, R. 1997. Covariation of sexual dichromatism and plumage colours in lekking and non-lekking birds: a comparative analysis. *Evolutionary Ecology*, 11, 217-235.

Burns, K.J. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus mal plumage. *Evolution*, 52, 1219-1224.

Clobert, J., Massot, M., Lecomte, J., Sorci, G., de Fraipont, M. & Barbault, R. 1994. Determinants of dispersal behavior : the common lizard as a case study. In: *Lizard Ecology: historical and experimental perspectives* (Ed. By L.J. Vitt & E.R. Pianka), pp183-206. Princeton: Princeton University Press.

Cote, J. & Clobert J. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society Biological Sciences Series B*, 274, 383-390.

Dauphin-Villemant, C., Leboulenger, F., Xavier, F. & Vaudry, H. 1990. Adrenal activity in the female Lacerta vivipara Jacquin associated with breeding activities. *General and Comparative Endocrinology*, 78, 399-413.

de Fraipont, M., Clobert, J., John-Alder, H. & Meylan, S. 2000. Pre-natal stress increases offspring philopatry. *Journal of Animal Ecology*, 69, 404-413.

Fitze, P., Le Galliard, J.F., Federici, P., Richard, M. & Clobert, J. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. *Evolution*, 59, 2451-2459.

Folstad, I. & Karter, A.J. 1992. Parasites, bright males, and the immunocompetence handicap. *The American Naturalist*, 139, 603-622.

Irwin, R.E. 1994. The evolution of plumage dichromatism in the New World Blackbirds: social selection on female brightness ? *The American Naturalist*, 144, 890-907.

Johnson, K. 1988. Sexual selection in pinion jays II: male choice and female-female competition. *Animal Behaviour*, 36, 1048-1053.

Laloi, D., Richard, M., Lecomte, J., Massot, M. & Clobert, J. 2004. Multiple paternity in clutches of common lizard Lacerta vivipara: Data from microsatellites markers. *Molecular Ecology*, 13, 719-723.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, 34, 292-305.

Langmore, N. 2000. Why Female Birds Sing. In: *Animal Signals* (Ed. By Y. Espmark, T. Amundsen & G. Rosenqvist G), pp 317-327. Trondheim: Tapir Academic Press.

LeBas, N.R. & Marshall, N.J. 2000. The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. *Proceedings of the Royal Society Biological Sciences Series B*, 267, 445-452.

Lecomte, J., Clobert, J. & Massot, M. 1993. Shift in behaviour related to pregnancy in *Lacerta vivipara*. *Revue d'Ecologie (Terre et Vie)*, 48, 99-107.

Lecomte, J., Clobert, J., Massot, M. & Barbault, R. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. *Ecoscience*, 1, 300-310.

Léna, J.P., de Fraipont, M. & Clobert, J. 2000. Affinity towards maternal odour and offspring dispersal in the common lizard. *Ecology Letters*, 3, 300-308.

Luque-Larena, J.J., Lopez, P. & Gosalbez, J. 2004. Spacing behavior and morphology predict promiscuous mating strategies in the rock-dwelling snow vole, *Chionomys nivalis*. *Canadian Journal of Zoology*, 82, 1051-1060.

Massot, M. 1992. Déterminisme de la dispersion chez le lézard vivipare. Ph.D. thesis, Université Paris XI.

Massot, M., Clobert, J., Pilorge, T., Lecomte, J. & Barbault, R. 1992. Density dependence in the common lizard : demographic consequences of a density manipulation. *Ecology*, 73, 1742-1756.

Meylan, S., Clobert, J. & Sinervo, B. 2007. Adaptive significance of maternal induced density-dependent phenotype. *Oikos* (in press).

Ord, T.J. & Stuart-Fox, D. 2006. Ornament evolution in dragon lizards: multiple gains and widespread losses reveal a complex history of evolutionary change. *Journal of Evolutionary Biology*, 19, 797-808.

Richard, M., Lecomte, J., de Fraipont, M. & Clobert, J. 2005. Age-specific mating strategies and reproductive senescence. *Molecular Ecology*, 14, 3147-3155.

Rowland, W.J., Baube, C.L. & Horan, T.T. 1991. Signalling of sexual receptivity by pigmentation pattern in female sticklebacks. *Animal Behaviour*, 42, 243-249.

SAS. 1992. SAS User's Guide: Statistics. Cary: SAS Institute.

Shier, D.M. & Randall, J.A. 2004. Spacing as a predictor of social organization in kangaroo rats (*Dipodomys heermanni arenae*). *Journal of Mammology*, 85, 1002-1008.

Sinervo, B., Miles, D.B., Frankino, W.A., Klukowski, M. & DeNardo, D.F. 2000a. Testosterone, endurance, and darwinian fitness: Natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior*, 38, 222-233.

Sinervo, B., Svensson, E. & Comendant, T. 2000b. Density cycles and an offspring quality and quantity game driven by natural selection. *Nature*, 406, 985-988.

Sinervo, B. & Clobert, J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science*, 300, 1949-1951.

Sinervo, B., Calsbeek, R., Comendant, T., Adamopoulou, C., Both, C. & Clobert, J. 2006. Genetic and maternal determinants of dispersal: the effect of sire genotype and size at birth in side-blotched lizards. *The American Naturalist*, 168, 88-99.

Trail, P.W. 1990. Why should lek-breeders be monomorphic? *Evolution*, 44, 1837-1852.

Vercken, E., Massot, M., Sinervo, B. & Clobert, J. 2007. Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. *Journal of Evolutionary Biology*, 20, 221-232.

Vercken, E., Massot, M., Sinervo, B. & Clobert, J. Female colour morphs in the common lizard display alternative offspring dispersal strategies with respect to environmental cues. Submitted.

Wauters L. & Dhondt, A.A. 1992. Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. *Animal Behaviour*, 43, 297-311.

Weiss, S.L. 2006. Female-specific color is a signal of quality in the striped plateau lizard (*Sceloporus virgatus*). *Behavioral Ecology*, 17, 726-732.

West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, 58, 155-183.

Woodley, S. & Moore, M.C. 1999. Female territorial aggression and steroid hormones in mountain spiny lizards. *Animal Behaviour*, 57, 1083-1089.

Variable	Difference between yellow and mixed focal females (n=225)	Difference between yellow and orange focal females (n=238)	Difference between orange and mixed focal females (n=245)
Scratching time	f colour $F_{1,222}$=5.38, **p=0.021**	f colour $F_{1,235}$=0.14, p=0.71	f colour $F_{1,242}$=9.46, **p=0.0023**
Number of biting attempts	f colour χ^2_1=3.3, p=0.08 o colour χ^2_1=6.89, **p=0.009** f colour*o colour χ^2_2=9.2, **p=0.01**	f colour χ^2_1=1.03, p=0.31 o colour χ^2_1=0.92, p=0.34 f colour*o colour χ^2_2=0.99, p=0.61	f colour χ^2_1=8.8, **p=0.003** o colour χ^2_1=3.09, p=0.08 f colour*o colour χ^2_2=10.38, **p=0.006**
Number of escape attempts	f colour χ^2_1=10.6, **p=0.001** o colour χ^2_1=0.26, p=0.61	f colour χ^2_1=13.35, **p=0.0003** o colour χ^2_1=25.66, **p<0.0001**	f colour χ^2_1=0.29, p=0.6 o colour χ^2_1=18.77, **p<0.0001**

Table 1: Results of F-tests and chi-squares tests for colour effects on behavioural variables (f= focal female; o=opponent female). Significant p-values are in bold.

Figure Legends

Figure 1: Time spent scratching depending on the colour of the focal female.

Error bars are 95 % confidence intervals (+/- 2 s.e.).

Figure 2: Mean number of biting attempts depending on the colour of the focal female colour or the opponent female or both. (a) Focal female colour. (b) Opponent female colour. (c) Interaction between the colours of the focal female and the opponent female.

Error bars are 95 % confidence intervals (+/- 2 s.e.).

Figure 3: Mean number of escape attempts depending on the colour of the opponent female.

Error bars are 95 % confidence intervals (+/- 2 s.e.).

Figure 1

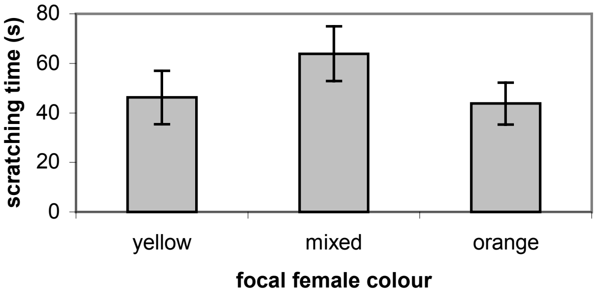

80
60
40
20
0
scratching time (s)
yellow
mixed
orange
focal female colour

Figure 2

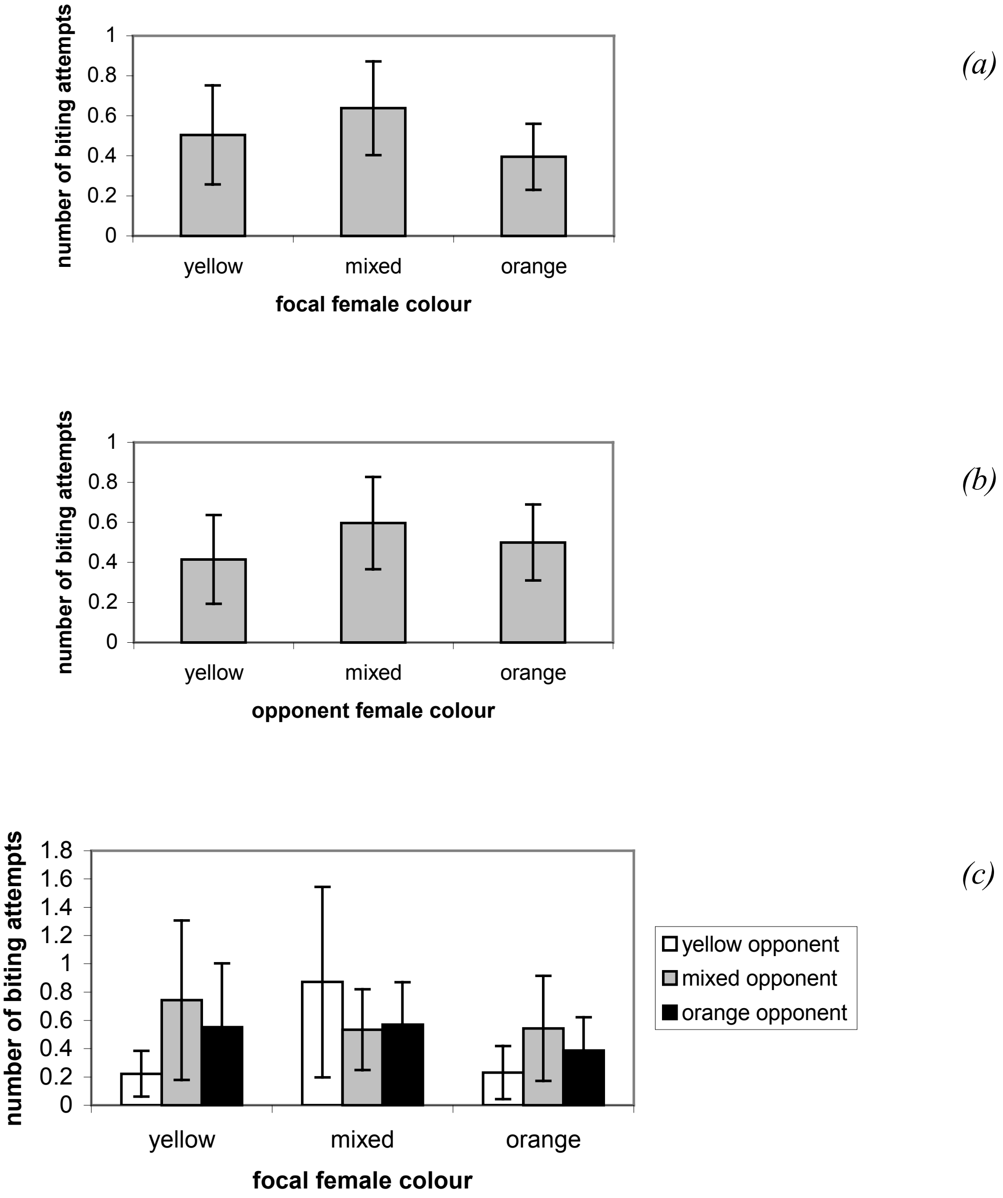
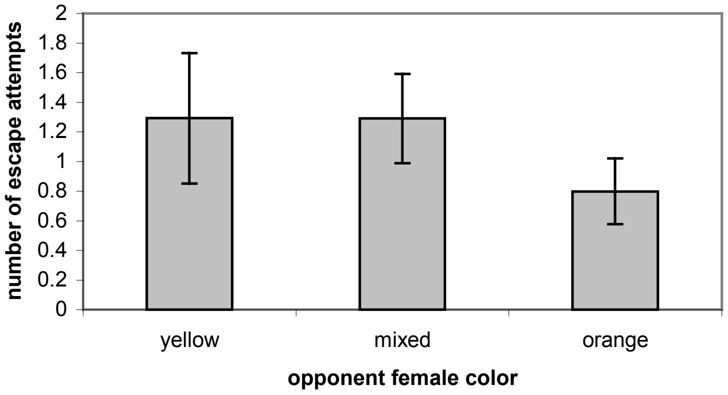

(a)
number of biting attempts
1
0.8
0.6
0.4
0.2
0
yellow
mixed
orange
focal female colour
(b)
number of biting attempts
1
0.8
0.6
0.4
0.2
0
yellow
mixed
orange
opponent female colour
(c)
number of biting attempts
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
yellow
mixed
orange
focal female colour
☐ yellow opponent
▨ mixed opponent
■ orange opponent

Figure 3


number of escape attempts
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
yellow
mixed
orange
opponent female color

ANNNEXE IV: Female colour polymorphism in the common lizard (*Lacerta* vivipara) signals for alternative strategies in social encounters

Article en préparation

Female colour polymorphism in the common lizard (*Lacerta vivipara*) signals for alternative strategies in social encounters

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Abstract

Colour variation in females is expected to play a role in intra-specific communication by signalling for traits that are socially relevant. However, in some cases, the information carried by colour signals is not sufficient and other cues should be used by conspecifics, as chemosensory cues. In the common lizard, females display three types of ventral colouration: yellow, orange and mixed. These ventral colours have been shown to affect the outcome of dyad encounters in laboratory experiments. However, it was not proved that females used the colour signal to assess the competitive ability and the social strategy of their opponent. In lacertids, chemical signals are often implicated in intraspecific communication, and could be used by females to acquire information, correlated or not with ventral colour, that can be useful in social interactions. We performed dyad encounters in which the ventral colour of the opponent was visible or not, and studied the response of the focal female. We found that females used the colour signal displayed by their opponent to adjust their own behaviour, but we could not determine whether they used other cues in complement. In addition, females of different colours appeared to differ in the degree of plasticity of their social behaviour, which could be related to the maintenance of colour polymorphism in this species.

Keywords: *female colour polymorphism, common lizard, competitive interactions, multiple signals, behavioural plasticity.*

Introduction

Variation in colour is an intriguing phenomenon found in a wide number of animal taxa, and it has been an extensive subject of interest for ecologists (e.g., in insects, Chapuisat 2004; in spiders, Oxford and Gillespie, 1998; in fishes, Olendorf et al. 2006; in reptiles, Sinervo et al. 2000; in birds Roulin 2004). However, if colour variation between males has been highly documented, and typically described as a product of sexual selection (Darwin 1871, Andersson 1994), variation in females has often be ignored or disregarded, merely considered as a by-product of sexual selection in males (Lande 1980).

Since a few years, increasing evidence has shown that selection has acted directly on females to favour the evolution of conspicuous traits (Burns 1988, Rowland et al. 1991, Irwin 1994, Bleiweiss 1997, Ord and Stuart-Fox 2006). Such traits might signal for female competitive ability (West-Eberhard 1983), dominance status (in pipefishes, Berglund and Rosenqvist 2001; in pinyon jays, Johnson 1988) or individual quality (in red-winged blackbirds, Johnsen et al. 1996; in bluethroats, Amundsen et al. 1997; in striped plateau lizards, Weiss 2006), and therefore might be selected by social competition (West-Eberhard 1983).

Female conspicuous traits in general, and female colour in particular, are thus likely to play a role in social interactions, as they give information about the individual's phenotype (Amundsen et al. 1997, Sinervo et al. 2000). However, if colour signals are used directly for communication in several species (for mate choice, Beeching et al. 1998, Amundsen and Forsgren 2001, Jones and Hunter 1993, LeBas and Marshall 2000; for sex recognition, Cooper and Burns 1987), it seems that in other cases, this information is complemented or even replaced with other cues (other visual signals, Zucker 1994; chemosensory signals, Lopez and Martin 2001, Hews and Bernard 2001). Indeed, colour signals do not always reflect all the characteristics of an individual that are potentially useful to its conspecifics (as age, Amundsen et al. 1997; size, Martin and Forsman 1999, Lopez et al. 2006; asymmetry, Martin and Lopez 2000, Lopez et al. 2006; parasitic load, Olsson and Madsen 1995; immune response, Lopez et al. 2006; dispersal status Aragon et al. 2006a), and alternative sources of information might be used in social interactions. In addition, different signals may be used at different spatial and temporal scales (e.g., visual signals accessible at longer distance than chemical signals, or persistence of chemical signals even in the absence of their issuer). The multiplicity of signals thus allows to convey composite messages, and redundant signals may be used in different contexts (Lopez et al. 1998, 2003).

In the common lizard *Lacerta vivipara*, females display a polymorphism in ventral colour (yellow, orange, or mixed), which is correlated with many other traits. In particular, females of different colours display alternative strategies in reproduction (Vercken et al. 2007) and offspring dispersal (Vercken et al. submitted). In addition, female ventral colour has been shown to be associated with differences in individual behaviour during social interactions (Vercken and Clobert submitted). When facing another female, female common lizards behave differently depending on their own ventral colour, or their opponent's colour, or both. Ventral colour thus appears to play a role in social communication in this species. However, we could not be sure that females used other females' colour directly as a signal in social interactions, and that they did not used other cues indicative of the strategy of their opponent. In lacertids, several studies have documented the role of chemosensory cues in intraspecific communication (Léna and de Fraipont 1998, Aragon et al. 2001, 2006a), and especially in individual recognition (Aragon et al. 2001, Léna and de Fraipont 1998). The presence and relative concentration of pheromonal components from the pre-cloacal and femoral gland secretions vary consistently among individuals (Alberts 1990, 1992), and convey information on individual identity that may be used in social interactions (Lopez et al. 2003, 2006). Such chemosensory cues could be used, alone or in complement of the colour signal, to assess the competitive ability and behavioural strategy of conspecifics and to adjust one's behaviour in consequence.

To test for the role of ventral colour as a direct signal in social interactions, we studied the behaviour of females facing another female whose ventral colour was visible or hidden, during laboratory staged encounters. We also offered females the choice between night shelters bearing the scent marks of other females of different ventral colours. We found that ventral colour was used directly in social encounters, but it could be reinforced by other cues. Females of different colour also reacted differently to the experimental treatment, which suggests that the plasticity of social behaviour could be colour-dependent.

Methods

The species

Lacerta vivipara is a small (adult snout-vent length from 50 to 70 mm), live bearing lacertid lizard, which is found throughout Europe and Asia. The four populations we studied are located on Mont Lozère (in southern France, altitude 1455 m). In these populations, males emerge from hibernation in mid-April, followed by yearlings, and females in mid-May. Mating occurs at female emergence, gestation lasts for two months, and parturition starts in July and lasts for two to three weeks. Females lay a clutch of, on average, five soft-shelled eggs (range 1-12). Offspring hatch within two hours after laying and are immediately independent of their mother. A more detailed description of life history can be found in Clobert et al. (1994). In our populations, adult females display a ventral coloration varying from pale yellow to bright orange, whereas adult males are almost always orange. Juveniles start by being melanic, and slowly turn to a pale green ventral coloration when yearlings. Stability of ventral colour arises with sexual maturity (around two years).

Data set

240 females were captured on the different sites in June 2006 and brought to the laboratory. At each capture, females were measured (snout vent-length or SVL) and weighed. Ventral colouration was assessed visually by comparison to a colour reference. Female ventral colour fell into three categories: pale yellow, bright orange or mixed colouration (mixture of yellow and orange). This classification was proved to reflect differences in colour spectrum, discrete alternative reproductive strategies (Vercken et al. 2007) and behavioural patterns (Vercken and Clobert submitted). Females were housed in plastic terraria with damp soil, a shelter and water *ad libitum*. They were exposed to natural daylight and heated by electric bulbs from 9h to 12h and from 14h to 17h. Females were kept in the laboratory until

parturition. They were involved in the shelter choice experiment the night after parturition. They encountered other females either the day after parturition or the next day, or both. After all experiments were conducted, females were fed and released with their offspring at the female's capture point.

Choice of night shelter

97 females participated to this experiment. A female (focal female) was introduced in a plastic terrarium (25 x 15 x 15 cm) containing two night shelters that had been used by unfamiliar females of different ventral colours until their parturition (at least for 2 weeks). Those females (referred as owner females) had laid the same day as the focal female so that the scents on the shelters were fresh. The focal female was introduced at 17h, and allowed to explore the terrarium during one hour with a light on. Then the light was turned off, and the position of the female (in or out, and in what shelter) was assessed at 22h.

Laboratory staged encounters

204 females participated to this experiment. Trials were conducted during the heating hours in order to match the natural activity pattern of the species. One female (focal female) encountered successively two females (opponents) on two consecutive days. The opponent females had the same ventral colour, which could be different from the focal female colour. In one encounter, the belly of the opponent was covered with green paint (Snazaroo Face Paint, Grass Green 444) so that the original ventral colour was not visible anymore. In the second encounter, the belly of the opponent was slightly stained with diluted white paint (Snazaroo Face Paint, White 000) so that the original ventral colour was still visible.

The focal female was introduced in a plastic terrarium (25 x 15 x 15 cm) containing a small heating wire (allowing basking for one female only) and left for 10 minutes, so that it could explore the terrarium and find the heating source. Then the opponent was introduced and the behaviour of both females was monitored for 15 minutes. Individuals of this species displayed two sets of behaviour, one related to their activity in the terrarium (walking, scratching the terrarium walls, basking on the heating wire, de Fraipont et al. 2000, Aragon et al. 2006b), and the other related to the presence of another individual in the terrarium (bite attempts, contact avoidance, search for physical contact without aggression). Females were considered searching for physical contact when they moved directly in direction of the other female but without showing any sign of aggression (open mouth, squirming tail, exaggerated walking movement, chase, or combination of such behaviours, Aragon et al. 2006b). When the female walked all around the terrarium and finally bumped on the other female, it was not considered as a deliberate attempt for physical contact. In the same way, contact avoidance was described when the female reacted to a movement of the other female in its direction by moving away.

The two females were always unfamiliar, either from different populations, or with non-overlapping home ranges in the same population. This kind of experimental design has been used successfully before with this species (de Fraipont et al. 2000, Belliure et al. 2004, Aragon et al. 2006b, Cote and Clobert 2007) and ventral colour was shown to affect the outcome of female encounters (Vercken and Clobert submitted).

Statistical Analysis

The focal females entered a night shelter in only 57% of trials. In 98% of trials, the focal female was found next to a shelter, and away from the other. We analysed the proportion of shelters chosen (either really entered by the focal female or where the female was found next to), and the proportion of shelters rejected depending on the colour of the focal female and the colour of the female that had used the shelter before (chi-square tests, FREQ procedure, SAS Institute).

For the second experiment, we analysed for each encounter only the behaviour of the focal female, whereas the behaviour of the opponent female was disregarded because it could not be considered as independent. As the focal female was used in two trials, we used mixed models that included a random female effect. Continuous variables (time spent walking, scratching or basking) were analysed using mixed models (MIXED procedure, SAS Institute), whereas variables that followed a Poisson distribution (number of interactions) were analysed using mixed log-linear regressions analysis (GLIMMIX procedure, SAS Institute). We tested the effects of focal female colour, opponent colour, painting treatment, focal female SVL, and difference in SVL between females. Estimations and test statistics were calculated with a restricted maximum likelihood approach. F-tests were used to assess significance of fixed effects. Random female effects always accounted for a significant part of variance (all $p<0.0005$), and thus were always included in models.

In the above analyses, type III sum of squares was used in all cases. We started with a general model including all the potential effects and their interactions (up to three-ways interactions). We then dropped the non-significant effects (backward selection), starting with the most complex interaction terms. Only the results of the final model are reported.

Colour effects were interpreted by comparing alternately the three different colour pairs. In this case, we used a Bonferroni correction to assess significance of effects (the significance threshold for the critic probability being lowered to 0.017).

Results

Choice of night shelter

Focal female colour had no effect on the probability of entering a shelter (χ^2_2=1.33, p=0.51, n=97). In addition, there was no effect of focal female colour or owner female colour on the probability of choosing a night shelter (χ^2_4=2.89, p=0.58, n=55), or on the probability of rejecting a shelter (χ^2_4=4.63, p=0.33, n=97). We did not find either any effect of focal female colour or owner female colour on the probability of choosing a night shelter when including all the trials where focal females had been found next to (but not necessarily inside) a shelter (χ^2_4=2.12, p=0.71, n=95).

Laboratory staged encounters

Time spent scratching the terrarium walls, time spent basking on the heating wire and number of contact avoidance never responded to females' colours (alone or in interaction) or to painting treatment (all p>0.15). However, both colour effects and painting treatment effects were found, alone or in interaction, in the analysis of the three other behavioural variables: time spent walking, number of bite attempts, number of searches for physical contacts. The visibility of the ventral colour of the opponent female thus affects both the individual and social behaviour of the focal female in the variables that are sensitive to colour effects.

Time spent walking depended on female SVL ($F_{1,65}$=8.84, p=0.004), opponent female's colour ($F_{2,65}$=4.21, p=0.015), and the interaction between focal female's colour and painting treatment ($F_{2,65}$=3.5, p=0.036). Orange females tended to increase their activity when facing an opponent whose colour was hidden (Figure 1), whereas the opposite trend was found for yellow and mixed females (difference between yellow and mixed females $F_{1,46}$=1.17, p=0.28; between yellow and orange females $F_{1,44}$=3.26, p=0.08; between orange and mixed females $F_{1,37}$=5.75 p=0.022).

Number of bite attempts depended on opponent female’s colour ($F_{2,65}$=4.85, p=0.01), and painting treatment ($F_{1,65}$=7.14, p=0.0095). Focal females were more aggressive towards orange opponents (mean number of bite attempts: 0.74) than towards yellow (0.30) or mixed opponents (0.15). Focal females tended to bite more often their opponent when they could see her colour (mean number of bite attempts when the opponent colour was visible: 0.48; mean number of bite attempts when the opponent colour was hidden: 0.25).

Number of searches for physical contact were affected by the interaction between focal female’s colour, opponent female’s colour, and painting treatment ($F_{4,56}$=2.48, p=0.054). The responses of yellow females are opposite in the two painting treatments (Figure 2): yellow females are more attracted towards mixed and orange opponents when their colour is visible, and more attracted to yellow opponents when their colour is hidden. On the other hand, the responses of mixed and orange females, although modified in intensity, are similar between treatments: mixed females are less attracted to mixed opponents than to yellow or orange opponents, whereas orange females are less attracted to yellow opponents than to mixed or orange opponents (difference between yellow and mixed females $F_{2.40}$=4.52, p=0.017; between yellow and orange females $F_{2,38}$=4.34, p=0.020; between mixed and orange females $F_{2.31}$=0.01, p=0.99).

Discussion

Repeatability of the behavioural assays

In this experiment, we found significant effects of focal female colour or opponent female colour, or both, on several behavioural variables. In a previous study, some of these variables were also found to depend on the colour of the females interacting, although the effects were not always similar to what we found in this experiment (Vercken and Clobert submitted). Indeed, if we pool the results of the two experiments (laboratory staged encounters performed in 2005, and encounters where the colour of the opponent was visible performed in 2006), we obtain repeatable patterns for the variables in common, yet often modulated by an annual effect. For scratching time, the interaction between both females' colours was significant alone ($p=0.028$ and $p=0.039$), and in interaction with year ($p=0.029$ and $p=0.009$). For the number of biting attempts, the effect of the colour of the opponent was significant alone ($p<0.0001$) and in interaction with year ($p<0.0001$), whereas the effect of the interaction between both females' colours was significant only in interaction with year ($p=0.002$). Finally, the number of contact avoidance was affected by the interaction between both females' colours, but only in interaction with year ($p=0.013$).

These results mean that, although some general behavioural trends appear conservative, a large part of individual behaviour is temporally variable. Indeed, annual effects have been found recurrently to affect individual behaviour in this species (natal dispersal, Massot and Clobert 2000). In addition, the local frequencies of yellow and orange females had been experimentally modified (increased or decreased) between the two experiments in the populations where the females came from. Therefore, the social environment experienced by the females prior to the laboratory encounters was different in the two years, and is likely to have influenced female behaviour when facing opponents of different colours. However, this experiment confirms the role of ventral colour in social interactions, as several behavioural variables respond either to the colour of the focal female, or the colour of the opponent, or both.

Effect of the female scent marks

Females did not select night shelters on the basis of colour-related chemical scents. This might mean that either females do not use chemical signals to identify other females' colour when they are not present, or that our experimental setting did not allow to highlight such a behaviour. For instance, females might have assessed that the terrarium was empty and thus that they were not likely to meet other females, or females do not avoid females of a certain colour specifically when it comes to choosing a shelter in an unfamiliar environment. At this stage however, we do not have enough evidence to draw any clear conclusion from this experiment.

Effect of the painting treatment

In all variables that responded to the colour of at least one of the females, we found an effect of the painting treatment. This means that the focal female was influenced by the colour signal of her opponent, and when this signal was not available, her behaviour was modified. However, if the behaviour of the focal female was strictly determined by the colour signal she perceives, we would expect to find a significant effect of the opponent female colour in the group where it was visible, and no effect in the group where it was hidden. Such opposed effects would generate an interaction between the painting treatment and the colour of the opponent. This is not what we found. Indeed, we found such an interaction in one case (for the number of searches for physical contact), but for the other variables (time spent walking and number of bite attempts), the treatment effect was significant either alone (number of bite attempts), or in interaction with the colour of the focal female (time spent walking). This means that the painting treatment, by hiding ventral colour, most probably does not totally suppress the social signal displayed by the opponent female, but only modifies it.

Are there multiple signals?

A first explanation to these results would be that focal females perceive another signal correlated with ventral colour, and thus have partial information concerning their opponent's social strategy. Females of different colour might have different chemical signatures, which would allow other females to identify potential competitors even in their absence. Alternatively, the behaviour of the opponent females might have provided information about their social strategy to the focal females. Indeed, in previous study, we showed that female behaviour depended on her ventral colour (Vercken and Clobert submitted), and as the colour of the focal female was visible, the behaviour of the opponent female was likely to be characteristic of her own colour-related strategy. In any case, whatever the nature of the other signal, it was not consistent with the colour signal available to the focal female in the group where the colour of the opponent was hidden. This could have altered the behaviour of focal females, sufficiently to induce a treatment effect, but not enough to induce an interaction between the treatment and the colour of the opponent female.

Such multiple signals, though correlated, are not strictly redundant because female behaviour is significantly affected by the visibility of the colour signal. Ventral colour is likely to be genetically determined, and is stable throughout an individual's life (Vercken et al. 2007), although some components of colour seem to be temporally variable and subject to environmental effects (Meylan et al. 2007, Vercken et al. in prep1, J.-F. Le Galliard, pers. com.). Therefore, it is possible that ventral colour do not reflect punctual variations in an individual's state (health, age, sexual receptivity, motivational state…), and other cues might be used by conspecifics to acquire more precise information about the actual general state of an individual (Zucker 1994, Lopez and Martin 2001, Hews and Bernard 2001). Indeed, ventral colour has been found to reflect differences in female social behaviour towards unfamiliar individuals, most probably related to differences in competitive ability and social dominance (Vercken and Clobert submitted). However, a female's motivational and physiological state is likely to strongly influence the outcome of agonistic interactions. Therefore, the social dominance between two females is expected to result from a balance between their respective competitive strategies (as indicated by their ventral colour), their motivation (as indicated by their behaviour), and their physiological state (a lower competitor being able to compensate for it with a good general condition that may be indicated by chemosensory cues). In addition, chemosensory cues have been shown to be implied in individual recognition and kin recognition in this species (Léna et al. 1998), and thus may modulate the behavioural strategies depending on female colour, familiarity and relatedness. Studies to come should focus on the characterisation of colour-specific chemical profiles (analyses of faeces and secretions from the femoral glands) in order to discriminate the different components, fixed and variable, that describe female phenotype.

Plasticity of social behaviour

In our experiment, opponent females were painted green in one of the treatment groups, i.e. focal females had to face a new signal. Indeed, the number of biting attempts was lower when the colour of the opponent was hidden with green paint, which might indicate that focal females did not know what the 'new strategy' was. However, the ability of females to adapt to a new signal (i.e., the plasticity of their social behaviour) might also depend on their own ventral colour. In this experiment, the time spent walking by orange and mixed females was affected by the painting treatment, whereas it was not the case for yellow females. In addition, the number of searches for physical contacts for mixed and orange females depended on the opponent female colour in a similar way whatever the painting treatment, whereas yellow females displayed different responses to the colour of their opponent in the two painting treatments. Mixed and orange females might thus be more sensitive to other cues (chemical or behavioural) that allow them to assess correctly their opponent's strategy, and thus to be more open to behavioural plasticity. On the other hand, in previous studies, yellow females appeared less plastic in their offspring dispersal behaviour (Vercken et al. submitted, Vercken et al. in prep2), and seem also to be less plastic in their social behaviour. If the different colour morphs play distinct social strategies, they should adjust differently their behaviour depending on the colour of their opponent, thus they are expected to differ in the plasticity of their social behaviour.

If yellow females are indeed higher competitors and thus socially dominant (Vercken and Clobert submitted), they might not need to adjust their behaviour in function of other females and always play a dominant/aggressive strategy. On the other hand, the other strategies (mixed and orange) might benefit from adjusting their behaviour to their opponent's strategy and physiological (or motivational) state in order to achieve a dominant status when possible, and to avoid the costs of agonistic interactions when facing a higher competitor. Behavioural plasticity in response to the social environment might thus be a key element in the maintenance of alternative female strategies in this species, by affecting the fitness pay-offs of colour-specific social encounters.

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REFERENCES

Alberts AC. 1990. Chemical properties of femoral gland secretions in the desert iguana *Dipsosaurus dorsalis*. Journal of Chemical Ecology 16: 13-25.

Alberts AC. 1992. Pheromone self-recognition in desert iguanas. Copeia 1992:229-232.

Amundsen T, Forsgren E, Hansen LTT. 1997. On the function of female ornaments: male bluethroats prefer colorful females. Proceedings of the Royal Society Biological Science Series B 264: 1579-1586.

Amundsen T, Forsgren E. 2001. Male mate choice selects for female coloration in a fish. Proceedings of the National Academy of Science USA 98:13155-13160.

Andersson M. 1994. Sexual Selection. Princeton University Press, Princeton, 624 p.

Aragon P, Lopez P, Martin J. 2001. Chemosensory discrimination of familiar and unfamiliar conspecifics by lizards : implications of field spatial relationships between males. Behavioral Ecology and Sociobiology 50: 128-133.

Aragon P, Massot M, Gasparini J, Clobert J. 2006a. Socially acquired information through chemical cues in the common lizard, *Lacerta vivipara*. Animal Behaviour 72: 965-974.

Aragon P, Clobert J, Massot M. 2006b. Individual dispersal status influences space use of conspecific residents in the common lizard, *Lacerta vivipara*. Behavioral Ecology and Sociobiology 60: 430-438.

Beeching SC, Gross SH, Bretz HS, Hariatis E. 1998. Sexual dichromatism in convict cichlids: the ethological significance of female ventral coloration. Animal Behaviour 56: 1021-1026.

Belliure J, Meylan S, Clobert J. 2004. Prenatal and postnatal effects of corticosterone on behaviour in juveniles of the common lizard *Lacerta vivipara*. Journal of Experimental Zoology 301A: 401-410.

Berglund A, Rosenqvist G. 2001. Male pipefish prefer dominant over attractive females. Behavioral Ecology 12: 402-406.

Bleiweiss R. 1997. Covariation of sexual dichromatism and plumage colours in lekking and non-lekking birds: a comparative analysis. Evolutionary Ecology 11: 217-235.

Burns KJ. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus mal plumage. Evolution 52: 1219-1224.

Chapuisat M. 2004. Evolution : social selection for eccentricity. Current Biology 14: R1003-R1004.

Clobert J, Massot M, Lecomte J, Sorci G, de Fraipont M, Barbault R. 1994. Determinants of dispersal behavior: the common lizard as a case study. In: Lizard Ecology: historical and experimental perspectives (LJ Vitt, ER Pianka, eds), pp 183-206. Princeton University Press, Princeton.

Cote J, Clobert J. 2007. Social personalities influence natal dispersal in a lizard. Proceedings of the Royal Society Biological Sciences Series B 274: 383-390.

Cooper WE Jr, Burns N. 1987. Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. Animal Behaviour 35: 526-532.

Darwin C. 1871. The Descent of Man, and Selection in Relation to Sex. John Murray, London, 2 vol.

de Fraipont M, Clobert J, John-Alder H, Melan S. 2000. Pre-natal stress increases offspring philopatry. Journal of Animal Ecology 69: 404-413.

Hews DK, Benard MF. 2001. Negative association between conspicuous visula display and chemosensory behaviour in two phrynosomatid lizards. Ethology 107: 839-850.

Irwin RE. 1994. The evolution of plumage dichromatism in the New World Blackbirds: social selection on female brightness? The American Naturalist 144: 890-907.

Johnsen TS, Hengeveld JD, Blank JL, Yasukawa K, Nolan V. 1996. Epaulet brightness and condition in female red-winged blackbirds. Auk 113: 356-362.

Johnson K. 1988. Sexual selection in pinion jays II: male choice and female-female competition. Animal Behaviour 36: 1048-1053.

Jones IL, Hunter FM. 1993. Mutual sexual selection in a monogamous seabird. Nature 362: 238-239.

Lande R.1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34: 292-305.

LeBas NR, Marshall NJ. 2000. The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. Proceedings of the Royal Society Biological Science Series B 267: 445-452.

Léna JP, de Fraipont M. 1998. Kin recognition in the common lizard. Behavioral Ecology and Sociobiology 42: 341-347.

Lopez P, Aragon P, Martin J. 1998. Iberian rock lizards (*Lacerta monticola cyreni*) assess conspecific information using composite signals from faecal pellets. Ethology 104: 809-820.

Lopez P, Martin J. 2001. Pheromonal recognition of females takes precedence over the chromatic cue in male Iberian wall lizards, *Podarcis hispanica*. Ethology 107: 901-912.

Lopez P, Aragon P, Martin J. 2003. Responses of female lizards, *Lacerta monticola*, to males' chemical cues reflecting their mating preference for older males. Behavioral Ecology and Sociobiology 55: 73-79.

Lopez P, Amo L, Martin J. 2006. Reliable signaling by chemical cues of male traits and health state in male lizards, Lacerta monticola. Journal of Chemical Ecology 32: 473-488.

Martin J, Forsman A. 1999. Social costs and development of nuptial coloration in male *Psammodromus algirus* lizards: an experiment. Behavioral Ecology 10: 396-400.

Martin J, Lopez P. 2000. Chemoreception, symmetry and mate choice in lizards. Proceedings of the Royal Society Biological Science Series B 267: 1265-1269.

Massot M, Clobert J. 2000. Processes at the origin of similarities in dispersal behaviour among siblings. Journal of Evolutionary Biology 13: 707-719.

Meylan S, Clobert J, Sinervo B. 2007. Adaptive significance of maternal induced density-dependent phenotype. Oikos (in press).

Olendorf R, Rodd FH, Punzalan D, Houde AE, Hurt C, Reznick DN, Hughes KA. 2006. Frequency-dependent survival in natural guppy populations. Nature 441: 633-636.

Olsson M, Madsen T. 1995. Female choice on male quantitative traits in lizards – why is it so rare? Behavioral Ecology and Sociobiology 36: 179-184.

Ord TJ, Stuart-Fox D. 2006. Ornament evolution in dragon lizards: multiple gains and widespread losses reveal a complex history of evolutionary change. Journal of Evolutionary Biology 19: 797-808.

Oxford GS, Gillespie RG. 1998. Evolution and ecology of spider coloration. Annual Review of Entomology 43: 619-643.

Roulin A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. Biological Review of the Cambridge Philosophical Society 79: 815-848.

Rowland WJ, Baube CL, Horan TT. 1991. Signalling of sexual receptivity by pigmentation pattern in female sticklebacks. Animal Behaviour 42: 243-249.

SAS. 1992. SAS User's Guide: Statistics. SAS Institute, Cary.

Sinervo B, Svensson E, Comendant T. 2000. Density cycles and an offspring quality and quantity game driven by natural selection. Nature 406: 985-988.

Vercken E, Massot M, Sinervo B, Clobert J. 2007. Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. Journal of Evolutionary Biology 20: 221-232.

Vercken, E., M. Massot, B. Sinervo and J. Clobert. Female colour morphs in the common lizard display alternative offspring dispersal strategies with respect to environmental cues. Submitted.

Vercken E, Clobert J. Female colour polymorphism and social dominance in the common lizard (*Lacerta vivipara*). Submitted.

Vercken E, Sinervo B, Clobert J. Female reproductive success is sensitive to the social environment in the common lizard (*Lacerta vivipara*). In preparation.

Vercken E, Sinervo B, Clobert J. Social environment-dependent dispersal strategies in juvenile common lizards (*Lacerta vivipara*). In preparation.

Weiss SL. 2006. Female-specific color is a signal of quality in the striped plateau lizard (*Sceloporus virgatus*). Behavioral Ecology 17: 726-732.

West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. Quarterly Review of Biology 58: 155-183.

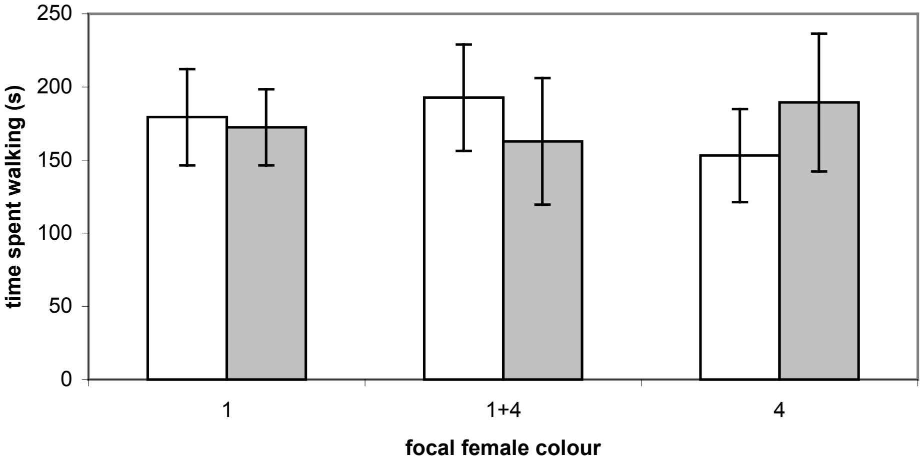
Zucker N. 1994. A dual status-signalling system: a matter of redundancy or differing roles? Animal Behaviour 47: 15-22.

Figure Legends

Figure 1 : Time spent walking in function of the colour of the focal female when the colour of the opponent female was visible (white bars) or hidden (gray bars). Error bars are 95 % confidence intervals (+/- 2 s.e.).

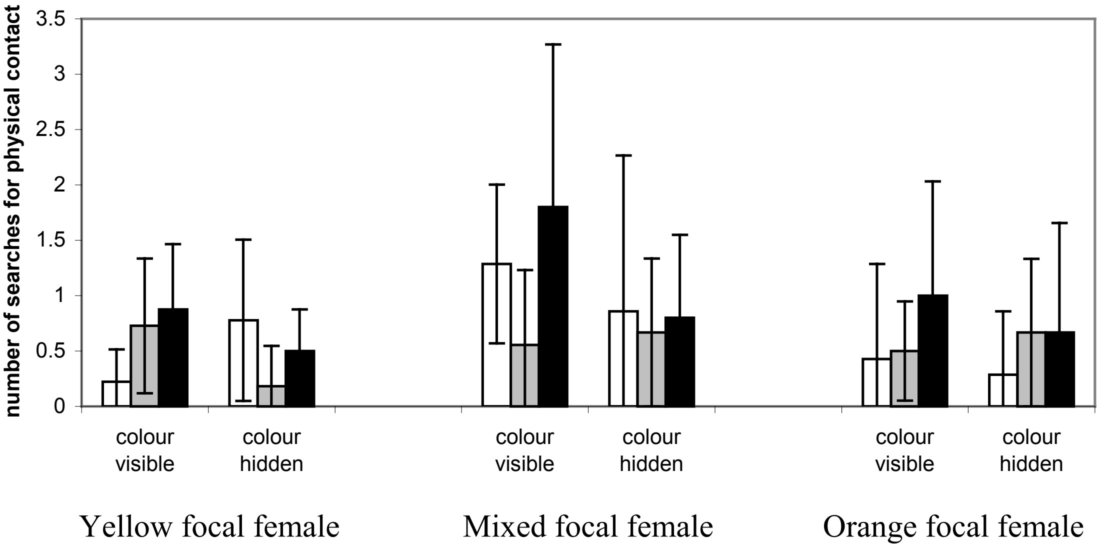
Figure 2 : Number of searches for physical contacts displayed by the focal females of different ventral colours for the two painting treatment in function of the colour of the opponent female (yellow, white bars; mixed, gray bars; orange, black bars). Error bars are 95 % confidence intervals (+/- 2 s.e.).

Figure 1



250
200
150
100
50
0
time spent walking (s)
1
1+4
4
focal female colour

Figure 2


number of searches for physical contact
3.5
3
2.5
2
1.5
1
0.5
0
colour visible
colour hidden
colour visible
colour hidden
colour visible
colour hidden
Yellow focal female
Mixed focal female
Orange focal female

ANNNEXE V: Female reproductive success is sensitive to the social environment in the common lizard (*Lacerta vivipara*)

Article en préparation

Female reproductive success is sensitive to the social environment in the common lizard (*Lacerta vivipara*)

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Abstract

Colour polymorphism often plays a role in intra-sexual competition by signalling alternative reproductive strategies. Such polymorphism has to be maintained in natural populations: overdominance, disruptive selection, and negative frequency-dependent selection are all evolutionary processes that can potentially select for genetic diversity. Although frequency-dependent selection has become a major concept in evolutionary biology, its empirical evidence remain scarce, and other mechanisms might have been underestimated. Therefore, experimental studies involving a manipulation of local colour morphs frequencies and studying its consequences on morphs fitness are needed to understand better how colour polymorphisms are maintained in natural populations. In the common lizard, females display three classes of ventral colouration (yellow, orange and mixed) that are associated with alternative strategies in reproduction, dispersal and social behaviour. Frequency-dependent selection appears as a potential mechanism for the maintenance of this polymorphism in populations, but other mechanisms such as differential responses to the abiotic environment or overdominance could also be implicated. We analysed the response of female reproductive parameters to an experimental manipulation of colour morphs frequencies in natural populations. We found that juvenile phenotype at birth was affected by the local frequencies of colour morphs, which indicates that female fitness is sensitive to the social environment. In addition, clutch hatching success was affected by the interaction between female colour and the frequencies of colour morphs in the population. Mixed females seem to benefit from overdominance effects modulated by the social environment, which could be related to the existence of alternative social strategies.

Keywords: *female colour polymorphism, social environment, alternative strategies, condition-dependent overdominance.*

Introduction

Colour polymorphisms within populations are widespread in the animal kingdom, and can be found whenever there is some variability in the abiotic or biotic environment (Galeotti et al. 2003, Munday 2003, Roulin et al. 2004). Recently, there has been a renewed interest in the study of colour polymorphism mainly because colour signals have been found to be of major importance in inter- and intra-sexual selection (signals of alternative reproductive and/or behavioural strategies, in reptiles Thompson and Moore 1991; in birds Roulin 2004; in insects Sirot et al. 2003; in fishes Gross 1991). Indeed, colour signals are often correlated with morphological, physiological or behavioural traits that constitute phenotypic syndromes characterising alternative strategies. For instance, in the side-blotched lizard (*Uta stansburiana*), males display three colour morphs (genetically determined) signalling three different reproductive strategies: sneaker, territorial and cooperative (Sinervo and Lively 1996). In females damselflies (*Ischnura elegans*), three female colour morphs have been identified which differ in their reproductive strategies (andromorph versus gynomorph) and probably in their dispersal pattern (Svensson and Abbott 2005).

Evolutionary conditions favouring the maintenance of polymorphisms have been extensively discussed (reviewed in Charlesworth 1987, Barton and Turelli 1989). Overdominance or selective advantage to heterozygous individuals (Wallace 1968, Gillespie and Langley 1974), disruptive selection or ‘niche variation hypothesis’ (Van Valen 1965, Hedrick 1986, Galeotti et al. 2003), and negative frequency-dependent selection by preys, predators or mates, i.e. ‘rare phenotype advantage’ (Paulson 1973, Allen 1988, Endler 1988, O’Donald and Majerus 1988, Partridge 1988) are among the main mechanisms able to maintain high levels of genetic variation within populations.

Up to now, the maintenance of colour polymorphisms has been mainly explained by negative frequency-dependent selection (Jones et al. 1977, Thompson et al. 1993, Lank 1995, Hughes et al. 1999, Andres et al. 2002). Frequency-dependent selection has become a central concept in evolutionary biology (Lewontin 1974, Heino et al. 1998) and is often argued to explain phenotypic diversity within populations on a theoretical basis (Asmussen et al. 2004, Billiard et al. 2005, Schneider 2005). However, empirical evidence of frequency-dependent selection in natural populations remain scarce (in side-blotched lizards, Sinervo et al. 2000; in damselfies Van Gossum et al. 2001, Svensson et al. 2005; in guppies Olendorf et al. 2006), and that for several reasons.

First, a major difficulty in field studies arises from the fact that, to detect and quantify frequency-dependent selection, fitness correlates for the different morphs must be estimated across several populations with different local morphs frequencies (Svensson et al. 2005). However, if these populations differ in some ecological factors, it is possible that morphs frequencies vary among populations because of the existence of a ratio-cline (i.e., graded alternations in the frequency of the morphs in a polymorphic system, Galeotti et al. 2003). In that case, the variation in both morph frequency and fitness between populations would come from the geographical variation in one ecological factor, and thus would not be directly related as in the case of frequency-dependent selection. To avoid this confusion, the populations where the fitness of the different morphs is estimated should be close enough geographically so that major ecological factors do not vary significantly among populations.

Second, the importance of other mechanisms of polymorphism maintenance might have been overlooked. For instance, some studies have argued that niche variation was involved in the maintenance of some colour polymorphism, while mechanisms such as over- or under-dominance have rarely been investigated in this framework. At least in one case, frequency dependent selection was however suggested to interact with other selection processes such as overdominance (in the side-blotched lizard, heterozygotes are favoured in several social contexts because they can express different alleles, Sinervo and Zamudio 2001).

Assessing the respective influence of the different mechanisms of polymorphism maintenance requires to compare the fitness response of the different morphs in several colour environments (characterised by local colour morph frequencies). Fitness responses are however difficult to analyse through correlative approaches because of many confounding factors such as morph-dependent sensitivity to the abiotic environment. An additional difficulty is that the expression of colour often includes a part of environmental determination (some degree of plasticity), which adds to other potential confounding factors and thus limits the power of the analyses of the respective importance of the different mechanisms of polymorphism maintenance. Up to now, very few studies (for instance, Sinervo et al. 2001) have experimentally manipulated colour morph frequency and examined its consequences on the subsequent fitness of each morph. However, such experiments are deeply needed to go further in the study of the mechanisms by which colour polymorphisms and the associated alternative strategies are maintained in natural populations.

In the common lizard *Lacerta vivipara*, discrete female colour variants coexist in several neighbouring populations. These females differ in ventral colour (yellow, orange, or a mixed colouration) and display complex alternative strategies in reproduction (Vercken et al. 2007), dispersal (Vercken et al. submitted) and behaviour (Vercken and Clobert submitted). Even if the mechanisms allowing for the maintenance of this polymorphism remain obscure, frequency-dependent selection is expected to play a role. Indeed, female reproductive success was affected by the temporal variation in the relative frequency of one colour morph in a natural population (Vercken et al. 2007). Moreover, social and competitive behaviours were found to correlate with the ventral colours of both individuals interacting in laboratory-staged experiments (Vercken and Clobert submitted). Such interactions between individual colour and the colour of the social environment could probably generate frequency-dependent effects on female reproductive success. However, other mechanisms could be implicated such as morph-dependent responses to the physical environment (Vercken et al. submitted) or potential overdominance (Vercken et al. 2007).

In order to test these hypotheses, we experimentally increased the relative frequency of two female colour morphs in different populations during two years, and we analysed the response of female reproduction to these experimental treatments. If negative frequency dependent selection is the main mechanism for polymorphism maintenance, we expect that the fitness of each colour morph will be negatively affected by an increase of its own frequency in the population, and positively affected by a decrease of its own frequency. Alternatively, if niche differentiation is the principal mechanism, we expect that only the morph with an increased frequency will suffer from fitness loss because a fraction of this morph will end up in unsuitable habitat, the other morphs fitness being unchanged Finally, if over or under-dominance is involved, we should observe a non linear response of the heterozygous phenotypes in the different colour environments. In addition, to estimate the importance of condition dependence in the expression of ventral colour, we analysed the variation in individual colour in response to the experimental change in colour morph frequencies.

Methods

The Species

Lacerta vivipara is a small (adult snout-vent length from 50 to 70 mm) live bearing lacertid lizard, found throughout Europe and Asia. We studied four populations located on Mont Lozère (Southern France, altitude 1420 m). In these populations, adult males emerge from hibernation in mid-April, followed by yearlings, and adult females in mid-May. Mating occurs at female emergence, and gestation lasts for two months. Parturition starts in mid-July and lasts for two or three weeks. Females lay an average clutch of five soft-shelled eggs (range 1-12). Offspring hatch within one or two hours after laying and are immediately independent of their mother. The activity season ends in late September and juveniles are the last to enter hibernation. A more detailed description of life history can be found in Massot et al. (1992). In this population, adult females display a ventral colouration varying from pale yellow to bright orange, whereas adult males are almost always orange. Juveniles start by being melanic, and slowly turn to a pale green ventral colouration when yearlings. Stability of ventral colour arises with sexual maturity (usually at two years in the Mont Lozère population).

Data Set

From 2004 to 2006, 773 females were temporarily removed from the four populations. Each year, from the end of June, females were captured and kept in the laboratory until parturition. At capture, females were measured (snout-vent length or SVL) and weighted. Body condition was calculated as the residual from the relationship between body mass and SVL. Females were housed in plastic terraria with damp soil, a shelter and water *ad libitum*. They were exposed to natural daylight and were heated 6 h per day with an electric bulb. Female ventral colouration was estimated visually using a colour reference, and fell into three distinct classes: pale yellow, bright orange and mixed colouration (mixture of yellow and orange), which have been shown to reflect spectrophotometrical differences (Vercken et al. 2007). Female ventral colour was also measured with a spectrophotometer (Ocean Optics USB2000). Data analysis was handled with the aid of the Color Project 1 software, developed by Jean-Marc Rossi (Laboratoire d'Ecologie, Université Pierre et Marie Curie, Paris). The software allowed us to calculate several parameters quantifying colour, and in particular the hue and the chroma, which have been found to be correlated with the visual classification of ventral colour (Vercken et al. 2007). At birth, offspring were individually marked by toe-clipping and sexed by counting ventral scales (Lecomte et al. 1992). Asymmetry was estimated by the absolute value of the difference between the number of left and right ventral scales. Offspring and their mother were measured and weighed. They were then released in the field either in their population of origin or in another population (see below).

Frequency experiment

The four studied populations differed in female density, and in female colour variants frequencies. The respective values of density (estimated from the recapture rate by the Lincoln-Petersen index), orange female frequency and yellow female frequency in the different populations are given in Table 1. We distinguished two "high-orange" populations (A and B) from two "high-yellow" populations (C and D). We increased the local frequency of yellow females in the "high-orange" populations, and the local frequency of orange females in the "high-yellow" populations with reciprocal transplants (orange females from population A were exchanged with yellow females from population D, and orange females from population B were exchanged with yellow females form population C). In 2004, 251 females were captured, and released with their offspring after parturition, either in their population of origin (mixed females, yellow females from "high-orange" populations, orange females from “high-yellow” populations) or transplanted to another population (yellow females from “high-yellow” populations, orange females from “high-orange” populations). In their new population, immigrant females were released at the capture point of a native transplanted female in order not to modify female density at the local scale. Total population densities were not modified, therefore the frequencies of mixed females were not modified either. The same manipulation was performed in 2005 (282 captured females, see Table 1 for the number of transplanted females in 2004 and 2005). In 2006, the 240 females captured were all released with their offspring at their own capture point. In 2004, the local frequencies experienced by females during gestation were not modified, and this year is thus considered as a “control” year. In 2005 and 2006, the females from populations A and B experienced an “increased-yellow” treatment (Y+ treatment), whereas females from populations C and D experienced an “increased-orange” treatment (O+ treatment).

In a previous experiment of reciprocal transplants, the majority of transplanted females was found to remain around their release site (Massot et al. 1994). In our experiment, 24 out of 98 females released on their site of origin after parturition and 22 out of 102 transplanted females in 2004 were captured again in 2005. Thus there was no difference in apparent survival rate between resident and transplanted females. Most transplanted females (91%) were captured within 20 meters of their release site, and 36% within 10 meters. Therefore, we may assume that the reciprocal transplant experiment had persistent effects on the social structure of the populations, although preserving their spatial structure.

Statistical analyses

We tested the stability of female coloration using both visual classification and colour spectrum. 94 females were captured at least twice throughout the study. The stability of ventral colour class was estimated by a general linear model (GLM procedure, SAS Institute) testing for the effect of the ventral colour in the first capture occasion on the ventral colour in the second capture occasion, with ventral colours being additively scored as 0 = yellow, 1 = mixed and 2 = orange (following Sinervo et al. 2001). The stability of colour spectrum was estimated by paired t-tests (TTEST procedure, SAS Institute) comparing the measures of chroma and hue made on the first capture occasion with the measures made on the second capture occasion.

We analysed the response of female reproduction (clutch size, clutch hatching success, clutch sex-ratio, mean juvenile SVL, mean juvenile weight, mean juvenile body condition, mean juvenile asymmetry) to several factors: year, population, frequency treatment, maternal ventral colour and maternal SVL. We tested for all simple effects and for the following interactions: year by population, year by treatment, year by ventral colour, ventral colour by treatment, and year by ventral colour by treatment. A significant year effect or year by population effect would mean that the different populations have different mean reproductive parameters, or different annual effects. In that case, the treatment effects estimated over two population replicates could be distorted by significant differences between replicates. A significant year by treatment effect would mean that the frequency treatments have modified female reproduction in comparison with the control year, with different effects for the two treatments. A significant year by ventral colour by treatment effect would mean that the reproduction of the different colour morphs have been affected differently by the two frequency treatments.

We analysed continuous variables (clutch size and juvenile characteristics) with general linear models (GLM procedure, SAS Institute). For variables that constituted proportions (clutch hatching success and clutch sex-ratio), we used logistic-linear regression analyses (GENMOD procedure, SAS Institute). F-tests and log-likelihood ratio tests (χ^2

values) were used to assess significance of effects. Type III sum of squares was used in all cases.

We started with a general model including all the potential effects and the interactions mentioned above. We then dropped the non-significant effects (backward selection), starting with the most complex interaction terms. Only the results of the final model are reported. Colour effects were interpreted by comparing alternately the three different treatment or colour pairs. In that case, we used a Bonferroni correction to assess significance of effects (the significance threshold for the p-value being lowered to 0.017).

Results

The classification of ventral colour on a second capture occasion was highly dependent on the classification made on the first capture occasion ($F_{1,92}$=197.27, p<0.0001). Only 8 females were classified differently in different occasions, and the change always occurred between two nearby colour classes. The measure of hue made on the second capture occasion was not significantly different from the measure made on the first capture occasion (t=-1.39, p=0.17), but the two measures of chroma were significantly different (t=-4.15, p<0.0001).

Clutch size depended on population ($F_{3,719}$=8.07, p<0.0001), year ($F_{1,719}$=21.25, p<0.0001), and female SVL ($F_{1,719}$=268.89, p<0.0001), but it was not affected by frequency treatment (p=0.8).

Clutch hatching success did not depend on population (p=0.11), but it was affected by the interaction between year, ventral colour and frequency treatment (χ^2_2=22.51, p<0.0001). Mixed female had a higher clutch hatching success in O+ populations than in Y+ populations (year by treatment χ^2_1=26.77, p<0.0001, n=235), whereas it was not the case for orange females (χ^2_1=2.13, p=0.14, n=224, although the trend is similar) or for yellow females (χ^2_1=1.48, p=0.22, n=254, Figure 1).

Clutch sex-ratio did not respond to any of the factors tested in this study (all p>0.2).

Juvenile SVL did not depend on population (p=0.09), but it was affect by year ($F_{1,690}$=126.96, p<0.0001) and by female SVL ($F_{1,690}$=9.76, p=0.019). Juvenile SVL was higher in the last year of the experiment than in the first year, and positively correlated with mother's SVL.

Juvenile weight did not depend on population (p=0.07), but it was affected by year ($F_{1,688}$=25.57, p<0.0001), female SVL ($F_{1,688}$=20.62, p<0.0001) and by the interaction between year and frequency treatment ($F_{1,688}$=4.16, p=0.042). O+ treatment had a strong positive effect on juvenile weight in comparison with the control year ($F_{1,344}$=24.97, p<0.0001), whereas Y+ treatment had only a minor positive effect ($F_{1,343}$=4.89, p=0.028, Figure 2a).

Juvenile body condition did not depend on population (p=0.2), but it was affected by female SVL ($F_{1,688}$=14.84, p=0.0001) and by the interaction between year and frequency treatment ($F_{1,688}$=8.76, p=0.0032). Y+ treatment had a strong negative effect on juvenile weight in comparison with the control year ($F_{1,343}$=5.72, p=0.017), whereas O+ treatment had no effect ($F_{1,34}$=2.15, p=0.14, Figure 2b)

Juvenile asymmetry did not depend on population (p=0.34), but it was affected by year ($F_{1,685}$=11.72, p=0.0007) and the interaction of female colour and female SVL ($F_{2,685}$=6.48, p=0.0016). Juvenile asymmetry increased with female age for mixed females, whereas no such relationship was found for yellow or orange females (difference between yellow and mixed females $F_{1,468}$=12.03, p=0.0006; between orange and mixed females $F_{1,443}$=7.4, p=0.0068; between yellow and orange females $F_{1,458}$=0.68, p=0.41).

Discussion

We did not find any difference between populations in female reproduction, except in clutch size. Treatment effects on other variables can thus be interpreted safely as they do not include any confounding replicate effect. Clutch hatching success, juvenile weight and juvenile body condition were affected by local morphs frequencies. Social environment experienced by females in the beginning of gestation thus affects reproductive allocation and offspring development, and ultimately female fitness.

Stability of female coloration

In a previous study analysing 14 years of data (Vercken et al. 2007), we found that female colour was significantly stable over age and was heritable within female lineages. In addition, none of the environmental factors examined were found to influence either female colour stability or heritability. However, these results were demonstrated using only a visual classification of ventral colour (the spectrophotometrical measure being only available in the last year of the long term study). Although this classification was demonstrated to be correlated with the colour spectrum indeed (chroma and hue), some quantitative variation in spectrum variables may not have been detected. Therefore, even though the analyses of the stability and heritability of ventral colour strongly militate for a genetic control of colouration, it is likely that some components of the colour spectrum are nevertheless open to environmental influences. Indeed, in an earlier experiment, the intensity of coloration (brightness) was found to be affected by population density (Meylan et al. 2007). In addition, an experimental manipulation of female corticosterone plasma level induced a change in chroma and hue (J.-F. Le Galliard, pers. com.). However, these later modifications in the spectrum (as well as females' corticosterone level) were not found when the population density was modified, i.e. the social stress did not seem to induce variation in chroma and hue. In our experiment however, hue appeared stable through years but the measure of chroma was significantly different between two capture occasions. Yet, the visual classification of colour was not altered by these modifications. Therefore it seems that, as visual classification is based on both chroma and hue, individual variations in chroma only from one year to another do not affect significantly our global perception of individual colour. Thus the experimental manipulation of local morphs frequencies was not biased by an alteration of individual colour in response to the modification of the social environment.

Effects of female morph frequencies on reproductive parameters

Juvenile condition was significantly better in O+ populations than in Y+ populations, regardless of female ventral colour. We did not find a different response of orange and yellow females to the modification of orange and yellow female frequencies, i.e. orange and yellow females had the same fitness whatever their colour environment. This last result was not expected under the hypothesis of a negative frequency-dependence scenario where the fitness of orange and yellow female would differ with respect to their own frequencies. Populations where the proportion of yellow females is low thus seem to constitute a better reproductive environment for all colour morphs. Such a result is not compatible with the hypothesis of colour-based niche partitioning either, because orange female fitness is not negatively affected by an increase of its own frequency. At this stage however, we cannot totally discard these two mechanisms of colour polymorphism maintenance because such mechanisms could operate on components of fitness not examined here, or the colour morph classification used might not directly reflect the genetic determinism of the colour variation in this species.

Only mixed females displayed a different response to the variations in local morph frequency, with much higher clutch hatching success in O+ than in Y+ environments. If mixed colour females are heterozygous phenotypes between orange and yellow homozygous phenotypes, then the above results support the hypothesis of a colour environment-dependent overdominance which might in turn explain the maintenance of female colour polymorphism. If ventral colour is considered as a continuous character (because of the continuity of the colour spectrum), such an interpretation would nevertheless be correct if ventral colour was correlated with a threshold trait that determines discrete alternative strategies. Intermediate values of colour would thus be correlated with a strategy associated with colour-dependent fitness payoffs. Is such an overdominance mechanism plausible? Several elements strongly militate in its favour. First, while the colour spectrum of mixed females is intermediate between those of yellow and orange females, the ecological responses of mixed females are never intermediate (Vercken et al. 2007, Vercken et al. submitted). Second, the mean reproductive success of mixed-coloured females calculated over 14 years is superior to the other two colour types (Vercken et al. 2007). Third, orange and yellow females are similarly influenced by the natural variation of yellow female frequency (Vercken et al. 2007) as we found experimentally here (see above), while this is not the case for mixed-coloured females. In both cases, we found different fitness responses for the different colour morphs with respect to variation in colour morphs frequencies, this interaction being driven by the distinctive response of mixed coloured females. However, because density and relative mixed female frequency were not constant in our long term study as opposed to our experiment, the direction of the responses are hardly comparable. All these results therefore support the idea of a simple determinism of the genetic component of the ventral colour of females common lizard with an over or under-dominance effect of which direction and intensity are modulated by the colour environment.

Social stress, female reproductive success and alternative strategies

All colour morphs experienced negative effects on offspring body condition when in a population where the frequency of yellow females had been increased. Negative effects of yellow female frequency on female reproductive success have also been found in a long term population survey (Vercken et al. 2007). In this species, ventral coloration does not play any role in crypsis or thermoregulation (Vercken et al. 2007), and most probably arises through social selection (West Eberhard 1983). Actually, ventral coloration of females is likely to be implicated in intra-sexual communication, by signalling differences in competitive ability or social behaviour. Indeed, social and competitive interactions between females might cause such colour-dependent effects on female fitness and juvenile phenotype (Comendant et al. 2003, Van Gossum et al. 2005). In laboratory experiments, females of different ventral colours were found to differ in aggressiveness and competitive ability (Vercken and Clobert submitted). Yellow females are thought to be socially dominant, orange females to be submissive, and mixed females to play the role of social challengers. When a female of any colour experiences an increase in the frequency of her yellow neighbours she should suffer from increased social stress. On the contrary, a female of any colour surrounded by many orange neighbours should have higher fitness on average due to lower social stress. Whereas yellow and orange strategies are likely to have equal fitness payoffs in the different colour environments, if mixed-coloured females are heterozygotes, they may benefit from playing a condition-dependent behavioural strategy which can be described as a “bully” strategy: play a submissive strategy (orange) against higher competitors (yellow) with some costs, play a dominant strategy (yellow) against lower competitors (orange) with some benefits. Such a response could also be expected if ventral colour was a continuous character correlated with continuous behavioural differences. Mixed females would thus play an intermediate strategy of social dominance: these females would suffer from fitness costs when dominated by yellow neighbours, but they also would have high benefits when dominating orange neighbours. In both cases, mixed coloured females could thus increase more substantially their fitness than the other two morphs when shifting from a yellow to an orange prevailing environment. Female stress during gestation has been shown to strongly affect female reproduction and offspring phenotype in this species (de Fraipont et al. 2000, Meylan et al. 2004, Belliure et al. 2004), and thus is a potential mediator of such colour-dependent maternal effects. This scenario relies however of some untested hypotheses of which the implication in intra-sexual communication is not the least. Indeed, female ventral colour might also constitute some inter-sex communication and play a role in the assortative mating strategy which is recurrently found in this species (Richard et al 2005, Eizaguirre et al 2007). However, the presence of many heterozygote phenotypes and their potential overdominance effect militate against this possibility.

Conclusion

The present research suggests that ventral colour polymorphism in female common lizards is maintained through overdominance effects of which direction and intensity depend on the colour environment. Therefore, it can be viewed as a sort of interaction between over-dominance and frequency-dependent selection. To gain more generality, other fitness components should be examined (Widemo 1998) such as morph dependent survival (Olendorf et al. 2006), or morph-dependent offspring dispersal strategies (Sinervo and Clobert 2003), which may respond more directly to morph frequency or to other environmental factors. Condition-dependent colour development should also be better studied and understood in order to asses the importance of the different mechanisms of polymorphism maintenance.

Acknowledgements

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REFERENCES

Allen JA. 1988. Frequency-dependent selection by predators. Philosophical Transactions of the Royal Society B Biological Sciences 319: 485-503.

Andrés JA, Sanchez-Guillén RA, Cordero Rivera A. 2002. Evolution of female colour polymorphism in damselflies : testing the hypotheses. Animal Behaviour 63: 677-685.

Asmussen MA, Cartwright RA, Spencer HG. 2004. Frequency-dependent selection with dominance: a window onto the behavior of the mean fitness. Genetics 167: 499-512.

Barton NH, Turelli M. 1989. Evolutionary quantitative genetics: how little do we know. Annual Review of Genetics 23: 337-370.

Belliure J, Meylan S, Clobert J. 2004. Prenatal and postnatal effects of corticosterone on behaviour in juveniles of the common lizard *Lacerta vivipara*. Journal of Experimental Zoology 301A: 401-410.

Billiard S, Faurie C, Raymond M. 2005. Maintenance of handedness polymorphism in humans: a frequency-dependent selection model. Journal of Theoretical Biology 235: 85-93.

Charlesworth B. 1987. The heritability of fitness. In: Sexual Selection: Testing the Alternatives (JW Bradbury, MB Andersson, eds), pp 21-40. J. Wiley, Chichester.

Comendant T, Sinervo B, Svensson EI, Wingfield J. 2003. Social competition, Corticosterone and survival in female lizard morphs. Journal of Evolutionary Biology 16: 948-955.

de Fraipont M, Clobert J, John-Alder H, Meylan S. 2000. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. Journal of Animal Ecology 69: 404-413.

Eizaguirre C, Laloi D, Massot M, Richard M, Federici P, Clobert J. 2007. Condition-dependence of reproductive strategy and the benefits of polyandry in a viviparous lizard. Proceedings of the Royal Society Biological Sciences Series B 274: 425-430.

Endler JA. 1988. Frequency-dependent predation, crypsis and aposematic coloration. Philosophical Transactions of the Royal Society B Biological Sciences 319: 505-523.

Galeotti P, Rubolini D, Dunn PO, Fasola M. 2003. Colour polymorphism in birds : causes and functions. Journal of Evolutionary Biology 16: 635-646.

Gillespie JH, Langley CH. 1974. A general model to account for genetic variation in natural populations. Genetics 76: 837-848.

Gross MR. 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. Philosophical Transactions of the Royal Society B Biological Sciences 332: 59-66.

Hedrick PW. 1986. Genetic polymorphism in heterogeneous environments: a decade later. Annual Review of Ecology and Systematics 17: 535-566.

Heino M, Metz JAJ, Kaitala V. 1998. The enigma of frequency-dependent selection. Trends in Ecology and Evolution 13: 367-370.

Hughes KA, Du L, Rodd H, Reznick DN. 1999. Familiarity leads to female mate preference for novel males in the guppy, *Poecilia reticulata*. Animal Behaviour 58: 907-916.

Jones JS, Leith BH, Rawlings P. 1977. Polymorphism in Cepaea: a problem with too many solutions? Annual Review of Ecology and Systematics 8: 109-143.

Lank DB, Smith CM, Hanotte O, Burke TA, Cooke F. 1995. Genetic polymorphism for alternative mating behavior in lekking male ruff, *Philomachus pugnax*. Nature 378: 59-62.

Lecomte J, Clobert J, MassotM. 1992. Sex identification in juveniles of *Lacerta vivipara*. Amphibia-Reptilia 13: 21-25.

Lewontin RC. 1974. The Genetic Basis of Evolutionary Change. Columbia Press, New York, 346 p.

Massot M, Clobert J, Pilorge T, Lecomte J, Barbault R. 1992. Density dependence in the common lizard : demographic consequences of a density manipulation. Ecology 73: 1742-1756.

Massot M, Clobert J, Lecomte J, Barbault R. 1994. Incumbent advantage in common lizards and their colonizing ability. Journal of Animal Ecology 63: 431-440.

Meylan S, de Fraipont M, Clobert J. 2004. Maternal size, stress and offspring philopatry: an experimental study in the common lizard (*Lacerta vivipara*). Ecoscience 11: 123-129.

Meylan S, Clobert J, Sinervo B. 2007. Adaptive significance of maternal induced density-dependent phenotype. Oikos (in press).

Munday PL, Eyre PJ, Jones GP. 2003. Ecological mechanisms for coexistence of colour polymorphism in a coral-reef fish: an experimental evaluation. Oecologia 137:519-526.

O'Donald P, Majerus ME. 1988. Frequency-dependent sexual selection. Philosophical Transactions of the Royal Society B Biological Sciences 319: 571-586.

Olendorf R, Rodd FH, Punzalan D, Houde AE, Hurt C, Reznick DN, Hughes KA. 2006. Frequency-dependent survival in natural guppy populations. Nature 441: 633-636.

Partridge L. 1988. The rare-male effect: what is its evolutionary significance? Philosophical Transactions of the Royal Society B Biological Sciences 319: 525-539.

Paulson DR. 1973. Predator polymorphism and apostatic selection. Evolution 27: 269-277.

Richard M, Lecomte J, de Fraipont M, Clobert J. 2005. Age-specific mating strategies and reproductive senescence. Molecular Ecology 14: 3147-3155.

Roulin A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. Biological Review of the Cambridge Philosophical Society 79: 815-848.

SAS. 1992. SAS User's Guide : Statistics. SAS Institute, Cary.

Schneider KA. 2005. Competitive divergence in non-random mating populations. Theoretical Population Biology 68: 105-118.

Sinervo B, Lively CM. 1996. The rock-paper-scissors game and the evolution of alternative male reproductive strategies. Nature 380: 240-243.

Sinervo B, Zamudio K. 2001. Genetic correlations between the sexes, fitness differentials, and the evolution of alternative reproductive strategies. Journal of Heredity 98: 198-212.

Sinervo B, Bleay C, Adamopoulou C. 2001. Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. Evolution 55: 2040-2052.

Sinervo B, Svensson E, Comendant T. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406:985-988.

Sinervo B, Clobert J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. Science 300: 1949-1951.

Sirot LK, Brockmann HJ, Marinis C, Muschett G. 2003. Maintenance of a female-limited polymorphism in *Ischnura ramburi* (Zygoptera : Coenagrionidae). Animal Behaviour 66: 763-775.

Svensson EI, Abbott J. 2005. Evolutionary dynamics and population biology of a polymorphic insect. Journal of Evolutionary Biology 18: 1503-1514.

Svensson E, Abbott J, Hardling R. 2005. Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. The American Naturalist 165: 567-576.

Thompson CW, Moore MC. 1991. Syntopic occurrence of multiple dewlap color morphs in male tree lizards, *Urosaurus ornatus*. Copeia 2: 493-503.

Thompson CW, Moore IT, Moore MC. 1993. Social, environmental and genetic factors in the ontogeny of phenotypic differentiation in a lizard with alternative male reproductive strategies. Behavioral Ecology and Sociobiology 33: 137-146.

Van Gossum H, Stoks R, De Bruyn L. 2001. Reversible frequency-dependent switches in male mate choice. Proceedings of the Royal Society Biological Sciences Series B 268: 83-85.

Van Gossum H, Stoks R, De Bruyn L. 2005. Lifetime fitness components in female colour morphs of a damselfly: density- or frequency-dependent selection? Biological Journal of the Linnean Society 86: 515-523.

Van Valen L. 1965. Morphological variation and the width of ecological niche. The American Naturalist 99: 377-390.

Vercken, E., M. Massot, B. Sinervo and J. Clobert. 2007. Colour polymorphism in females and alternative reproductive strategies in the common lizard *Lacerta vivipara*. Journal of Evolutionary Biology 20: 221-232.

Vercken, E., M. Massot, B. Sinervo and J. Clobert. Female colour morphs in the common lizard display alternative offspring dispersal strategies with respect to environmental cues. Submitted.

Vercken E, Clobert J. Female colour polymorphism and social dominance in the common lizard (*Lacerta vivipara*). Submitted.

Wallace B. 1968. Topics in population genetics. Norton, New York, 481 p.

West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. Quarterly Review of Biology 58: 155-183.

Widemo F. 1998. Alternative reproductive strategies in the ruff, *Philomachus pugnax*: a mixed ESS? Animal Behaviour 56: 329-336.

Table 1: Female density, orange and yellow female frequencies for the four studied populations in 2004, and number of transplanted females in 2004 and 2005.

Population parameter	Population A	Population B	Population C	Population D
Adult female density	160	140	175	100
Orange female frequency	0.42	0.4	0.2	0.21
Yellow female frequency	0.36	0.25	0.37	0.42
Females transplanted in 2004	25	26	26	25
Females transplanted in 2005	23	23	19	19

Figure Legends

Figure 1: Mean clutch hatching success for yellow (□), mixed (▲), and orange females (■) in O+ (—) and in Y+ (---) populations in 2004 (control year), 2005 and 2006.

Figure 2: Mean juvenile characteristics in O+(■—■) and Y+ (□---□) populations in 2004 (control year), 2005 and 2006. (a) Juvenile weight. (b) Juvenile body condition. Error bars are 95% confidence intervals (+/- 2 s.e.).

Figure 1

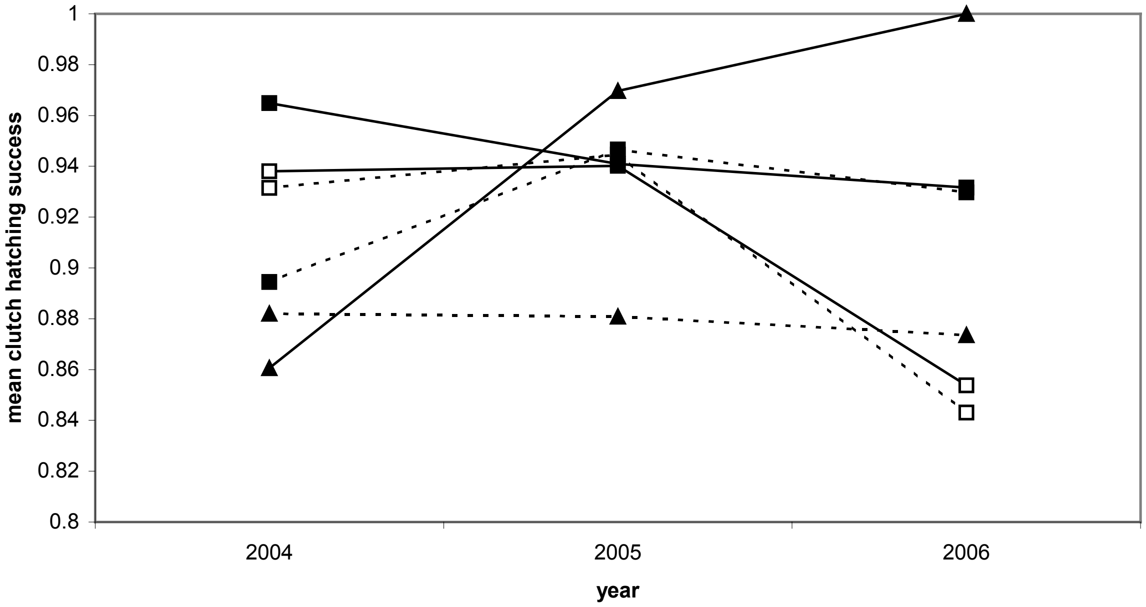
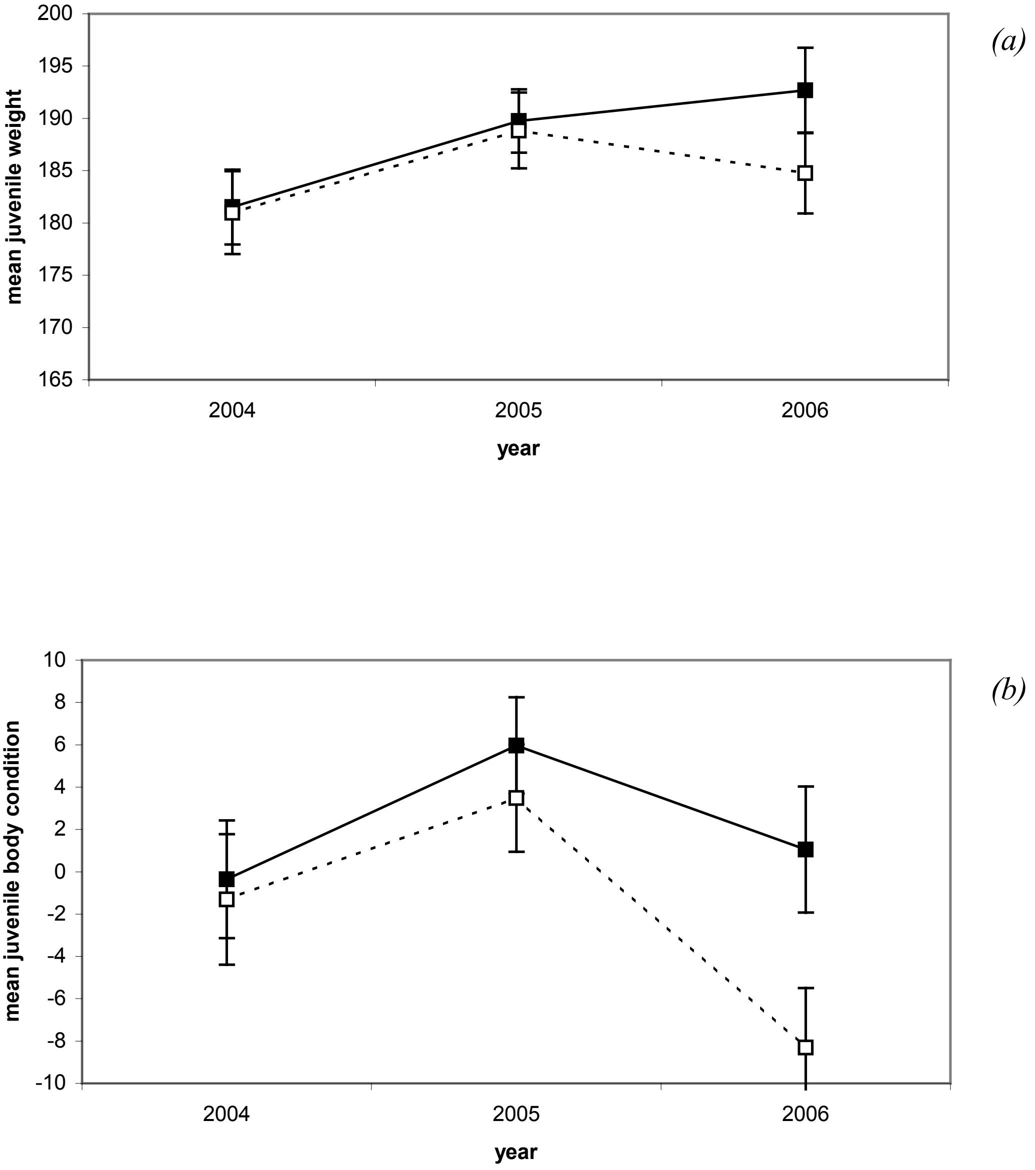

mean clutch hatching success
1
0.98
0.96
0.94
0.92
0.9
0.88
0.86
0.84
0.82
0.8
2004
2005
2006
year

Figure 2


(a)
mean juvenile weight
200
195
190
185
180
175
170
165
2004
2005
2006
year
(b)
mean juvenile body condition
10
8
6
4
2
0
-2
-4
-6
-8
-10
2004
2005
2006
year

ANNNEXE VI: Social environment-dependent dispersal strategies in juvenile common lizards (*Lacerta vivipara*)

Article en préparation

Social environment-dependent dispersal strategies in juvenile common lizards (*Lacerta vivipara*)

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Abstract

Environmental structure is known to maintain polymorphisms in natural populations. Dispersal can affect the social environment experienced by alternative morphs, and morphs are expected to adopt different dispersal strategies influenced by their social environment. The interplay between the spatial structure of the environment and frequency-dependent selection on morphs might lead to the emergence of alternative, frequency-dependent dispersal strategies. Colour polymorphisms often signal for alternative strategies that create heterogeneity in the social environments. Thus, in the case of a colour polymorphism, dispersal is expected to be both individually and environmentally colour-dependent. In the common lizard, natal dispersal is known to be highly plastic, influenced by maternal effects, and sensitive to the social environment. In this species, females display three classes of ventral colouration (yellow, orange and mixed) that are associated with alternative strategies in reproduction, dispersal and social behaviour. Female reproduction was previously shown to be affected by the local frequencies of colour morphs. We therefore predicted that offspring dispersal would be affected by the colour of the social environment in interaction with maternal colour, and thus that the different colour morphs would disperse differently in response to a variation in local colour morphs frequencies. We found that natal dispersal depended on the interaction between maternal ventral colour and the local frequency treatment, supporting the hypothesis of colour-based alternative dispersal strategies determined by differential competitive abilities and/or social strategies.

Keywords: *female colour polymorphism, alternative strategies, natal dispersal, frequency-dependence, social competition.*

Introduction

Dispersal has been recognized as a key parameter in population persistence and species evolution (Hanski 2001, Barton 2001). Recently, heterogeneity in habitats was found to promote polymorphism through the evolution of different dispersal tactics (Doebeli and Ruxton 1997). Spatial structure is expected to be widespread, since in nature most populations are not isolated and are connected by migratory flows to other neighbouring populations (Clobert et al. 2001). Dispersal is thus a way to create spatial structure within populations, by shaping local density, relatedness and social environment (Whitlock 2001, Hanski 2001). Because dispersal is a complex trait, open to the influence of many abiotic and biotic factors (Clobert et al. 2001, Clobert et al. 2004, Bowler and Benton 2005), we may expect that whenever some alternative strategies evolve within a population they should also differ in dispersal. For instance, in the side-blotched lizard *Uta stansburiana*, offspring dispersal was found to be among the traits characterizing alternative male reproductive strategies (Sinervo and Clobert 2003, Sinervo et al. 2006a). Indeed, by their action on local density and relatedness, dispersal or philopatry of alternative reproductive strategies will affect the social environment of individuals, which is known to have a feedback effect on the selective pressures acting on the evolution of dispersal (Clobert et al. 2004). Thus, the success of distinct strategies should depend on the social composition of local environment (Sinervo and Clobert 2003, Sinervo et al 2006b), and individuals playing distinct strategies may benefit differently from dispersal as a function of this local environment. Therefore, dispersal is thought to play a role in the maintenance of genetic variation in general (Hanski 1999, Whitlock 2001), and of strategy polymorphisms in particular (Frank 1986, Johst et al. 1999, Parvinen 2002).

Variation in colour is found in many animal taxa, particularly vertebrates (Galeotti et al. 2003). Apart from mechanistic roles in thermoregulation and predator avoidance, variation in individual colour is expected to be mainly implicated in social communication. In particular, colour signals have been demonstrated to advertise individual health, competitive ability, dominance status,etc (Johnson 1988, Amundsen et al. 1997, Berglund and Rosenqvist 2001, Weiss 2006) and, in some cases, alternative social strategies (Sinervo and Lively 1996, Thompson and Moore 1991, Formica et al. 2004). Indeed, it was demonstrated both theoretically and empirically that individuals playing different social strategies gained advantage from signalling their strategy by some conspicuous characters or 'green beards' (Hamilton 1964a and b, Dawkins 1989, Jansen and Van Baalen 2006, Sinervo et al. 2006b). In addition, in populations where frequency-dependent selection is operating, as dispersal affects the social environment experienced by alternative genotypes, optimal dispersal is likely to be frequency-dependent (Murren et al. 2001). In other words, dispersal is expected to be both individually and environmentally colour-dependent. Indeed, whenever the local neighbourhood is spatially variable in its colour composition, individuals of different strategies (i.e., of different colours) should disperse in a different way with respect to this social environment. Such association between colour morphs and dispersal strategies, although expected, has only been found once (Sinervo and Clobert 2003) and this study was furthermore correlative in the way that the colour composition of the local environment was not manipulated. However, experimental approaches are deeply needed to better characterise such traits association.

In the common lizard (*Lacerta vivipara*), offspring dispersal has been shown to be strongly influenced by female density (Léna et al 1998) and various maternal effects (maternal age, Ronce et al. 1998; maternal parasitic load, Sorci et al. 1994; local relatedness, Le Galliard et al. 2003a; maternal stress, de Fraipont et al. 2000; multiple factors Massot and Clobert 2000, Massot et al. 2002), such that females social environment is strongly expected to affect offspring dispersal. In this species, discrete female colour variants coexist in most ovoviviparous populations (E. Vercken, pers. obsv.). These females differ in ventral colour (yellow, orange, or a mixed coloration) and display complex alternative strategies in reproduction (Vercken et al. 2007), non-social dispersal (response to the quality of the environment, Vercken et al. submitted), and behaviour (Vercken and Clobert submitted). Although the mechanisms allowing for the maintenance of this polymorphism are still unclear, some degree of frequency-dependent selection is likely to be involved. Indeed, we found that female reproductive success was affected by the experimental manipulation of the local frequencies of colour morphs (Vercken et al. in prep) and we hypothesized that female contest competition and social stress were responsible for these frequency-dependent effects. We therefore expected that offspring dispersal would be affected by the colour of the social environment, and thus that the different colour morphs would disperse differently in response to a variation in local colour morphs frequencies (interaction between individual colour and environmental colour).

In order to test this hypothesis, we manipulated the colour morph frequencies at the local scale in four different populations. We then followed offspring dispersal in response to an increase or decrease in yellow and orange female frequencies. We found that offspring dispersal responded to the social environment experienced by the mother during gestation, and to the interaction between the local frequencies of colour morphs and maternal ventral colour.

Methods

The Species

Lacerta vivipara is a small (adult snout-vent length from 50 to 70 mm) live bearing lacertid lizard, found throughout Europe and Asia. We studied four populations located on Mont Lozère (Southern France, altitude 1420 m). In these populations, adult males emerge from hibernation in mid-April, followed by yearlings, and adult females in mid-May. Mating occurs at female emergence, and gestation lasts for two months. Parturition starts in mid-July and lasts for two or three weeks. Females lay an average clutch of five soft-shelled eggs (range 1-12). Offspring hatch within one or two hours after laying and are immediately independent of their mother. Juvenile dispersal takes place within the first ten days of life (Léna et al. 1998). The activity season ends in late September and juveniles are the last to enter hibernation. A more detailed description of life history can be found in Massot et al. (1992). In this population, adult females display a ventral colouration varying from pale yellow to bright orange, whereas adult males are almost always orange. Juveniles start by being melanic, and slowly turn to a pale green ventral colouration when yearlings. Stability of ventral colour arises with sexual maturity (usually at two years in the Mont Lozère populations).

Data Set

From 2004 to 2006, 773 females were temporarily removed from the four populations. Each year, from the end of June, females were captured and kept in the laboratory until parturition. Females were housed in plastic terraria with damp soil, a shelter and water *ad libitum*. They were exposed to natural daylight and were heated 6 h per day with an electric bulb. Female ventral colouration was estimated visually using a colour references, and fell into three distinct classes: pale yellow, bright orange and mixed coloration (mixture of yellow and orange), which have been shown to reflect spectrophotometrical differences (Vercken et al. 2007).

We obtained 3029 living juveniles. At birth, offspring were individually marked by toe-clipping, measured, weighed, and sexed by counting ventral scales (Lecomte et al. 1992). They were then released with their mother either in their population of origin or in another population (see below).

Recapture sessions in fall and spring allowed us to map the location of juveniles after dispersal. Dispersers were defined as individuals that had moved more than 30 meters between their release point and their last recapture point (upper 95% confidence limit of the home range diameter). Philopatric individuals were defined as individuals that had moved less than 20 meters (average home range diameter) (Clobert et al. 1994, Massot and Clobert 2000). Individuals moving more than 30 meters were never found to come back on their natal territory. Juveniles that had moved between 20 and 30 m were not assigned any dispersal status, and were excluded from the analysis. We obtained dispersal status for 503 juveniles.

Frequency experiment

The four studied populations differed in female density, and in the frequencies of female colour variants. We distinguished two “high-orange” populations (A and B) from two “high-yellow” populations (C and D). During two years (2004 and 2005), we increased the local frequency of yellow females in the “high-orange” populations, and the local frequency of orange females in the “high-yellow” populations with reciprocal transplants of females and their clutch after parturition. In their new population, immigrant females were released at the capture point of a native transplanted female in order not to modify female density at the local scale. Total population densities were not modified, therefore the frequencies of mixed females were not modified either.

The respective values of density (estimated from the recapture rate by the Lincoln-Petersen index), orange female frequency and yellow female frequency in the different populations are given in Table 1, with the numbers of females transplanted in each population in 2004 and 2005. Transplanted females did not have lower survival than resident females, and remained on their release site after the experiment (Vercken et al. in prep). Therefore, the reciprocal transplant experiment had persistent effects on the social structure of the populations, although preserving their spatial structure.

In 2004, the local frequencies experienced by females during gestation were not modified, and this year is thus considered as a “control” year with respect to pre-natal effects. In 2005 and 2006, the females from populations A and B experienced an “increased-yellow” treatment (Y+ treatment) during gestation, whereas females from populations C and D experienced an “increased-orange” treatment (O+ treatment). In all years, juveniles from populations A and B experienced a Y+ post-natal treatment, and juveniles from populations C and D a O+ post-natal treatment.

Statistical analyses

Dispersal status was considered as a binomial variable (0 : philopatric offspring; 1 : disperser), and therefore was analysed using logistic-linear regression analysis (GENMOD procedure, SAS Institute). Log-likelihood ratio tests (χ^2 values) and type III sum of squares were used to assess significance of effects. The analysis of dispersal often raises a statistical issue due to overdispersion of data, induced by the non-independence among siblings (Massot and Clobert 1995, 2000). The DSCALE option of the GENMOD procedure allowed us to correct for overdispersion (Clobert et al. 1993, Massot et al. 2002). We analysed the response of juvenile dispersal to several variables: individual characteristics were described by body size (snout-vent length or SVL) and sex; maternal characteristics by the ventral colour of the mother; environmental parameters by year, population, the frequency treatment in the population of origin of the mother (pre-natal frequency effect), and the frequency treatment in the population were the juveniles were released (post-natal frequency effect). We tested for all simple effects and for the following interactions: year by population, year by treatment, year by ventral colour, ventral colour by treatment, and year by ventral colour by treatment. A significant year effect or year by population effect would mean that the different populations have different mean dispersal rates, or different annual effects. In that case, the treatment effects estimated over two population replicates could be distorted by significant differences between replicates. A significant year by treatment effect would mean that the frequency treatments have modified juvenile dispersal in comparison with the control year, with different effects for the two treatments. A significant year by ventral colour by treatment effect would mean that offspring dispersal of the different colour morphs have been affected differently by the two frequency treatments.

We started with a general model including all the potential effects and the interactions mentioned above. We then dropped the non-significant effects (backward selection), starting with the most complex interaction terms. Only the results of the final model are reported. Colour effects were interpreted by comparing alternately the three different treatment or colour pairs. In that case, we used a Bonferroni correction to assess significance of effects (the significance threshold for the p-value being lowered to 0.017).

Results

Juvenile dispersal was not affected either by population (p=0.076) or by female colour morph frequency that they experienced after birth (p=0.081). However juvenile dispersal was affected by the interaction between year and maternal colour (χ^2_2=13.97, p=0.0009, n=503), by the interaction between year and the frequency of colour morphs experienced by their mother during gestation (χ^2_2= 6.73, p=0.0095), and by the interaction between year, maternal colour and the frequency treatment experienced by the mother (χ^2_2= 6.18, p=0.045).

The interaction between year and maternal colour was not significant when comparing the response of juveniles from mixed or orange mothers (χ^2_1= 1.45, p=0.22, n=331), but it was significant when comparing the response of juveniles from yellow or mixed mothers (χ^2_1= 13.34, p=0.0003, n=351) or the response of juveniles from yellow or orange mothers (χ^2_1= 5.8, p=0.016, n=328). Dispersal of juveniles from orange or mixed females tended to decrease during the three-year period, whereas dispersal of juveniles yellow females appeared stable over the same period.

Juvenile dispersal was not affected by the increase in the frequency of orange females (χ^2_1= 0.07, p=0.78, n=251), but dispersal decreased significantly in response to an increase in the frequency of yellow females (χ^2_1= 11.28, p=0.0008, n=254).

Finally, the interaction between year, maternal colour and frequency treatment during gestation was not significant when comparing the response of juveniles from mixed or orange mothers (χ^2_2= 1.21, p=0.27, n=331) or the response of juveniles from yellow or orange mothers (χ^2_2= 1.85, p=0.17, n=328), but it was significant when comparing the response of juveniles from yellow or mixed mothers (χ^2_2= 6.2, p=0.0127, n=351). Dispersal of juvenile from mixed females decreased significantly in response to an increase in the frequency of yellow females but did not respond to an increase in the frequency of orange females, whereas the same trend was observed but it was not significant for juveniles from orange females, and juveniles from yellow females were not affected at all by the variation in colour frequencies (Figure 1).

Discussion

Juvenile dispersal was found to respond to the local frequencies of female colour morphs experienced during gestation, in interaction with maternal ventral colour. Female reproductive success was also shown to respond to the local frequencies of female colour morphs in interaction with female colour (Vercken et al. in prep). Frequency-dependent processes (Heino et al. 1998, Molofsky et al. 1999) and morph-specific dispersal strategies (Frank 1986, Johst et al. 1999, Parvinen 2002) are known to promote genetic diversity within populations, and might contribute to the maintenance of stable polymorphisms.

Plasticity of morph-specific dispersal strategies

In all treatments, dispersal rate of offspring from yellow females was constant and intermediate (around 0.3): they did not respond to the local frequencies of colour morphs in their dispersal strategies. In a previous study (Vercken et al. submitted), dispersal of offspring from yellow females also appeared insensitive to several environmental factors. Therefore, it is possible that yellow females play a fixed dispersal strategy. Indeed, yellow females appear to be socially dominant over other morphs such that the dispersal of their offspring is likely to be less influenced by social competition. However, an increase in yellow female density affects offspring phenotype for all females whatever their ventral colour (Vercken et al. in prep), such that offspring dispersal of yellow female was expected to be influenced by the local colour environment at birth. This is not what we found. This might suggest that the cost to derive a plastic dispersal strategy in yellow females is too high with respect to the benefits that their offspring can expect from it. Alternatively, variation in the frequency of yellow females might be spatially correlated such that leaving one’s natal place will not allow to shift from one’s native colour environment. Juveniles from mixed or orange females dispersed more in control and O+ populations (around 0.5), and less in Y+ populations (between 0.13

and 0.22). In other words, dispersal of offspring born to orange and mixed coloured females was condition-dependent, and this plasticity arose through maternal effect. Females are thus able to assess precisely the colour composition of their social environment, and to use this information to influence their offspring's development and phenotype. The evolution of such maternal effects requires that the environmental cues used by the females are reliable indicators of the future environment that will be experienced by their offspring. In this species, maternal effect on offspring dispersal have been recurrently found (maternal age, Ronce et al. 1998; maternal parasitic load, Sorci et al. 1994; local relatedness, Le Galliard et al. 2003a; maternal stress, de Fraipont et al. 2000; multiple factors Massot and Clobert 2000, Massot et al. 2002) such that the physiological machinery to modify the development of the behavioural phenotype (Meylan et al. submitted) is likely to be in place. Furthermore, the colour composition of the neighbourhood is likely to be stable and predictable since adult females have been proved to remain on the same territory for their entire life (Massot 1992). Finally, the colour signal itself, although open to environmental influences (Meylan et al. 2007, Vercken et al. in prep), has been proved to be heritable and strongly stable trough female life span (Vercken et al. 2007, Vercken and Clobert in prep). Nevertheless, there is still to demonstrate that offspring from mixed and orange females benefit from adapting their strategy to the social environment, whereas it is not the case for yellow females.

Social environment, local competition and morph-specific dispersal strategies

In this species, offspring dispersal is thought to have evolved both as a mechanism to avoid kin competition (Ronce et al. 1998, de Fraipont et al. 2000, Le Galliard et al. 2003a) and competition with conspecifics (Léna et al. 1998, Le Galliard et al. 2003a, Meylan et al. 2007). Furthermore, offspring at birth was found to have different social personalities which strongly influence their dispersal pattern (Cote and Clobert 2007). If offspring from mixed or orange females disperse more in control populations than offspring from yellow females, it could mean that they are more sensitive to competition than offspring from yellow females. In addition, offspring from mixed and orange females decreased their dispersal in Y+ populations. In another study (Vercken and Clobert submitted), yellow females were shown to be more aggressive than mixed or orange females such that yellow females are thought to be socially dominant. Therefore, in a population where the frequency of yellow females is high, the level of intraspecific competition is also expected to be high. Such a sensitivity of offspring dispersal to individual competitive ability is not surprising in this species since it was already demonstrated that various classes of age and sex characterized by differential competitive abilities was influencing differently offspring dispersal (kin interactions: Ronce et al. 1998; interactions with non-related conspecifics: Lena et al. 1998, Le Galliard et al. 2003a). In this context, two scenarios may explain the decrease in the dispersal rate of offspring from mixed and orange females in Y+ populations.

In a population where intraspecific competition is strong, cooperation to exploit and defend a territory against stronger competitors might be selected for (Jannett 1978, Jones et al. 1988, Lambin et al. 2001). As the benefits of this strategy often depend on the evolution of a reduced mobility (Le Galliard et al. 2003b, 2005), philopatry should be selected in such a context (Matthiopoulos et al. 1998, Lambin et al. 2001). If cooperative strategies are played by mixed and orange females, then the benefits associated with cooperation might be higher than the costs of within colour-morph competition in Y+ populations, which would decrease the selective pressure enhancing dispersal in mixed and orange morphs. Such types of trade-offs between competitive ability and cooperative behaviour correlated to different colour morphs has already been documented in another species of lizard (Sinervo and Lively 1996).

Another possible scenario would be that dispersing offspring from mixed and orange females experience higher settlement costs in Y+ populations, which increases the cost of dispersal and therefore select for reduced dispersal. In another lizard species, it was shown that the acquisition of a dominance status during settlement involved competitive contests (Stamps and Krishnan 1995). Aggressive behaviour during settlement was related to the probability that an individual would become socially dominant, and a territory owner (Stamps and Krishnan 1998). In an environment where yellow females are frequent, it might then be very costly for non-yellow individuals to disperse and try to settle in a place with too many yellow neighbours. The two above scenarios are not necessarily mutually exclusive and the effective dispersal pattern is likely to result from a balance between the relative benefits of philopatry and costs of dispersal.

The relevance and relative importance of each scenario in explaining the above results might be assessed by looking to the scale at which the colour environment is perceived. In the cooperation scenario, frequency-dependence is experienced at the local scale: the increase in the number or the frequency of yellow neighbours is an indicator of an increased level of local competition in the native area. Alternatively, in the settlement costs scenario, frequency-dependence is experienced at the population scale: the individuals assess the probability to enter contest competition with yellow individuals at dispersal distance. The interaction between the scale of frequency-dependence and the scale of dispersal is predicted to affect patterns of spatial distribution (Molofsky et al. 2002) such that the study of theses patterns might help discriminating among these alternative adaptive scenarios.

Conclusion

We found that, in the common lizard, offspring dispersal depended on maternal ventral coloration and on female colour morph frequency in maternal neighbourhood. This is the first experimental effect to be reported of an interaction between a female colour morph and her coloured social environment on her offspring dispersal profile. Yet the underlying selective processes remain at this point speculative. The analysis of spatial association patterns for all colour morphs could help understanding better what are the main selective forces driving colour-dependent dispersal. Although the reproductive success of the yellow and orange females appear to be equivalent on the long term (Vercken et al. 2007), the examination of the consequences of colour-dependent dispersal strategies on juvenile fitness might further help assessing the adaptive nature of colour-based alternative strategies.

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REFERENCES

Amundsen T, Forsgren E, Hansen LTT. 1997. On the function of female ornaments: male bluethroats prefer colorful females. Proceedings of the Royal Society Biological Sciences Series B 264: 1579-1586.

Barton NH. 2001. The evolutionary consequences of gene flow and local adaptation: future approaches. In: Dispersal (Clobert J, Danchin E, Dhondt AA, Nichols JD, eds), pp 329-340. Oxford University Press, Oxford.

Berglund A, Rosenqvist G. 2001. Male pipefish prefer dominant over attractive females. Behavioral Ecology 12: 402-406.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Review of the Cambridge Philosophical Society 80: 205-225.

Clobert J, Julliard R, McCleery RH. 1993. The components of local recruitment. In: The study of bird population dynamics using marked individuals (Lebreton JD, North P, eds), pp 281-294. Birkauser Verlag, Basel.

Clobert J, Danchin E, Nichols JD, Dhondt AA. 2001. Dispersal. Oxford University Press, 452p.

Clobert J, Ims RA, Rousset F. 2004. Causes, mechanisms and consequences of dispersal. In: Ecology, Genetics and Evolution of Metapopulations (Hanski I, Gaggiotti OE, eds), pp 307-335. Academic Press, San Diego.

Cote J, Clobert J. 2007. Social personalities influence natal dispersal in a lizard. Proceedings of the Royal Society Biological Sciences Series B 274: 383-390.

Dawkins R. 1989. The selfish gene (second edition). Oxford University Press, Oxford, 352 p.

de Fraipont M, Clobert J, John-Alder H, Meylan S. 2000. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. Journal of Animal Ecology 69: 404-413.

Doebeli M, Ruxton GD. 1997. Evolution of dispersal rates in metapopulation models: Branching and cyclic dynamics in phenotype space. Evolution 51: 1730-1741.

Formica VA, Gonser RA, Ramsay S, Tuttle EM. 2004. Spatial dynamics of alternative reproductive strategies: The role of neighbors. Ecology 85: 1125-1136.

Frank AS. 1986. Dispersal polymorphisms in subdivided populations. Journal of Theoretical Biology 122 : 303-309.

Galeotti P, Rubolini D, Dunn PO, Fasola M. 2003. Colour polymorphism in birds : causes and functions. Journal of Evolutionary Biology 16: 635-646.

Hamilton WD. 1964a. The genetical evolution of social behaviour I. Journal of Theoretical Biology 7: 1-16.

Hamilton WD. 1964b. The genetical evolution of social behaviour II. Journal of Theoretical Biology 7: 17-52.

Hanski I. 1999. Metapopulation ecology. Oxford University Press, Oxford, 313 p.

Hanski I. 2001. Population dynamic consequences of dispersal in local populations and in metapopulations. In: Dispersal (Clobert J, Danchin E, Dhondt AA, Nichols JD, eds), pp 283-298. Oxford University Press, Oxford.

Heino M, Metz JAJ, Kaitala V. 1998. The enigma of frequency-dependent selection. Trends in Ecology and Evolution 13: 367-370.

Jannett F. 1978. The density-dependent formation of extended maternal families of the montane vole, *Microtus montanus nanus*. Behavioral Ecology and Sociobiology 3: 245-263.

Jansen VAA, Van Baalen M. 2006. Altruism through beard chromodynamics. Nature 440: 663-666.

Johnson K. 1988. Sexual selection in pinion jays II: male choice and female-female competition. Animal Behaviour 36: 1048-1053.

Johst K, Doebeli M, Brandl R. 1999. Evolution of complex dynamics in spatially structured populations. Proceedings of the Royal Society Biological Sciences Series B 266 : 1147-1154.

Jones W, Waser P, Elliott N, Link N, Bush B. 1988. Philopatry, dispersal, and habitat saturation in the banner-tailed kangaroo rat, *Dipodomys spectabilis*. Ecology 69: 1466-1473.

Lambin X, Aars J, Piertney SB. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation. In: Dispersal (Clobert J, Danchin E, Dhondt AA, Nichols JD, eds), pp 110-122. Oxford University Press, Oxford.

Lecomte J, Clobert J, Massot M. 1992. Sex identification in juveniles of *Lacerta vivipara*. Amphibia-Reptilia 13: 21-25.

Le Galliard JF, Ferriere R, Clobert J. 2003a. Mother-offspring interactions affect natal dispersal in a lizard. Proceeding of the Royal Society Biological Sciences Series B 270: 1163-1169.

Le Galliard JF, Ferriere R, Dieckmann U. 2003b. The adaptive dynamics of altruism in spatially heterogeneous populations. Evolution 57: 1-17.

Le Galliard JF, Ferriere R, Dieckmann U. 2005. Adaptive evolution of social traits: Origin, trajectories, and correlations of altruism and mobility. The American Naturalist 165: 206-224.

Léna JP, Clobert J, de Fraipont M, Lecomte J, Guyot G. 1998. The relative influence of density and kinship on dispersal in the common lizard. Behavioral Ecology 9: 500-507.

Massot M. 1992. Movement patterns of the common lizard (*Lacerta vivipara*) in relation to sex and age. In: Proceedings of the 6th Ordinary General Meeting of the Societas Europaea Herpetologica, Budapest, 1991 (Korsos Z, Kiss I, eds), pp 21-36. Chapman & Hall, London.

Massot M, Clobert J, Pilorge T, Lecomte J, Barbault R. 1992. Density dependence in the common lizard : demographic consequences of a density manipulation. Ecology 73: 1742-1756.

Massot M, Clobert J. 1995. Influence of maternal food availability on offspring dispersal. Behavioral Ecology and Sociobiology 37: 413-418.

Massot M, Clobert J. 2000. Processes at the origin of similarities in dispersal behaviour among siblings. Journal of Evolutionary Biology 13: 707-719.

Massot M, Clobert J, Lorenzon P, Rossi JM. 2002. Condition-dependent dispersal and ontogeny of the dispersal behaviour : an experimental approach. Journal of Animal Ecology 71: 253-261.

Matthiopoulos J, Moss R, Lambin X. 1998. Models of red grouse cycles. A family affair ? Oikos 82: 574-590.

Meylan S, Clobert J, Sinervo B. 2007. Adaptive significance of maternal induced density-dependent phenotype. Oikos (in press).

Meylan S, de Fraipont M, Aragon P, Vercken E, Clobert J. Are dispersal-dependent personalities produced by phenotypic plasticity ? Submitted.

Molofsky J, Durrett R, Dushoff J, Griffeath D, Levin S. 1999. Local frequency dependence and global coexistence. Theoretical Population Biology 55: 270-282.

Molofsky J, Bever JD, Antonovics J, Newman TJ. 2002. Negative frequency-dependence and the importance of spatial scale. Ecology 83: 21-27.

Murren CJ, Julliard R, Schlichting CD, Clobert J. 2001. Dispersal, individual phenotype, and phenotypic plasticity. In: Dispersal (Clobert J, Danchin E, Dhondt AA, Nichols JD, eds), pp 261-272. Oxford University Press, Oxford.

Parvinen K. 2002. Evolutionary branching of dispersal strategies in structured metapopulations. Journal of Mathematical Biology 45: 106-124.

Ronce O, Clobert J, Massot M. 1998. Natal dispersal and senescence. Proceedings of the National Academy of Sciences of the USA 95: 600-605.

SAS. 1992. SAS User's Guide : Statistics. SAS Institute, Cary.

Sinervo B, Lively CM. 1996. The rock-paper-scissors game and the evolution of alternative male reproductive strategies. Nature 380: 240-243.

Sinervo B, Clobert J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. Science 300: 1949-1951.

Sinervo B, Calsbeek R, Comendant T, Both C, Adamopoulou C, Clobert J. 2006a. Genetic and maternal determinants of effective dispersal: the effect of sire genotype and size at birth in side-blotched lizards. The American Naturalist 168: 88-99.

Sinervo B, Chaine A, Clobert J, Calsbeek R, McAdam A, Hazard L, Lancaster L, Alonzo SH, Corrigan G, Hochberg M. 2006b. Self-recognition, color signals and cycles of greenbeard mutualism and transient altruism. Proceedings of the National Academy of Sciences USA 102: 7372-7377.

Sorci G, Massot M, Clobert J. 1994. Maternal parasite load increases sprint speed and philopatry in female offspring of the common lizard. The American Naturalist 144: 153-164.

Stamps JA, Krishnan VV. 1995. Territory acquisition in lizards: III. Competing for space. Animal Behaviour 49: 679-693.

Stamps JA, Krishnan VV. 1998. Territory acquisition in lizards: IV. Obtaining high status and exclusive home ranges. Animal Behaviour 55: 461-472.

Thompson CW, Moore MC. 1991. Syntopic occurrence of multiple dewlap color morphs in male tree lizards, *Urosaurus ornatus*. Copeia 2: 493-503.

Vercken E, Massot M, Sinervo B, Clobert J. 2007. Colour polymorphism in females and alternative reproductive strategies in the common lizard *Lacerta vivipara*". Journal of Evolutionary Biology 20: 221-232.

Vercken E, Massot M, Sinervo B, Clobert J. Female colour morphs in the common lizard display alternative offspring dispersal strategies with respect to environmental cues. Submitted.

Vercken E, Clobert J. Female colour polymorphism and social dominance in the common lizard (*Lacerta vivipara*). Submitted.

Vercken E, Sinervo B, Clobert J. Female reproductive success is sensitive to the social environment in the common lizard (*Lacerta vivipara*). In preparation.

Weiss SL. 2006. Female-specific color is a signal of quality in the striped plateau lizard (*Sceloporus virgatus*). Behavioral Ecology 17: 726-732.

Whitlock MC. 2001. Dispersal and the genetic properties of metapopulations. In: Dispersal (Clobert J, Danchin E, Dhondt AA, Nichols JD, eds), pp 273-282. Oxford University Press, Oxford.

Table 1 : Female density, orange and yellow female frequencies for the four studied populations in 2004, and number of transplanted females in 2004 and 2005.

Population parameter	Population A	Population B	Population C	Population D
Adult female density	160	140	175	100
Orange female frequency	0.42	0.4	0.2	0.21
Yellow female frequency	0.36	0.25	0.37	0.42
Females transplanted in 2004	25	26	26	25
Females transplanted in 2005	23	23	19	19

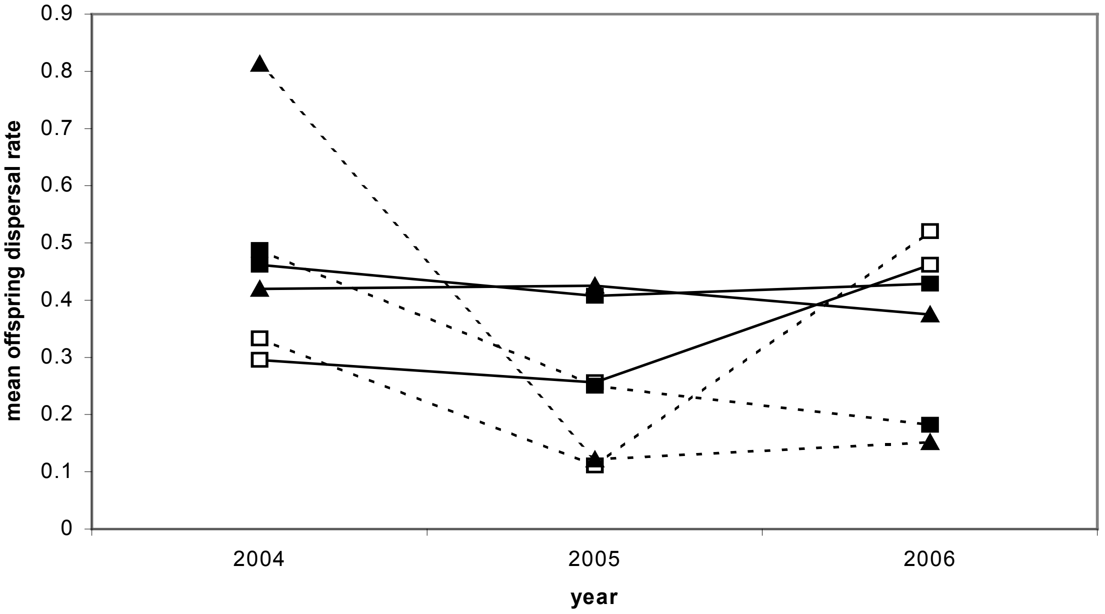

Figure 1 : Mean offspring dispersal rate for yellow (□), mixed (▲), and orange mothers (■) in O+ (—) and in Y+ (---) populations.

ANNNEXE VII: Juvenile growth and survival in different social environments in the common lizard (*Lacerta vivipara*): does variation in local competition select for alternative reproductive strategies?

Article en préparation

Juvenile growth and survival in different social environments in the common lizard (*Lacerta vivipara*): does variation in local competition select for alternative reproductive strategies ?

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Abstract

Colour polymorphism is expected to play a role in intra-specific communication and to signal alternative strategies. Although colour-based alternative reproductive strategies in males have been extensively documented, the study of colour polymorphism and alternative strategies in females is still recent, and few examples have been provided so far. Alternative strategies may be maintained in populations if they are condition-dependent, if they achieve equal mean fitness pay-offs, or if they are under negative frequency-dependent selection. The study of both adult and juvenile colour-specific fitness in different social environments should help determining how the different strategies are maintained in natural populations.

In the common lizard, females display three classes of ventral colouration (yellow, orange and mixed) that are associated with alternative strategies in reproduction, dispersal and social behaviour. Frequency-dependent overdominance appears as a potential mechanism for polymorphism maintenance, as frequency-dependent effects were demonstrated on reproduction and offspring dispersal of mixed females. Such effects are likely to be mediated by contest competition and social stress, which are expected to affect also offspring fitness. We analysed the response of juvenile growth and survival to an experimental manipulation of colour morphs frequencies in natural populations. We found that correlates of juvenile fitness were indeed affected by the local frequencies of colour morphs, but not in interaction with maternal colour. In addition, the observed trend was opposed to our predictions. These results suggest that local differences in density might have affected juvenile development independently of maternal reproductive strategy, through non-adaptive environmental effects.

Keywords: *female colour polymorphism, frequency-dependence, overdominance, juvenile growth, juvenile survival, non-adaptive maternal effects.*

Introduction

Colour polymorphism is found in a wide number of animal taxa, and thus it has been an extensive subject of interest for ecologists (e.g., in insects, Chapuisat 2004; in spiders, Oxford and Gillespie, 1998; in fishes, Olendorf et al. 2006; in reptiles, Sinervo et al. 2000; in birds Roulin 2004). Apart from mechanistic roles in predation avoidance (by crypsis or aposematism) and thermoregulation, colour variation is expected to be implicated in intra-specific communication, as it may signal for socially relevant individual characteristics, and in particular alternative reproductive strategies (Gross 1996, Roulin 2004). However, even though alternative strategies in males have been described in many species (Gross 1991, Thompson et al.1993, Lank et al. 1995), the study of female polymorphism has received little attention until the past few years.

Recently, evidence from comparative studies has shown that selection has acted directly on females to favour the evolution of conspicuous traits (Burns 1988, Rowland et al. 1991, Irwin 1994, Bleiweiss 1997, Ord and Stuart-Fox 2006). Such traits might signal for female competitive ability (West-Eberhard 1983), dominance status (Johnson 1988, Berglund and Rosenqvist 2001) or individual quality (Johnsen et al. 1996, Amundsen et al. 1997, Weiss 2006), and therefore might be indicative of alternative reproductive or social strategies (Amundsen 2000, Roulin 2004). For instance, in damselflies (*Ischnura* elegans, Svensson et al. 2005) or in capuchinbirds (*Perissocephalus tricolor*, Trail 1990), some females display a male-like colouration that allows them to avoid sexual harassment. In the side-blotched lizard (*Uta stansburiana*), females of different colour play alternative strategies in reproduction (r/K strategies, Sinervo et al. 2000) and social competition (Comendant et al. 2003).

Such alternative strategies may be maintained in populations under different mechanisms. First, if alternative strategies are not genetically determined but condition-dependent, individuals adopt the best strategy considering their own status or competitive ability, and all strategies do not provide equal fitness pay-offs (Gross 1996). Second, genetically-based alternative strategies may achieve equal lifetime fitness pay-offs, because of different life-history trade-offs (Shuster and Wade 1991). Finally, alternative strategies may also be maintained by negative frequency-dependence, with fitness advantage to the rare strategy (Maynard-Smith 1982, Heino et al. 1998). To understand how alternative strategies are maintained in a population, one should try to measure both female reproductive success and juvenile fitness associated with each strategy, when the frequencies of the different strategies vary. In the common lizard (*Lacerta vivipara*), discrete female colour variants coexist in several populations. These females differ in ventral colour (yellow, orange, or a mixed coloration) and display complex alternative strategies in reproduction (Vercken et al. 2007), dispersal (Vercken et al. submitted), and behaviour (Vercken and Clobert submitted). One colour morph (mixed) was shown to be frequency-dependent for reproductive success and natal dispersal in populations where the local frequency of yellow or orange females had been increased (Y+ and O+ populations). Offspring body condition was higher in O+ populations than in Y+ populations for all colour morphs, and mixed females also benefited from an increase in clutch hatching success in O+ populations (Vercken et al. in prep 1). Frequency-dependent overdominance thus appeared as a potential mechanism allowing for the maintenance of colour polymorphism in this species. Offspring dispersal was also higher in O+ populations than in Y+ populations (Vercken et al. in prep 2). As yellow females appeared to be more aggressive and to have a higher competitive ability than mixed or orange females (Vercken and Clobert submitted), all these results were consistent with the hypothesis that the intensity of social competition between females depended on both their own ventral colour and the colour of their neighbours, and was responsible for the observed frequency-dependent effects. An increase in the frequency of yellow females was thought to strengthen the local competition and therefore to accentuate the social stress experienced by females.

Social stress would have affected negatively female reproductive success and/or juvenile phenotype (Comendant et al. 2003, Van Gossum et al. 2005, Silverin 1998), and favoured philopatric strategies because of high settlement costs (Stamps and Krishnan 1995, 1998). Such a stress was thus likely to also affect offspring fitness through post-natal effects on development and survival. Therefore, we predicted that juvenile fitness would be lower in Y+ populations than in O+ populations because of the costs due to an increased social competition, as attested by the poor juvenile condition at birth in Y+ populations. On the other hand, the populations where the frequency of orange females had been increased seemed to constitute a favourable environment, especially for mixed females (Vercken and Clobert in prep 1). Thus we predicted that juvenile fitness would be higher in O+ populations, with overdominance effects on offspring from mixed females.

To test this hypothesis, we followed offspring growth and survival before hibernation in populations where the relative frequency of two female colour morphs (yellow and orange) had been experimentally increased. These two variables are good general indicators of juvenile fitness, because size at two years determines the age at first reproduction (Lorenzon et al. 2001, Leturque 2002). Surprisingly, we found that juveniles grew faster and had higher survival in Y+ populations than in O+ populations, which is opposed to our predictions. We did not find any difference between colour morphs in the different social environments. Such a pattern could instead be explained by different social constraints (density and intensity of social stress) depending on the environment that have opposed fitness effects on adult females and juveniles.

Methods

The Species

Lacerta vivipara is a small (adult snout-vent length from 50 to 70 mm) live bearing lacertid lizard, which is found throughout Europe and Asia. We studied four populations located on Mont Lozère (Southern France, altitude 1420 m). In these populations, adult males emerge from hibernation in mid-April, followed by yearlings, and adult females in mid-May. Mating occurs at female emergence, and gestation lasts for two months. Parturition starts in mid-July and lasts for two or three weeks. Females lay an average clutch of five soft-shelled eggs (range 1-12). Offspring hatch within one or two hours after laying and are immediately independent of their mother. The activity season ends in late September and juveniles are the last to enter hibernation. A more detailed description of life history can be found in Massot et al. (1992). In this population, adult females display a ventral coloration varying from pale yellow to bright orange, whereas adult males are almost always orange. Juveniles start by being melanic, and slowly turn to a pale green ventral colouration when yearlings. Stability of ventral colour arises with sexual maturity (usually at two years in the Mont Lozère population).

Data Set

From 2004 to 2006, 773 females were temporarily removed from the four populations. Each year, from the end of June, females were captured and kept in the laboratory until parturition. Females were housed in plastic terraria with damp soil, a shelter and water *ad libitum*. They were exposed to natural daylight and were heated 6 h per day with an electric bulb. Female ventral coloration was estimated visually using a colour reference, and fell into three distinct classes: pale yellow, bright orange and mixed coloration (mixture of yellow and orange), which have been shown to reflect spectrophotometrical differences (Vercken et al. 2007).

We obtained 3029 living juveniles. At birth, offspring were individually marked by toe-clipping and sexed by counting ventral scales (Lecomte et al. 1992). Offspring and their mother were measured (snout-vent length or SVL) and weighed. They were then released in the field either into their population of origin or into another population (see below). Recapture sessions were achieved in fall 2004, 2005 and 2006, and in spring 2005 and 2006. We were thus able to estimate juvenile growth in 2004, 2005 and 2006, and juvenile survival before hibernation in 2004 and 2005.

Frequency experiment

The four studied populations differed in female density, and in female colour variants frequencies. We distinguished two "high-orange" populations (A and B) from two "high-yellow" populations (C and D). During two years (2004 and 2005), we increased the local frequency of yellow females in the "high-orange" populations (Y+ populations), and the local frequency of orange females in the "high-yellow" populations (O+ populations) with reciprocal transplants of females and their clutch after parturition. In their new population, immigrant females were released at the capture point of a native transplanted female in order not to modify female density at the local scale. Total population densities were not modified, therefore the frequencies of mixed females were not modified either.

The respective values of density (estimated from the recapture rate by the Lincoln-Petersen index), orange female frequency and yellow female frequency in the different populations are given in Table 1, with the number of females transplanted in each population in 2004 and 2005. Transplanted females did not have lower survival than resident females, and remained on their release site after the experiment (Vercken et al. in prep1). Therefore, the reciprocal transplant experiment had persistent effects on the social structure of the populations, although preserving their spatial structure.

Survival Analysis

We obtained 2153 capture histories constituted of 3 capture occasions (birth in the lab, recapture in fall, and recapture in spring the following year). Juvenile apparent survival rate (including mortality and emigration) was estimated using the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) extended to group effects (Clobert et al. 1987, 1988, Lebreton et al. 1992). As migration rate is low in this population (Massot et al. 1992), we considered the apparent survival rate as representative of the actual survival rate. The computer program MARK (White 1998) was used to fit models. Models were compared by Akaike Information Criterion (AIC) and we retained the most parsimonious of them (lowest AIC, Anderson et al. 1994). We tested the effects of year, frequency treatment, maternal ventral colour, juvenile SVL at birth and their interactions independently on survival probabilities. Capture probabilities were considered either fixed, or year-dependent. To increase our statistical power, we pooled together the juveniles from yellow or orange females, and opposed them to the juveniles from mixed females. To verify our method, we also performed the analysis with the three colour classes, and the same model was selected. Therefore, we will only present the model results obtained with the first method.

Growth analyses

We analysed the response of juvenile growth (difference in SVL between birth and first recapture in fall) to several factors: number of days between birth and recapture, year, population, frequency treatment experienced by juveniles, maternal ventral colour, maternal SVL, juvenile sex and SVL, the interactions between frequency treatment and maternal colour, between frequency treatment and population, between frequency treatment and year, between frequency treatment and sex, and three-factors interaction including all of these variables. The analysis of siblings raises a statistical issue because, they cannot be considered as independent statistical units (Massot and Clobert 1995, 2000). However, because of the small number of siblings recaptured in our study, we did not include a random family effect in the models. Nevertheless, we always included maternal SVL as a covariate to account for potential family effects.

We used general linear models (GLM procedure, SAS Institute), F-tests were used to assess significance of effects. Type III sum of squares was used in all cases. We started with a general model including all the potential effects and interactions (listed above). We then dropped the non-significant effects (backward selection), starting with the most complex interaction terms. Only the results of the final model are reported.

Results

Juvenile growth was affected by the number of days between birth and recapture ($F_{1,520}$=83.81, p<0.0001), the population ($F_{3,520}$=31.28, p<0.0001), maternal SVL ($F_{1,520}$=8.36, p=0.004), juvenile SVL ($F_{1,520}$=6.29, p=0.012), juvenile sex ($F_{1,520}$=6.05, p=0.014) and frequency treatment ($F_{1,520}$=36.79, p<0.0001). The mean increase in juvenile SVL was higher in Y+ populations (9.96 mm) than in O+ populations (9.01 mm).

Juvenile capture probability varied between years, whereas juvenile survival probability was affected by the interaction between year and frequency treatment (see Table 2 for model results). Juvenile survival did not differ between treatments in 2004 (juvenile survival rate in Y+ populations: 0.39, in O+ populations: 0.41), but it was higher in Y+ populations (0.55) than in O+ populations (0.42) in 2005.

Discussion

Juvenile fitness components were found to respond to the local frequencies of female colour morphs. Both juvenile growth rate and survival were higher in populations where the local frequency of yellow females had been increased (Y+ populations) than in populations where the local frequency of orange females had been increased (O+ populations). Contrary to our predictions, negative pre-natal effects (Vercken et al. in prep1) were counterbalanced by positive post-natal effects, and there was no significant difference anymore between the colour morphs in their response to the change in their social environment. Offspring fitness was thus higher for all colour morphs in populations where contest competition is stronger, which can be explained by differences in density and dispersal rates between experimental treatments.

Post-natal effects of the social environment on juvenile fitness

As natal dispersal rate was higher in O+ populations than in Y+ populations in 2005, apparent survival rate could have been under-estimated in O+ populations. In that case, the differences in survival between experimental treatments would be merely statistical artefacts. However, those differences in survival are consistent with the differences in growth rate: juveniles in Y+ populations have both a higher growth rate and a higher survival, which rather supports the hypothesis of a biologically significant fitness difference across treatments.

As yellow females are thought to be socially dominant (Vercken and Clobert submitted), we hypothesized that the experimental increase in the frequency of yellow females had generated strong social competition and social stress, with negative effects on female reproduction and/or juvenile phenotype at birth. Y+ populations would thus be unfavourable environments, and juvenile growth and survival was expected to be lower in these populations.

However, we observed the exact opposite: juveniles from Y+ populations experienced higher growth and survival than juveniles from O+ populations, whatever the colour of their mother. This result thus does not support the hypothesis of increased competition costs in Y+ populations, associated with lower juvenile fitness. Yet, the negative responses of female reproduction and juvenile phenotype at birth in Y+ populations do not support either the hypothesis of a better social environment in Y+ populations. Instead, the fitness difference between experimental treatments could result indirectly from differences in dispersal rate. Indeed, juveniles from O+ populations have higher mean dispersal rate than juveniles from Y+ populations. Dispersal is usually thought to be costly, in particular during the transient phase (Hamilton and May 1977, Motro 1983). Dispersing individuals thus often have reduced survival during transience and settlement (Bélichon et al. 1996). In the common lizard though, a previous study demonstrated that juveniles did not suffer from settlement costs (Massot et al. 1994). However, there might be significant fitness costs during the transient phase. Dispersers are on average more active at birth (Clobert et al. 1994, de Fraipont et al. 2000), which can increase their predation rate, and thus decrease their survival in comparison with philopatric individuals. In addition, disperser have a lower feeding rate than philopatric individuals (Meylan et al. submitted), which could affect growth and survival negatively (Le Galliard et al. 2005). Therefore, lower growth and survival rates in O+ populations might come from higher dispersal rates, at least partly.

On the other hand, density increased in O+ populations during the experiment, because of higher reproductive success of mixed females. Juvenile growth and survival are probably density-dependents, as an increase in density was found to affect juvenile fitness negatively in a previous experiment (Massot et al. 1992). In our experiment, density (an juvenile density in particular) increased in O+ populations, with cumulative effects in 2005 (due to the sum of two reproductive seasons), which could have reduced juvenile growth and survival in these populations. As a result, the environment the most favourable to females (where their reproductive success is higher) would be the least favourable to juveniles because of increased density, whatever the colour of their mother.

Pre-natal effects on juvenile phenotype: constraint or adaptation ?

The modification of the social environment had fitness consequences at several levels: female reproduction, pre-natal and post-natal components of juvenile phenotype. We found that offspring fitness was higher in Y+ populations, in which juvenile phenotype was of lower quality. It is possible that the reduced physical condition of juveniles born in Y+ populations is not a negative consequence of increased social stress, but rather a part of maternal strategy in order to produce locally adapted offspring. Indeed, it has been known for long that different selective pressures in different environments may select for alternative life-history strategies (Volis et al. 2002, Parker and Begon 1986, Doligez and Clobert 2003, Fox 2000). In O+ populations, juveniles are in better physical condition, have higher dispersal rate, but lower growth and survival. If all of these effects are involved in the production of an optimal phenotype depending on the local environmental conditions, then they could be part of adaptive strategies. Alternatively, some of these effects might be non-adaptive consequences of the modification of the environment (due to higher social stress or increased density).

In our experiment, the environment experienced by females during gestation was not always the same that their offspring experienced after birth. Indeed, juveniles from orange mothers captured in Y+ populations were released into O+ populations, and the opposite was true for juveniles from yellow mothers captured in O+ populations. If the modifications of juvenile phenotype at birth in response to variations in the social environment were adaptive, we would expect higher fitness for juveniles released into the same environment that their mother experienced during gestation, because of a pre-adaptation to these environmental conditions. That is to say, we would expect to find a significant interaction between the release and the capture sites, which is not the case (p=0.69). Thus, even if females from different environments produce juveniles that differ in morphology and behaviour, this initial difference does not confer any advantage in these given environmental conditions, and such effects are not likely to be part of adaptive maternal strategies. Post-natal development and juvenile fitness is thus determined only by local environmental conditions, and not by pre-natal effects. In a previous study, where the population density had been experimentally manipulated, similar results were found: clutch size and juvenile size at birth did not affect either juvenile growth or survival (Meylan et al. 2007). In addition, the juvenile phenotype induced by the modification of population density did not appear adaptive (Meylan et al. 2007). All these results suggest that the effects of density or social environment on post-natal juvenile phenotype are most probably not included in an adaptive maternal strategy, but would rather be constrained by the pre- and post-natal environments.

Females in Y+ populations would thus have been forced to reduce their clutches (for mixed females) or to produce lower-quality juveniles because of a strong social stress during gestation, and the increased juvenile fitness in these populations would only be a positive side-effect of the decrease in local density. On the other hand, females in O+ populations would produce larger clutches or higher-quality juveniles because of more favourable environmental conditions, but their offspring would suffer from the increase in local density experienced in their post-natal environment.

Conclusion

We found differential offspring growth and survival in populations where the local frequencies of colour morphs had been modified. Offspring fitness seemed to be higher in populations where the reproductive success of adult females was lower. However, the adaptive nature of such environmentally-induced maternal effects is not supported. Variability in the social environment between population may generate different environmental constraints (strong social stress versus high density) that affect either female or juvenile fitness negatively. Differences in juvenile and adult fitness between populations may lead to different equilibrium states, which would explain the coexistence in nature of both types of populations (Volis et al. 2002, Kneitel and Chase 2004). The study of the evolution of morph frequency in the manipulated populations in following years could thus help understanding better the role of the different components of the social environment on the evolution of different equilibrium states in colour morphs frequencies and investigating the possibility of alternative population dynamics under different environmental regimes.

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REFERENCES

Amundsen T, Forsgren E, Hansen LTT. 1997. On the function of female ornaments: male bluethroats prefer colorful females. Proceedings of the Royal Society Biological Sciences Series B 264: 1579-1586.

Amundsen T. 2000. Female ornaments: Genetically Correlated or Sexually Selected ? In: Animal Signals: Signalling and Signal Design in Animal Communication (Espmark Y, Amundsen T, Rosenqvist G, eds), pp 133-154. Tapir Academic Press, Trondheim.

Anderson DR, Burnham KP, White GC. 1994. AIC model selection in overdispersed capture-recapture data. Ecology 75: 1780-1793.

Bélichon S, Clobert J, Massot M. 1996. Are there differences in fitness components between philopatric and dispersing individuals? Acta Oecologica 17: 503-517.

Berglund A, Rosenqvist G. 2001. Male pipefish prefer dominant over attractive females. Behavioral Ecology 12: 402-406.

Bleiweiss R. 1997. Covariation of sexual dichromatism and plumage colours in lekking and non-lekking birds: a comparative analysis. Evolutionary Ecology 11: 217-235.

Burns KJ. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus mal plumage. Evolution 52: 1219-1224.

Chapuisat M. 2004. Evolution : social selection for eccentricity. Current Biology 14:R1003-R1004

Clobert J, Lebreton JD, Allainé D. 1987. A general approach to survival rate estimation by recapture or resighting of marked birds. Ardea 75:133-142.

Clobert J, Perrins CM, McCleery RH, Gosler AG. 1988. Survival rate in the great tit *Parus major* in relation to sex, age and immigration status. Journal of Animal Ecology 57: 287-306.

Clobert J, Massot M, Lecomte J, Sorci G, de Fraipont M, Barbault R. 1994. Determinants of dispersal behavior : the common lizard as a case study. In: Lizard Ecology : historical and experimental perspectives (Vitt LJ, Pianka ER, eds), pp183-206. Princeton University Press, Oxford.

Comendant T, Sinervo B, Svensson EI, Wingfield J. 2003. Social competition, Corticosterone and survival in female lizard morphs. Journal of Evolutionary Biology 16: 948-955.

Cormack RM. 1964. Estimates of survival from the sighting of marked animals. Biometrika. 51: 429-438.

de Fraipont M, Clobert J, John-Alder H, Meylan S. 2000. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. Journal of Animal Ecology 69: 404-413.

Doligez B, Clobert J. 2003. Clutch size reduction as a response to increased nest predation rate in the collared flycatcher. Ecology 84: 2582-2588.

Fox CW. 2000. Natural selection on seed beetle egg size in the field and the lab: Variation among environments. Ecology 81: 3029-3035.

Gross M. 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. Philosophical Transactions of the Royal Society Biological Sciences 332: 59-66.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology and Evolution 11: 92-98.

Hamilton WD, May RM. 1977. Dispersal in stable habitats. Nature 269 : 578-581.

Heino M, Metz JAJ, Kaitala V. 1998. The enigma of frequency-dependent selection. Trends in Ecology and Evolution 13: 367-370.

Irwin RE. 1994. The evolution of plumage dichromatism in the New World Blackbirds: social selection on female brightness ? The American Naturalist 144: 890-907.

Johnsen TS, Hengeveld JD, Blank JL, Yasukawa K, Nolan V. 1996. Epaulet brightness and condition in female red-winged blackbirds. Auk 113: 356-362.

Johnson K. 1988. Sexual selection in pinion jays II: male choice and female-female competition. Animal Behaviour 36: 1048-1053.

Jolly GM. 1965 Explicit estimates from capture-recapture data with both dead and immigration-stochastic models. Biometrika 52: 225-247.

Kneitel JM, Chase JM. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecology Letters 7: 69-80.

Lank DB, Smith CM, Hanotte O, Burke T, Cooke F. 1995. Genetic polymorphism for alternative mating behaviour in lekking male ruff (*Philomacus pugnax*). Nature 378: 59-62.

Le Galliard JF, Ferriere R, Clobert J. 2005. Juvenile growth and survival under dietary restriction: are males and females equal? Oikos 111: 368-376.

Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992 Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62: 67-118.

Lecomte J, Clobert J, Massot M. 1992. Sex identification in juveniles of *Lacerta vivipara*. Amphibia-Reptilia 13 : 21-25.

Leturque H. 2002. Evolution du sexe-ratio et de la dispersion en populations structurées. Phd Thesis, Biologie de l'Evolution et Ecologie, Université Montpellier II.

Lorenzon P, Clobert J, Massot M. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. Evolution 55: 392-404.

Maynard Smith J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge, 226 p.

Massot M, Clobert J, Pilorge T, Lecomte J, Barbault R. 1992. Density dependence in the common lizard : demographic consequences of a density manipulation. Ecology 73 : 1742-1756.

Massot M, Clobert J, Lecomte J, Barbault R. 1994. Incumbent advantage in common lizards and their colonizing ability. Journal of Animal Ecology 63: 431-440.

Massot M, Clobert J. 1995. Influence of maternal food availability on offspring dispersal. Behavioral Ecology and Sociobiology 37: 413-418.

Massot M, Clobert J. 2000. Processes at the origin of similarities in dispersal behaviour amog siblings. Journal of Evolutionary Biology 13: 707-719.

Meylan S, Clobert J, Sinervo B. 2007. Adaptive significance of maternal induced density-dependent phenotype. Oikos (in press).

Motro U. 1983. Optimal rates of dispersal. III. Parent-offspring conflict. Theoretical Population Biology 23: 159-168.

Olendorf R, Rodd FH, Punzalan D, Houde AE, Hurt C, Reznick DN, Hughes KA. 2006. Frequency-dependent survival in natural guppy populations. Nature 441: 633-636.

Ord TJ, Stuart-Fox D. 2006. Ornament evolution in dragon lizards: multiple gains and widespread losses reveal a complex history of evolutionary change. Journal of Evolutionary Biology 19: 797-808.

Oxford GS, Gillespie RG. 1998. Evolution and ecology of spider coloration. Annual Review of Entomology 43: 619-643.

Parker GA, Begon M.1986. Optimal egg size and clutch size: Effects of environment and maternal phenotype. The American Naturalist 128: 573-592.

Roulin A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. Biological Review of the Cambridge Philosophical Society 79: 815-848.

Rowland WJ, Baube CL, Horan TT. 1991. Signalling of sexual receptivity by pigmentation pattern in female sticklebacks. Animal Behaviour 42: 243-249.

SAS. 1992. SAS User's Guide: Statistics. SAS Institute, Cary.

Seber GAF. 1965. A note on the multiple-recapture census. Biometrika 52: 249-259.

Shuster SM, Wade MJ. 1991. Equal mating success among male reproductive strategies in a marine isopod. Nature 350: 608-610.

Silverin B. 1998. Stress in birds. Poultry and Avian Biology Reviews 9: 153-168.

Sinervo B, Svensson E, Comendant T. 2000. Density cycles and an offspring quality and quantity game driven by natural selection. Nature 406: 985-988.

Svensson EI, Abbott J, Härdling R. 2005. Female polymorphism, Frequency Dependence, and Rapid Evolutionary Dynamics in Natural Populations. The American Naturalist 165: 567-576.

Thompson CW, Moore IT, Moore MC. 1993. Social, environmental, and genetic factors in the ontogeny of phenotypic differenciation in a lizard with alternative male reproductive strategies. Behavioral Ecology and Sociobiology 33: 137-146.

Trail PW. 1990. Why should lek-breeders be monomorphic? Evolution 44: 1837-1852.

Van Gossum H, Stoks R, De Bruyn L. 2005. Lifetime fitness components in female colour morphs of a damselfly : density- or frequency-dependent selection? Biological Journal of the Linnean Society 86: 515-523.

Vercken E, Massot M, Sinervo B, Clobert J. 2007. Colour polymorphism in females and alternative reproductive strategies in the common lizard *Lacerta vivipara*. Journal of Evolutionary Biology 20: 221-232.

Vercken E, Massot M, Sinervo B, Clobert J. Female colour morphs in the common lizard display alternative offspring dispersal strategies with respect to environmental cues. Submitted.

Vercken E, Clobert J. Female colour polymorphism and social dominance in the common lizard (*Lacerta vivipara*). Submitted.

Vercken E, Sinervo B, Clobert J. Female reproductive success is sensitive to the social environment in the common lizard (*Lacerta vivipara*). In preparation.

Vercken E, Sinervo B, Clobert J. Social environment-dependent dispersal strategies in juvenile common lizards (*Lacerta vivipara*). In preparation.

Volis S, Mendlinger S, Ward D. 2002. Differentiation among populations of *Hordeum spontaneum* along a gradient of environmental productivity and predictability: life history and local adaptation. Biological Journal of the Linnean Society 77: 479-490.

Weiss SL. 2006. Female-specific color is a signal of quality in the striped plateau lizard (*Sceloporus virgatus*). Behavioral Ecology 17: 726-732.

West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. Quarterly Review of Biology 58: 155-183.

White G. 1998. Mark and recapture survival rate estimation. http://www.cnr.colostate.edu/~gwhite/mark/mark.htm

Table 1 : Female density, orange and yellow female frequencies for the four studied populations in 2004, and number of transplanted females in 2004 and 2005.

Population parameter	Population A	Population B	Population C	Population D
Adult female density	160	140	175	100
Orange female frequency	0.42	0.4	0.2	0.21
Yellow female frequency	0.36	0.25	0.37	0.42
Females transplanted in 2004	25	26	26	25
Females transplanted in 2005	23	23	19	19

Table 2: Model selection for capture probability and survival rate. AIC (number of parameters) are reported for the different models. The selected model (lowest AIC) is in bold.

P Phi	CONSTANT	YEAR
CONSTANT	3219.7 (2)	3206.8(3)
YEAR	3220.2 (3)	3207.5 (4)
TREATMENT	3219.0 (3)	3206.5 (4)
MATERNAL COLOUR	3221.7 (3)	3208.7 (4)
SVL	3221.4 (3)	3208.3 (4)
YEAR BY TREATMENT	3216.0 (5)	**3203.0** (6)
YEAR BY COLOUR	3223.9 (5)	3211.2 (6)
YEAR BY SVL	3223.1 (5)	3210.7 (6)
TREATMENT BY COLOUR	3222.8 (5)	3210.2 (6)
TREATMENT BY SVL	3218.8 (5)	3206.6 (6)
COLOUR BY SVL	3219.2 (5)	3206.8 (6)
YEAR BY TREATMANT BY COLOUR	3217.8 (9)	3210.7 (10)
YEAR BY SVL BY COLOUR	3225.5 (9)	3206.6 (10)
TREATMENT BY SVL BY COLOUR	3216.9 (9)	3206.2 (10)
YEAR BY TREATMENT BY SVL BY COLOUR	3222.9 (13)	3210.4 (14)

ANNNEXE VIII: Alternative strategies affect spacing behaviour in female common lizards (*Lacerta vivipara*)

Article en préparation

Alternative strategies affect spacing behaviour in female common lizards (*Lacerta vivipara*)

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Abstract

Spacing patterns are determined by the relative sensitivities of individuals regarding both the habitat characteristics and the presence of other individuals. Therefore, spacing behaviour is expected to differ between distinct classes of individuals, and in particular between alternative strategies. Indeed, as social interactions deeply affect the success of alternative strategies, the spatial distribution of the different strategies should be interrelated. Therefore, the analysis of spatial organization of alternative strategies can help understanding the social mechanisms connecting alternative strategies. In the common lizard, females display a polymorphism in ventral colour (yellow, orange, or mixed) correlated with alternative strategies in reproduction, dispersal, and competitive behaviour. Females are often spatially aggregated around discrete resources in nature, and we predicted that colour morphs should not distribute randomly among these groups, depending on the presence of other morphs and of related individuals. In order to test this hypothesis, we analysed the degree of home range overlap with un-related or related females of each colour morph. We found that females of different colour displayed different spacing behaviours in relation with the presence of the different colour morphs, most probably related to differences in competitive ability. The presence and relative frequency of the different colour morphs might thus spatially structure the social environment, and allow individuals to take adaptive settlement decisions.

Keywords: *spacing behaviour, alternative strategies, female competition, social dominance.*

Introduction

Spacing patterns characterize the mode of distribution of individuals in a population in space and time. The spatial distribution of individuals ultimately affects individual fitness by modulating the respective influence of several factors that contribute to selection (Formica et al. 2004). Indeed, both ecological (food, habitat) and biotic factors (predation, Cowlishaw 1999; parasitism, Boulinier et al. 1996; intraspecific competition, Shier and Randall 2004; kin competition, Gundersen and Andreassen 1998; or kin interactions, Hatchwell et al. 2001) determine the quality of a territory, and spatial variation in these factors will generate spatial heterogeneity in reproductive success (number and quality of mates, offspring survival, Andersson 1994). Different classes of individuals are likely to be more or less sensitive to the intensity of these various selective factors and thus to distribute differently in the environment. Therefore, spacing behaviour is expected to differ between individuals, according to their age (Brotons 2000, Luque-Larena et al. 2004), sex (Wauters and Dhondt 1992, Luque-Larena et al. 2004), or dominance status (Wauters and Dhondt 1992, Formica et al. 2004).

Alternative strategies are complex phenotypic syndromes that differ in a number of traits, such as morphology (Svensson et al. 2005), life-history (Sinervo et al. 2000), or behaviour (Ryan et al. 1992), which allow them to coexist in a population by exploiting differently the environment. The existence of social interactions is thought to be at the origin of the evolution of alternative strategies (Gross 1996). As social processes also affect the spatial organization of a population (the social tolerance of individuals correlating with the amount of overlap in home ranges, Shier and Randall 2004), the spatial distribution of alternative strategies should be especially sensitive to the presence or absence of other individuals depending on their strategy. Indeed, as the fitness of a strategy often depends on frequency-dependent processes (Maynard-Smith 1982, Gross 1996), the spatial distributions of the different strategies are expected to be interrelated. For instance, in the white-throated sparrow, male alternative reproductive strategies segregate into distinct spatial and social niches, which allow them to achieve equal mean fitness (Formica et al. 2004). In addition, alternative strategies may distribute differently not only with respect to the strategies of their conspecifics, but also in function of the presence of related individuals. Indeed, in the side-blotched lizard, one male strategy is characterised by the spatial association between genetically similar individuals, whereas another strategy is characterised by the spatial segregation of genetically similar individuals (Sinervo and Clobert 2003). The spatial organization of a population can thus predict its social organization, and social relationships between different classes of individuals, and between alternative strategies in particular, may be inferred from their degree of promiscuity with kin and non-kin in natural populations.

In the common lizard, females display a polymorphism in ventral colour (yellow, orange, or a mixed coloration) correlated with complex alternative strategies in reproduction (Vercken et al. 2007), dispersal in response to variations of the physical environment (Vercken et al. submitted), and behaviour (Vercken and Clobert submitted). In laboratory staged encounters, the outcome of social interactions was proved to depend on the strategy of both females in the pair, and alternative behavioural patterns between colour morphs were thought to reflect individual differences in competitive ability and social dominance (Vercken and Clobert submitted). Yellow females seemed to be the best competitors and to be socially dominant, whereas orange females would be subordinate individuals. Mixed females might have an intermediate dominance status, which would allow them to dominate orange females while avoiding the costs of competition with yellow females (Vercken et al., in prep1).

In this species, the habitat is heterogeneous, characterised by the distribution of discrete resources (rocks, trees, streams), and individuals aggregate around these resources. Males are territorial, especially during the mating season, whereas females are more promiscuous (Massot 1992), and thus show some degree of social tolerance. However, as competition for resources is thought to be strong between females in this species (Massot et al. 1992, Lecomte et al. 1994), it is likely that these social groups are not constituted of random individuals regarding their competitive ability, dominance status, and/or relatedness. Indeed, offspring dispersal in response to the variations of the social environment was found to be colour-dependent (Vercken et al. in prep2), which might generate colour-specific spacing patterns. In particular, offspring from mixed or orange females decreased their dispersal in response to an increase of the level of local competition (increase in the frequency of yellow females), which might be related to kin cooperation strategies in order to defend resources against higher competitors.

These results suggest that the social repartition of females with regard to the colour of their social environment and the local relatedness might depend on individual colour. Plastic spatial association patterns could allow the different strategies to optimise their fitness in response to the variations in the level of intraspecific competition. The most dominant females (yellow females) are expected to be more territorial than other females, and thus to have fewer neighbours. Subordinate females (mixed or orange females) in particular should avoid the vicinity of higher competitors. In addition, because of their particular dispersal strategies, mixed and orange females are expected to be close spatially to females of the same colour, and maybe to related females.

In order to test these hypotheses, we analysed the distribution patterns of females in a population using a long-term study. We tested if females of different ventral colours were often found within close distance of other unrelated females, and of siblings, and if this pattern was affected by the variations of the social environment.

Methods

The Species

Lacerta vivipara is a small (adult snout-vent length from 50 to 70 mm), live bearing lacertid lizard, which is found throughout Europe and Asia. The population we studied is located on Mont Lozère (Southern France, altitude 1420 m), and is divided into two contiguous zones that differ in structural diversity of the microhabitat (Clobert et al. 1994): a zone with high structural diversity and high lizard densities (high quality zone), and a zone with low structural diversity and lower lizard densities (low quality zone). In this population, the activity season lasts from May to September. Males emerge from hibernation in mid-April, followed by yearlings, and females in mid-May. Mating occurs at female emergence, and gestation lasts for two months (parturition starting in July and lasting for two to three weeks). Females lay a clutch of, on average, five soft-shelled eggs (range 1-12). Offspring hatch within two hours after laying and are immediately independent of their mother. A more detailed description of life history can be found in Clobert et al. (1994).

In this population, adult males are almost always orange whereas adult females can be classified into three colour classes: yellow, orange or a mixed coloration (mixture of yellow and orange). Juveniles start by being melanic, and slowly turn to a pale green ventral colouration when yearlings. Stability of ventral colour arises with sexual maturity (around two years). The visual assessment of ventral colour and classification into discrete colour classes was proved to reflect spectrophotometrical differences (Vercken et al. 2007).

Data set

From 1989 to 2002, females were temporarily removed from the population each year in the beginning of July (1009 females in the 13 years of study), and their capture point was marked. Adults are sedentary, especially in the reproductive period (Massot 1992, Clobert et al. 1994), such that their capture point in July is assumed to be the core area of their territory.

At capture, females were measured (snout-vent length or SVL), weighted, and female ventral colouration was estimated visually using a colour reference. Then, females were kept in the laboratory until parturition, and at birth, offspring were individually marked by toe-clipping and sexed by counting ventral scales (Lecomte et al. 1992). They were then released at the mother's last capture point. Recapture sessions in September and May allowed to record the movements of juveniles born in the laboratory. As natal dispersal takes place within 10 days after birth and is definitive (Léna et al. 1998), spatial position in September or May is assumed to be indicative of the location of an individual's future territory as an adult.

Statistical Analyses

The average home range diameter being around 20m (Massot 1992), we counted for each female the number of other females of each colour morph captured as adults the same year, and whose capture point was distant by less than 15m. Those were considered as 'neighbours', i.e., individuals with whom the female was likely to interact in nature. We analysed the number of yellow, mixed, or orange female neighbours with generalised linear model (GLM procedure, SAS Institute). We included the effects of female density, yellow female frequency, habitat zone, female SVL and female ventral colour as covariates, and the interactions of ventral colour and habitat zone with all the factors (up to three-ways interactions including both colour and habitat zone). The same analyses were performed using a 'neighbouring distance' ranging from 3 to 20 m, with no consequences on the results. Therefore we will present only the results obtained with a distance of 15m.

To increase our sample size for the analysis of the distance between related females, we included all recaptured sisters (females with the same mother), whatever their age at recapture and the year of recapture. We obtained data for 332 females, from 128 different mothers. We counted for each female the number of her sisters that were captured less than 15m away, and calculated the mean per family, to account for the non-independence of data. We analysed the mean number of neighbouring sisters per family with generalised linear model (GLM procedure, SAS Institute). We included the effect of maternal colour and habitat zone, and their interaction, as covariates.

Type III sum of squares was used in all cases. We started with a general model including all the potential effects and the interactions described above. We then dropped the non-significant effects (backward selection), starting with the most complex interaction terms. Only the results of the final model are reported.

Results

The number of yellow, mixed or orange neighbours was always affected by habitat zone (for yellow neighbours, $F_{1,877}=33.94$, $p<0.0001$; for mixed neighbours, $F_{1,875}=44.18$, $p<0.0001$; for orange neighbours, $F_{1,880}=51.53$, $p<0.0001$), density (for yellow neighbours, $F_{1,877}=356.9$, $p<0.0001$; for mixed neighbours, $F_{1,875}=155.28$, $p<0.0001$; for orange neighbours, $F_{1,880}=295.28$, $p<0.0001$), and female SVL (for yellow neighbours, $F_{1,877}=43.47$, $p<0.0001$; for mixed neighbours, $F_{1,877}=12.44$, $p=0.0004$; for orange neighbours, $F_{1,880}=22.32$, $p<0.0001$). Unsurprisingly, females had more neighbours, regardless of their colour, in the high density zone than in the low-density zone, and when density was high. In addition, large females had fewer neighbours than small females.

The mean number of yellow neighbours depended on female colour ($F_{2,877}=3.27$, $p=0.039$).Yellow females had more yellow neighbours (mean number of yellow neighbours: 6.6) than orange (5.6) or mixed females (5.6).

The mean number of mixed neighbours was affected by the frequency of yellow females, in interaction with female colour ($F_{2,877}=5.12$, $p=0.006$). All females had fewer mixed neighbours when the frequency of yellow females was high, but this relationship was stronger for mixed females (Figure 1).

The mean number of orange neighbours did not depend on female colour, alone or in interaction (all $p>0.1$).

The number of sisters living in the same area did not differ between colour morphs ($p=0.27$).

Discussion

According to our predictions, females of different colours do not distribute evenly in the environment. However, contrary to our expectations, we could not find any colour-based difference in kin association, which does not support the hypothesis of colour-related cooperative strategies. Actually, the costs of kin competition seem to be a major evolutionary constraint in this species (Ronce et al. 1998, Meylan et al. 2002, 2004, Le Galliard et al. 2003), and might always overcome the benefits of kin cooperation. Consequently, female spacing behaviour seems to depend mainly on the presence of yellow females, in interaction with the female's own strategy. If yellow females are indeed the highest competitors, then the spacing pattern might be representative of colour-specific sensitivities to the level of local competition.

Distribution of yellow females

Depending on their ventral colour, females differed in the number of yellow females with overlapping home range, yellow females having more yellow neighbours than orange or mixed females. Such a pattern could arise from three different reasons: first, yellow females might have specific habitat requirements, and thus find themselves aggregated in suitable habitat patches. If mixed and orange females had different ecological needs, or only larger niches, they should have fewer yellow neighbours than yellow females. However, if this scenario was true, we would expect to find a biased repartition of the three different colour morphs in the two habitat zones of the studied population, which is not the case (χ^2_2=0.29, p=0.87, n=1008). Therefore, colour morphs do not segregate into different ecological habitats.

A second hypothesis is that yellow females might show some attraction behaviour towards other yellow females (if ventral colour is a cue for relatedness: "green beard hypothesis", Dawkins 1976), and play a strategy of kin association. In that case, we would expect yellow females to have more sisters with overlapping home range than mixed or orange females (because mixed and orange females do not have as many neighbours of the same colour as yellow females). This is not what we found: thus, the aggregated distribution of yellow females is not related to a kin association strategy.

Finally, yellow females could have more yellow neighbours than mixed or orange females, if mixed and orange females intentionally avoided the vicinity of yellow females because of high competition costs with dominant females. This third scenario is indirectly supported by the spatial distribution pattern of females in function of their size: larger females that are probably more competitive (Vercken and Clobert submitted), have fewer neighbours than smaller females. Therefore it seems that non-dominant females or subordinate females avoid the close proximity of dominant females, probably because the costs of competition are higher for a female whose home range overlaps with the home range of a dominant female.

If this last scenario is true, it implies that the presence of yellow females is a strong selective pressure for mixed and orange females, and that these females select territories primarily on the basis of the presence and the density of yellow competitors. In addition, the presence of yellow females also seems to affect the settlement decision of mixed females with regard to the presence of other mixed females. The presence of yellow females could thus be a general indicator of environmental selective pressures that shape morph-specific adaptive spacing strategies.

Distribution of orange and mixed females

Contrary to our predictions, orange or mixed females are not closer to females of the same colour, or to related individuals than yellow females, even when the frequency of yellow females is high. On the contrary, mixed females become even more distant at high frequencies of yellow females. Therefore, it seems that mixed and orange females do not play kin cooperation strategies modulated by the level of competition of the social environment. Instead, the reduction in dispersal rate in response to the increase in the frequency of yellow females might be associated with reduced survival because of increased local kin competition. In that case, we would not observe any effect of the frequency of yellow females on the aggregation of adult mixed and orange females, but rather a negative effect on the density of those females. Indeed, the number of mixed neighbours is negatively affected by an increase in the frequency of yellow females for all colour morphs, which could result from a decreased density of mixed females. This scenario allows to explain the dispersal strategy of mixed and orange females. In the common lizard, kin competition is thought to be a major selective pressure acting on the evolution of dispersal (Ronce et al. 1998, Meylan et al. 2002, 2004, Le Galliard et al. 2003), and orange females are thought to be especially sensitive to kin competition (Vercken et al. 2007). However, mixed and orange females reduced their offspring dispersal in response to an increase of the frequency of yellow females, which is probably correlated with an increase in the level of competition and in the costs of dispersal (Vercken et al. in prep2). If the costs of dispersal in a highly competitive environment are higher than the costs of kin competition, then reduced dispersal is selected. Kin competition would thus affect all colour morphs, but colour-related differences in competitive ability would generate different dispersal and habitat choice strategies. The frequency of yellow females would determine the level of competition of the local environment, and thus generate a spatial heterogeneity in selective pressures, which selects for alternative spacing strategies.

Colour morphs, spacing strategies, and social competition

Yellow females have more neighbours than mixed or orange females, and more yellow female neighbours in particular. This implies that yellow females are aggregated in high densities areas. Within the population, and within the two habitat zones, the environment is heterogeneous: some areas are of high quality, with many resources, and thus have a high carrying capacity; other areas are of poorer quality, and have a lower carrying capacity. Yellow females could have a resource-based spatial repartition, and thus be more frequent in high-quality territories. On the other hand, if mixed and orange females tend to avoid areas with high yellow female frequency, they should be more frequent in low-quality territories.

In a previous experiment, the reproductive success of mixed females was found to be negatively affected by the frequency of yellow females (Vercken et al. in prep1). Thus, if mixed females avoid the vicinity of yellow females and are more frequent in areas where the frequency of yellow females is lower, they might benefit from a local selective advantage. Indeed, the mean reproductive success of mixed females appeared superior to yellow or orange females in a long-term study (Vercken et al. 2007), which might result from an adaptive habitat choice strategy. On the other hand, yellow and orange females seem to achieve equal mean fitness (Vercken et al. 2007, Vercken et al. in prep1), in spite of different competitive ability and social dominance. It is possible that orange females have lower energetic needs (due to lower aggressiveness, Vercken and Clobert submitted), or a different strategy of resources exploitation (less favourable thermoregulation areas, less valuable preys), and thus do not suffer from competition with yellow females. Orange females might also exploit a different 'temporal niche', and thus do not enter agonistic interactions with yellow females. Indeed, common lizards are not active during all the day hours, and different individuals might be spotted in the same vicinity at different times of the day (E. Vercken, pers. obs.). The first and last hours of daylight (before 10 am, after 5 pm), and the hottest hours (between 1 and 3 pm), usually show a reduced level of activity. These less favourable hours could thus be the main hours of activity for subordinate individuals (young or small individuals, and lower competitors), when the probability of agonistic interactions with dominant individuals is low. However, such individual differences in activity pattern remain to be tested.

Conclusion

We found colour-specific spacing patterns in female common lizards, which seem to result from differential sensitivities to intraspecific competition, and to morph-specific competition, whereas kin interactions do not seem to affect spacing behaviour. Such patterns might induce a spatial heterogeneity of the social environment, which is known to promote the evolution of alternative strategies (Heino et al. 1998). Social interactions between individuals of different strategies ultimately affect individual fitness (Vercken et al. in prep1), such that the existence of different social environments might allow individuals to take adaptive settlement decisions. Studies to come should aim at characterising more precisely morph-specific differences in habitat choice and resources exploitation. Precise behavioural data would help understanding better the social mechanisms that limit the costs of female competition in nature, making female spatial cohabitation possible.

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REFERENCES

Andersson M.1994. Sexual Selection. Princeton University Press, Princeton, 624 p.

Boulinier T, Ives AR, Danchin E. 1996. Measuring aggregation of parasites at different host population levels. Parasitology 112: 581-587.

Brotons L. 2000. Winter spacing and non-breeding social system of the Coal Tit *Parus ater* in a subalpine forest. Ibis 142: 657-667.

Clobert J, Massot M, Lecomte J, Sorci G, de Fraipont M, Barbault R. 1994. Determinants of dispersal behavior : the common lizard as a case study. In: Lizard Ecology : historical and experimental perspectives (Vitt LJ, Pianka ER, eds), pp183-206. Princeton University Press, Princeton.

Cowlishaw G. 1999. Ecological and social determinants of spacing behaviour in desert baboon groups. Behavioral Ecology and Sociobiology 45: 67-77.

Dawkins R. 1976. The selfish gene. Oxford University Press, Oxford, 224 p.

Formica V, Gonser RA, Ramsay S, Tuttle EM. 2004. Spatial dynamics of alternative reproductive strategies: the role of neighbors. Ecology 85: 1125-1136.

Gross MR. 1996. Alternative reproductive strategies and tactics : diversity within sexes. Trends in Ecology and Evolution 11: 92-98.

Gundersen G, Andreassen HP. 1998. Causes and consequences of natal dispersal in root voles, Microtus oeconomus. Animal Behaviour 56: 1355-1366.

Hatchwell BJ, Anderson C, Ross DJ, Fowlie MK, Blackwell PG. 2001. Social organization of cooperatively breeding long-tailed tits: kinship and spatial dynamics. Journal of Animal Ecology 70: 820-830.

Heino M, Metz JAJ, Kaitala V. 1998. The enigma of frequency-dependent selection. Trends in Ecology and Evolution 13: 67-370.

Le Galliard JF, Ferriere R, Clobert J. 2003. Mother-offspring interactions affect natal dispersal in a lizard. Proceeding of the Royal Society Biological Sciences Series B 270: 1163-1169.

Lecomte J, Clobert J, Massot M. 1992. Sex identification in juveniles of *Lacerta vivipara*. Amphibia-Reptilia 13: 21-25.

Lecomte J, Clobert J, Massot M, Barbault R. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. Ecoscience 1:300-310.

Léna JP, Clobert J, de Fraipont M, Lecomte J, Guyot G. 1998. The relative influence of density and kinship on dispersal in the common lizard. Behavioral Ecology 9: 500-507.

Luque-Larena JJ, Lopez P, Gosalbez J. 2004. Spacing behavior and morphology predict promiscuous mating strategies in the rock-dwelling snow vole, *Chionomys nivalis*. Canadian Journal of Zoology 82: 1051-1060.

Massot M. 1992. Déterminisme de la dispersion chez le lézard vivipare. PhD Thesis, Université Paris XI, Paris.

Massot M, Clobert J, Pilorge T, Lecomte J, Barbault R. 1992. Density dependence in the common lizard : demographic consequences of a density manipulation. Ecology 73: 1742-1756.

Maynard-Smith J. 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge. 226p.

Meylan S, Belliure J, Clobert J, de Fraipont M. 2002. Stress and body condition as prenatal and postnatal determinants of dispersal in the common lizard (*Lacerta vivipara*). Hormones and Behavior 42: 319-326.

Meylan S, de Fraipont M, Clobert J. 2004. Maternal size, stress and offspring philopatry : an experimental study in the common lizard (*Lacerta vivipara*). Ecoscience 11: 123-129.

Ronce O, Clobert J, Massot M. 1998. Natal dispersal and senescence. Proceedings of the National Academy of Sciences USA 95: 600-605.

Ryan MJ, Pease CM, Morris MR. 1992. A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: testing the prediction of equal fitnesses. The American Naturalist 139: 21-31.

Shier DM, Randall JA. 2004. Spacing as a predictor of social organization in kangaroo rats (*Dipodomys heermanni arenae*). Journal of Mammology 85: 1002-1008.

Sinervo B, Svensson E, Comendant T. 2000. Density cycles and an offspring quality and quantity game driven by natural selection. Nature 406: 985-988.

Sinervo B, Clobert J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. Science 300: 1949-1951.

Svensson E, Abbott J, Hardling R. 2005. Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. The American Naturalist 165: 567-576.

Vercken E, Massot M, Sinervo B, Clobert J. 2007. Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. Journal of Evolutionary Biology 20: 221-232.

Vercken E, Massot M, Sinervo B, Clobert J. Female colour morphs in the common lizard display alternative offspring dispersal strategies with respect to environmental cues. Submitted.

Vercken E, Clobert J. Female colour polymorphism and social dominance in the common lizard (*Lacerta vivipara*). Submitted.

Vercken E, Sinervo B, Clobert J. Female reproductive success is sensitive to the social environment in the common lizard (*Lacerta vivipara*). In preparation.

Vercken E, Sinervo B, Clobert J. Social environment-dependent dispersal strategies in juvenile common lizards (*Lacerta vivipara*). In preparation.

Wauters L, Dhondt AA. 1992. Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. Animal Behaviour 43: 297-311.

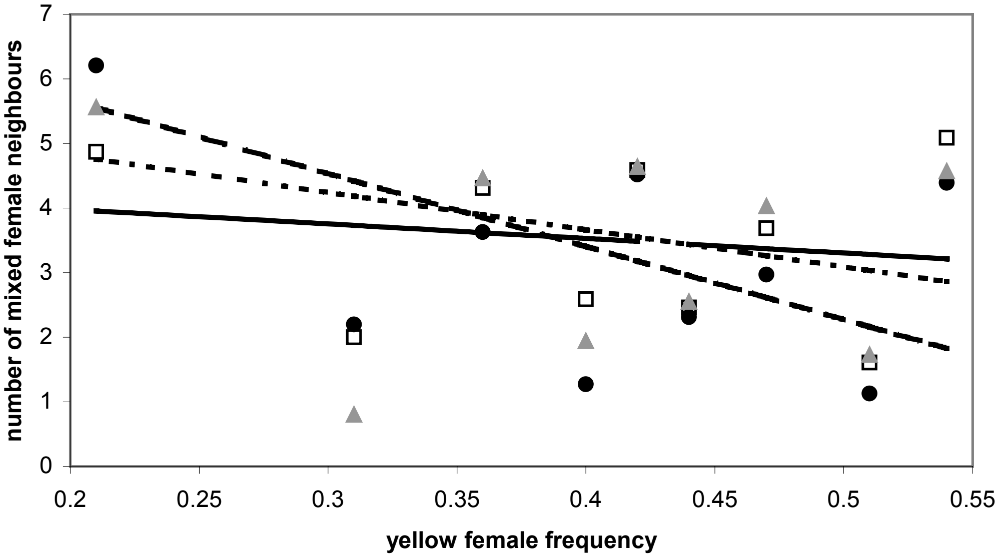

Figure 1: Effect of yellow female frequency on the number of mixed females neighbours (means per frequency and model fit) for yellow (white squares, solid line), mixed (black circles, long-dashes line) and orange females (grey triangles, short-dashed line).

ANNNEXE IX: Interaction between frequency- and density-dependence in cyclic dynamics : the case of the side-blotched lizard

Article soumis

Interaction between frequency- and density-dependence in cyclic dynamics : the case of the side-blotched lizard

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Abstract

The interaction between density-dependence and frequency-dependence has rarely been studied in demographic models, though it might deeply affect the dynamics of polymorphic populations. This interaction should be easily detected in polymorphic populations where density and morph frequency cycle, like *Uta stansburiana* populations which display two female colour morphs. We modelled this species female life history with a discrete time model and we analysed it with numerical simulations. We found that frequency-dependence appears destabilizing compared to density-dependence. Indeed, frequency-dependence enlarges the parameters range of existence for cyclic dynamics, and increases the probability of extinction for rare phenotypes. However, frequency-dependence theoretically favours the evolution of alternative phenotypes by increasing the dimensionality of the system, and allows for the persistence of rare phenotypes by negative frequency-dependent selection. These predictions may be deeply affected by the introduction of demographic stochasticity, which increases the extinction probability of rare phenotypes, especially in cyclic populations. However, the introduction of a spatial structure and the possibility for dispersal allow for the long-term persistence of the two morphs at the metapopulation scale. Thus in such systems, connectivity and dispersal seem to be major forces affecting the maintenance of rare polymorphisms in populations by means of rescue effect.

Keywords: *density-dependence; frequency-dependence; probability of extinction; dispersal; numerical simulations.*

Introduction

Density-dependent and frequency-dependent processes have traditionally been studied separately, as they were considered to belong respectively to the fields of ecology and evolutionary biology. Density-dependence implies that individual fitness, and therefore population regulation, are affected by local density, usually negatively. On the other hand, frequency-dependence refers to a situation where individual fitness, and therefore population regulation, are affected by the relative frequency of the different phenotypes coexisting in the population. These effects are usually mediated through variations in individual fecundity or survival, which are classically modelled as being sensitive to density, or phenotypes frequency, but hardly ever to both variables. However, frequency and density effects on population dynamics are likely to be linked since density determines the degree of competition in the population which affects the intensity of the frequency-dependent selection (Namkoong and Selgrade 1986).

Indeed, density dependence and frequency dependence should interact whenever the success of one strategy is affected by the proportion of individuals pursuing an alternative strategy, and resources required by individuals are limited. In that case, reproductive success is affected both by the frequency of the different strategies, and by the total number of individuals competing for the limited resource (Eadie and Fryxell 1992).

Moreover the idea that frequency dependence and density dependence can act simultaneously is not new, since population geneticists have been developing for a long time models where frequency- and density-dependent selection interact (Slatkin 1979, Namkoong and Selgrade 1986). However, these aspects have been rather neglected in other fields of population biology, especially in the study of population dynamics and demography, the only documented cases of frequency dependence in demographic studies being two-sex models with complex life cycles and mating systems (Caswell and Weeks 1986, Legendre et al.

1999). In these models, the introduction of frequency dependence generates nonlinearities, which may produce bifurcations leading eventually to chaos. The resulting fluctuations of the sex ratio may then trigger extinction under certain conditions (Caswell and Weeks 1986). These predictions seem even more realistic when the effect of demographic stochasticity is added (Legendre et al. 1999, Møller and Legendre 2001), and this is likely to be of extreme importance in the study of the dynamics of polymorphic populations (Calsbeek et al. 2002). Indeed frequency dependent selection is necessary for stable phenotypic polymorphisms to occur (Heino et al. 1998), but it may also initiate complex population dynamics in which one of the morphs is maintained at a low frequency. With the effects of demographic and environmental stochasticity, this rare morph can find itself repeatedly at the edge of extinction and its persistence over time is endangered. However, the distribution of frequency and density dependence between morphs produces complex nonlinearities which make the dynamical evolution of the population hard to predict. Nevertheless, in nature rare strategies can often be observed, sometimes at very low frequencies (Ferrière and Clobert 1992), and apparently manage to maintain themselves in the populations.

Stable polymorphisms require multidimensional feedback environments to emerge, as a consequence of Levin’s competitive exclusion principle, which means that the population must show some ‘structure’ which can be genetic, temporal, physiological or spatial (Heino et al.1998). Spatial structure is expected to be widespread, since in nature most populations are not isolated and are connected by migratory flows to other neighbouring populations (Clobert et al. 2001). This structure could then explain the persistence of rare strategies in natural populations, especially when dispersing ability is morph-dependent (Frank 1986). Therefore connectivity and dispersal are likely to affect local population dynamics, and may allow rare morphs to persist by supplying external sources of individuals and generating rescue effects.

In the case of a polymorphic population the interaction between density dependence and frequency dependence is expected to deeply affect the dynamics, even more when demographic stochasticity and spatial structure are accounted for.

Cyclic dynamics are likely to illustrate the interplay between density and frequency dependence: population cycles in density are often explained by negative feedbacks on density-dependent processes like survival or fecundity (Hassell 1975, Bellows 1981), whereas cycles in the frequency of different genotypes are usually related to frequency-dependent selection acting to maintain a mixed Evolutionary Stable Strategy (Brown and Vincent 1987). A population where density and gene frequencies cycle thus should be under the influence of both density and frequency-dependent processes, of which the respective selective strength may vary. These dynamics are also expected to be sensitive to demographic stochasticity (Calsbeek et al. 2002), which is known to blur the deterministic details of complex dynamics enough to decrease complexity in real populations (Smith and Meade, 1980) although this idea has been challenged (Dennis et al. 2001, Boukal & Berec 2002). Finally, in a metapopulation with local patches displaying cyclic dynamics, dispersal is thought to have a stabilizing effect on global dynamics (Doebeli 1995). Cyclic populations are then fully appropriate to study the effects of density- and frequency-dependence on the dynamics of a rare morph in the population.

The side-blotched lizard *Uta Stansburiana* displays stable population cycles, both on density and on the frequency of genetic morphs correlated with throat colour (Sinervo et al. 2000). Morphs differ in their reproductive strategies: orange-throated females produce many small eggs, whereas yellow-throated females produce fewer but larger eggs. They also differ in their spatial distribution, with orange individuals being overdispersed (Sinervo and Clobert 2003), and in their dispersal behaviour, for dispersal distance or intensity being higher for orange individuals. Both density and female morph frequency cycle with a two-year period, orange-throated females being favoured at low overall density and yellow-throated females at high density.

Sinervo et al. (2000) described these cycles and modelled interactions between orange and yellow females with an evolutionary game theory model. They drew the conclusion that the two female morphs were maintained in an evolutionary stable state of coexistence by frequency-dependent selection, and that stable cycles were due to time lag in population regulation by density-dependent natural selection. However, such a model does not allow for an analysis of the effect of population density, and as density exhibits strong cyclical variations in *Uta stansburiana*, it should affect individual fitness in a non-negligible way. In this article, we propose a complementary approach to the work of Sinervo et al., through the use of demographic models. We developed a simple discrete model based on the ecology of *Uta stansburiana*, allowing us to identify the critic parameters responsible for the cyclic dynamics, especially to test for the respective effects of density and frequency on the dynamics of these populations, and on the persistence of the orange morph in particular.

We first considered a deterministic model and analysed the conditions required for stable cycles to emerge, then we incorporated demographic stochasticity to follow long-term persistence of the population. Finally, we extended the model to a metapopulation and studied its dynamics in presence or in absence of several sources of stochasticity, for different patterns of dispersal.

METHODS

The Species

The side-blotched lizard *Uta stansburiana* exhibits male and female throat-colour morphs which are heritable and associated with distinct life history strategies (Sinervo et al. 2001, reviewed in Sinervo 2001 and Calsbeek and Sinervo 2003). Male morphs (orange, yellow and blue) are associated with three alternative mating strategies analogous to a rock-paper-scissors game (Sinervo and Lively 1996), and cycle in frequency with a four to five-year period. Female morphs (orange and yellow) are associated with two alternative reproductive strategies for clutch size and progeny size, and cycle in frequency with a two-year period, which is coupled to a population density cycle (Sinervo et al. 2000). We focus our analysis on the evolution of these two-year cycles, through the study of female demography. Coupled models of male and female strategies, which incorporate simple payoff matrices for each sex and various genetic models of inheritance can be found in Sinervo (2001).

Life-Cycle

Side-blotched lizards reach sexual maturity within their first year, and adult survival over winter is low. We set the population census in spring just before reproduction, because this is the time of year where most captures are made, and therefore where population parameters are evaluated most precisely. Life history was thus modelled by a life-cycle graph with one age class only (sexually mature individuals). The juvenile class is transient, and does not appear explicitly in the model.

Morphs were modelled as two different classes of individuals, influenced by each other's density and frequency, and in our model yellow and orange females can produce respectively only yellow or orange juveniles (this is not the case in nature where male colour contributes to determine offspring colour). Competitive interactions for resources take place before winter for adults, and in early spring for juveniles. Adults have a size advantage on juveniles, and so do yellow juveniles on orange ones. All density-dependent competitive functions are of exponential form. The forms of the transition functions (place and specificity of density and frequency feedbacks), have been chosen to match the field data and our knowledge of the species biology (Sinervo et al. 1992, Sinervo et al. 2000, B. Sinervo unpublished data).

The three annual reproduction events have been reduced to one, the fecundity parameters being modified to keep the same average annual reproductive rate. Fecundity is assumed to be the sum of a constant minimal fecundity and a density-dependent fecundity function. Yellow female fecundity is affected by total density, whereas orange female fecundity responds to orange female density only. Yellow females are described as "K-strategists": they produce smaller clutches but larger juveniles (Sinervo et al. 2000), and are less affected by competition (Svensson et al. 2001). On the other hand, orange females are "r-strategists": they produce larger clutches but smaller juveniles (Sinervo et al. 2000), and are more sensitive to competition (Svensson et al. 2001), and in particular by competition with other orange females (Svensson et al. 2002).

As orange females are more affected by competition, and as they exhibit much stronger frequency-dependence than yellow females (Sinervo et al. 2000, Comendant et al. 2003), we chose to add a frequency-dependent component in orange juvenile survival, with orange juvenile survival being negatively affected by orange juvenile frequency. Actually the negative density-dependent effect of yellow juveniles density on orange juveniles survival is mediated by the frequency of orange juveniles (see the model below), which means that a high frequency of orange juveniles in the population increases their sensitivity to the competition with the other morph. In order to compare the respective effects of density- and frequency-dependence on population dynamics, we also built an alternative "density-dependent" model where orange juvenile survival is affected by density only.

Model fitting

We designed the model as close as possible to our knowledge of *Uta stansburiana* ecology. The values of demographic parameters were estimated from the field data (for fecundities and survival rates B. Sinervo, personal communication, 2003, see also Sinervo et al. 1992, Sinervo et al. 2000, Svensson et al. 2002). Once these parameters fixed, we restrained the values of theoretical parameters (competition coefficients and competitive abilities) to the range allowing for cycles in density and morph frequencies. Finally, we chose in this range the values giving density and morph frequencies values closest to what is observed in nature.

Parameters values are listed in table 1. A sensitivity analysis was performed for all parameters, the results being detailed in table 1.

Several forms of frequency-dependence were tested (orange juvenile frequency mediating the effect of total juvenile density, of total density in spring…) but in most cases they did not lead to cyclic dynamics compatible with the constraints of the demographic parameters fitted in the model. Thus only the form of frequency-dependence described above was retained in the model.

ULM Software

The system modelled was non-linear because of several density-dependent and/or frequency-dependent processes, and did not allow for an analytical approach. We approached a numerical solution for the deterministic model (both the frequency-dependent and the density-dependent models), using the Newton's method (for details, see Stoer and Bulirsch

2002). The dynamical properties of the model were studied with numerical simulations, with the aid of the ULM (Unified Life Models) computer program (Legendre 2000). The ULM software is distributed freely and allows to model any species life-cycle graph, inter- and intra-specific competition, density-dependence and non-linear systems, environmental and demographic stochasticity, and coupled systems with metapopulations and migrations. It gives numerous kinds of results, including population trajectories and distributions, models sensitivities to changes in parameters, probabilities of extinction and extinction times, and bifurcation diagrams. It has been extensively verified (Caswell 2000) and used in quite a number of research articles (Legendre and Clobert 1995, Ferrière et al. 1996). ULM and Matlab program codes and for the deterministic model can be found in the appendices.

THE MODELS

Single population model

Annual population growth is described by equation 1, with $F_{y/o}$ the fecundity function for yellow and orange females respectively, $S_{y/o}$ the adult survival function, and $s_{y/o}$ the juvenile survival function:

$$\left(N_{y(t+1)}\ ,\ N_{o(t+1)}\right) = \begin{pmatrix} F_y\, s_y + S_y & 0 \\ 0 & F_o\, s_o + S_o \end{pmatrix} \left(N_{y(t)}\ ,\ N_{o(t)}\right) \quad (1)$$

For yellow females, adult survival S_y (equation 2) depends on total juvenile density n_{jt} and total adult density before winter (S_a N_t), with S_a the adult survival during the breeding season and N_t the total adult density. Φ_w is the maximal adult survival during winter, k_y is the coefficient of competition for yellow individuals, and a is the coefficient of competitive ability of juveniles with respect to adult survival.

$$S_y = S_a\ \Phi_w\ exp(-k_y\ (a\ n_{jt} + S_a\ N_t)) \quad (2)$$

Yellow juvenile survival s_y (equation 3) depends on yellow and orange adults densities in spring (S_y N_{yt}) and (S_o N_{ot}), and on yellow and orange juvenile densities n_{jy} and n_{jo}. φ_w is the maximal juvenile survival during winter, b is the relative competitive ability of juveniles compared to adults with respect to juvenile survival, and c is the size advantage of yellow over orange juveniles.

$s_y = \varphi_w \ exp(-k_y (S_y N_{yt}+ S_o N_{ot} + b (n_{jy} + c\, n_{jo}))$ (3)

Yellow female fecundity F_y (equation 4) depends on total adult density only, F being the maximal fecundity term common to both morphs in absence of competition, f_y being the minimal fecundity for yellow females and h_y being the coefficient of competition for reproduction for yellow females.

$F_y = f_y + F\, exp(-h_y\ N_t)$ (4)

For orange females, adult survival S_o (equation 5) depends on total juvenile and total adult density before winter, Φw being the maximal adult survival during winter, and k_o the coefficient of competition for orange individuals.

$S_o = S_a\ \Phi_w\ exp(-k_o (a\, n_{jt} + S_a N_t))$ (5)

Orange juvenile survival (equation 6) depends on yellow and orange adults densities in spring, on juvenile densities and on orange juvenile frequency π_o, φw being the maximal juvenile survival during winter. In the “density-dependent” model the same equation is used, with π_o being constant equal to 0.27, which is the mean of orange juveniles frequency observed in the frequency-dependent model.

$s_o = \varphi_w\ exp(-k_o (S_y N_{yt}+ S_o N_{ot} + b (n_{jo} + \pi_o\ n_{jy})))$ (6)

Orange female fecundity F_o (equation 7) depends on orange adults density, f_o being the minimal fecundity for orange females and h_o the coefficient of competition for reproduction for orange females.

$F_o = f_o + F\ exp(-h_o\ N_{ot})$ (7)

Metapopulation model

In the metapopulation model, three populations identical to the first one are connected. These populations are equidistant, and the probability to emigrate into one or another is equal. Dispersal takes place after competitive interactions, just before census.

Different forms of dispersal rate were used: fixed (equal to 0.2; this is always the case for yellow individuals), density-dependent ($N_t/150$), orange-density-dependent ($N_{ot}/50$), or frequency-dependent (π_o). These rates have been chosen to stay in a numeric range which is ecologically relevant (see Sinervo and Clobert 2003) and so that their mean values are comparable, in order to analyse only their dynamical influence on the system.

In the deterministic model, a symmetric dispersal rate between patches would be neutral since all patches display the same dynamics. Therefore, we introduced asymmetric dispersal (i.e. individuals from only one patch disperse) in the deterministic model in order to assess its effects on local and global dynamics.

Stochastic model

Demographic stochasticity was incorporated by regarding the variables as the realized values of random variables drawn from distributions, whose means are the values used in the deterministic model above. Parameters subject to demographic stochasticity included the survival rates, dispersal rates and fecundities. For survival and dispersal rates, we used a binomial law, and for fecundities a Poisson law. For instance, yellow juvenile survival is calculated for each yellow juvenile as the result of a binomial law with a mean equal to s_y, and yellow female fecundity is calculated for each yellow female as the result of a Poisson law with a mean equal to F_y.

Environmental stochasticity was modelled by having absolute juvenile survival to vary following beta distributions, whose mean are equal to the parameter fixed value in the deterministic model and whose standard deviation are equal to 0.3.

Probabilities of extinction were estimated from Monte Carlo simulations. A thousand trajectories were drawn over a 1000-year time horizon. In the metapopulation model, we distinguished between local (in one patch) and global (in all patches) extinctions.

RESULTS

Deterministic model

With this model, we could find a set of parameters allowing for two-year cycles in density and morph frequency characteristic of the studied population of *Uta stansburiana*. If we consider the sensitivity of the model to the different parameters (table 1), it appears that fecundity and juvenile survival are the most sensitive transitions. Indeed the most sensitive parameters in the model are the coefficient of competitive abilities k_o and b, the fecundity coefficient f_o, the maximal fecundity F and the maximal juvenile survival φ_w. The model is extremely sensitive to the form of the competitive functions and the values of the competitive parameters. Indeed the value of k_o is a critic value. If k_o is increased, the orange morph cannot persist in the system and gets extinct after a few generations. If k_o is decreased, the system does not cycle anymore and the orange morph is always the most frequent morph, even if the yellow morph persists in the population. Thus in our case, the orange morph is highly sensitive to competition, and this particularity is essential to the emergence of cyclic dynamics.

In what follows, we focused our analysis on the effects of variations in maximal fecundity and maximal juvenile survival on population dynamics.

First, only a limited range of values of maximal fecundity allow cycles to appear (fig. 1A), but this range is smaller in the density-dependent model than in the frequency-dependent model. Actually, for the value of maximal fecundity used in the model, the population display cyclic dynamics in the frequency-dependent model (although it is close to the bifurcation point), but not in the density-dependent model (figs 1A). The same results are found when the maximal juvenile survival varies (fig 1B). We studied the equilibrium states for the two models, represented by a growth function $G(N_{ot}, N_{yt})$. The equilibrium points, or fixed points, are defined as the couples (N_{ot}^*, N_{yt}^*) which verify $G(N_{ot}^*, N_{yt}^*) = (N_{ot}^*, N_{yt}^*)$. A fixed point is stable if the absolute value of the eigenvalue at this point is inferior to one, and unstable if it is superior to one. Thus, for the frequency-dependent model, the growth function has three fixed points, which are all unstable, whereas the composite of G with itself $G^2(N_{ot}, N_{yt})$ has two stable equilibrium points. Those fixed points define the stable 2-period cycle that is obtained for the frequency-dependent model. On the other hand, in the density-dependent model, the growth function G has four fixed points, among which one is stable and corresponds to the stable value of (N_{ot}, N_{yt}) observed in the deterministic model.

In addition, in the frequency-dependent model, the interaction between the two morphs generates cyclic dynamics in a region of the parameters space where the two morphs taken in isolation display stable dynamics (fig. 1A and fig. 1B). This is not the case in the density-dependent model, where population cycles are linked to the dynamics of the orange morph, and cycles only appear for parameters values generating cyclic dynamics for the orange morph in isolation (fig. 1A and fig. 1B). Thus frequency-dependence seems to favour the emergence of cyclic dynamics, and for a larger range of parameters values, compared to density-dependence. In all that follows, we will consider variations of maximal fecundity only, as variations of maximal juvenile survival give the same results.

Stochastic model

With demographic stochasticity, the dynamics are qualitatively the same as under the deterministic regime. In all cases, the probability of extinction for the orange morph is quite high whereas the yellow morph never gets extinct, and the interaction between the two morphs is crucial for cyclic dynamics to appear. The probability of extinction for the orange morph is slightly higher in the frequency-dependent model than in the density-dependent model (fig. 2). Thus the enhanced cyclicity generated by the frequency-dependence seems to have a destabilizing effect on the rare orange morph.

Metapopulation model

In the deterministic model, the introduction of (asymmetric) dispersal affects population dynamics at the local scale and limits the range of existence of cyclic dynamics (fig. 3A). At the metapopulation scale dispersal also slightly stabilizes the dynamics by reducing the dynamical possibilities for the emergence of cycles (fig. 3 B) compared to a model without dispersal, the amplitude of this shift increasing with the dispersal rate.

In the model with demographic stochasticity, the introduction of dispersal makes the probability of extinction fall, regardless of the form of the dispersal function (fig. 4).

Dispersal also affects between-patch synchronization: compared to isolated patches with equivalent dynamics connected patches are less synchronized, because demographic stochasticity makes density vary differently between patches. The flux of emigrants, which depends on local density, also varies between patches and so does its effect on local dynamics. The dispersal function then decreases between-patch synchronization, the lowest degree of synchrony corresponding to an orange-density dependent dispersal rate (table 2). Local probabilities of extinction are similar in all cases, but global probability of extinction is negatively affected by the level of synchrony. In the case of strong environmental stochasticity, the minimal global probability of extinction is then reached for an orange-density dependent dispersal rate (table 3).

DISCUSSION

Validity of the model

The model we developed considers only the species demography, and does not include an evolutionary approach. But the main aim of this work was to explore the parameter space allowing for cyclic dynamics to appear, and to study the influence of frequency- and density-dependence on these dynamics. We chose to focus the frame on *Uta stansburiana* ecology, in order to be able to compare its predictions to biological data. Our model seems to give a good approximation of the species demography and ecological characteristics, but several assumptions were made in the modelling which can be discussed with regard to the biological and ecological reality.

In this study, we modelled frequency-dependence by the proportion of orange juveniles. However, an individual perception of the morph frequencies is more likely to concern its immediate neighborhood than the entire population. As a matter of fact, an individual should interact preferentially with its neighbours, so its fitness should be affected mostly by its neighbours color. For *Uta stansburiana* males, spatial distribution is not random for colour and in particular, orange males are over-dispersed (Sinervo and Clobert 2003).

We also modelled the two morphs as two independent classes of individuals, which is certainly not realistic. Models of the allelic dynamics rather than the individuals could give different results. In particular, it is likely that the probability of extinction for the orange allele is far lower than what we observe for the orange morph in our model. Indeed the orange allele could be maintained in heterozygous individuals, in case of codominance or dominance of the yellow allele.

The next step in model building should integrate the alternative male strategies that drive a rock-paper-scissors cycle and examine the interaction between the two cycles. It seems also critical to build an allelic model and a cellular model to compare their predictions to the main results from the population-scale demographic model.

Deterministic model

With the deterministic model, we obtain two-years cycles in density and in morph frequency consistent with the species dynamics in the studied populations. However the parameters values used in the model correspond to period-two dynamics close to the bifurcation point. But we know that some polymorphic populations of *Uta stansburiana* in the Santa Cruz Islands display stable dynamics (B. Sinervo and T. Comendant, personal commuication, 2003). Actually, those stable populations have higher survival and lower fecundity than the continental populations, thus they are located in the region of the parameters space where dynamics are linear in our model. It follows that the cyclic populations should not be located too far from the bifurcation point in the parameters space, if the transition from cyclic to stable dynamics is possible in nature.

The specific value of the parameter k_o was also critical for the emergence of cyclic dynamics. It seems that the high sensitivity to competition of the orange morphs is responsible for an intrinsic instability of the system, independent of frequency-dependence, which allows for cyclic dynamics. However the cycles are triggered by the interactions between the two morphs, since the morphs taken in isolation do not cycle, or cycle for a different set of parameters values, which are not biologically relevant. The interaction between the orange and the yellow morph then increases the theoretical possibilities for cyclic dynamics, with or without frequency-dependence.

It has been known for long that within a scramble competition context, density-dependence can generate cyclic dynamics (May and Oster 1976, Guckenheimer et al. 1977, Hassell 1987) in a given region for a given set of parameters values. Yet it has been severely questioned if such parameters values were biologically meaningful outside viruses, bacteria or other micro-organism (Hassell, Lawton and May 1976, Doebeli and Koella 1994). However it has been suggested that in fact such complex dynamical behaviours were likely to be more widespread (Ferriere and Clobert 1992). In our system density-dependence is sufficient to generate cyclic dynamics, and frequency-dependence only enlarges the parameters range of emergence for such complex dynamics. Also, even if only one morph is affected by frequency-dependent selection, the interaction between the two morphs is necessary for cycles to appear. Then it is not one frequency-dependent morph displaying cyclic dynamics and making the other morph cycle by simple density-dependence. Frequency-dependence makes two morphs that are stable in isolation cycle, and for a larger range of demographic parameters than density-dependence per se.

When the population dynamics cycle, the orange morph is steadily found at low frequencies, and this may affect its persistence when demographic or environmental stochasticity is taken into account. Thus we added stochastic effects in our model in order to study long-term persistence of the orange morph and stability of the system.

Stochastic model

If frequency-dependence favours the emergence of cycles, then it could be seen as a destabilizing force for the population. Indeed, cyclic dynamics make the frequency of orange morph reach very low values, and thus it lowers its probability of persistence in the long term (see fig. 2). It is known that a phenotypic polymorphism can be adaptive when the environment varies and then be maintained by natural selection (Yoshimura and Clark 1991), but in the case of demographic stochasticity, a rare strategy is only expected to be more prone to extinction. Indeed, in our system the orange morph has a very high probability of extinction (superior to 0.9 for the frequency-dependent model). Yet we know that in nature some populations are missing the orange morph (A. Corl and B. Sinervo, personal communication 2003), whereas others have the orange morph but display cyclic dynamics which increase the probability of extinction for the orange morph. The metapopulation model allowed us to study the effects of connectivity and dispersal on the persistence of the orange morph and the likelihood of extinction-recolonization processes (rescue effect).

Dispersal

First of all, the introduction of dispersal in the deterministic model reduces the range of existence for cyclic dynamics and stabilizes the system also at the metapopulation level according with what was previously found (Hastings 1993, Doebeli 1995).

Moreover, it decreases strongly the probability of extinction, even for low dispersal rates (table 3). A metapopulation system then seems to allow the orange morph to persist at a global scale. In a metapopulation system with no dispersal, stochasticity generates spatially uncorrelated variance in fitness, which thereby favours dispersal and allows rescue effects. However, high dispersal synchronizes population dynamics, producing conditions selecting against dispersal (Holt and McPeek 1996). Thus, it is likely that the effective dispersal rate results from a trade-off between these two opposing forces, and that its value is intermediate, which is compatible with the different forms of dispersal rates we used in the model.

More surprisingly, the form of the dispersal function is neutral with respect to its effect on extinction probabilities, so dispersal does not have to be frequency-dependent in our system. However, dispersal has been shown empirically to be condition dependent, in particular with respect to density and, indeed it has been proven theoretically that condition-dependent dispersal strategies are superior over non plastic ones in many situations (McPeek and Holt 1992, Travis et al. 1999, Clobert et al. 2001). With a strong environmental stochasticity, the global probability of extinction is negatively correlated with the degree of synchrony between patches, so the lowest probability of extinction is obtained for the model with orange-density dependent dispersal rate. In our case, an orange density-dependent dispersal rate could be selected, since it is associated to the lowest degree of between-patches synchrony, whereas the highest is reached for a fixed dispersal rate (table 2).

Finally, we considered that dispersal is always successful. But this is hardly ever the case in nature, and dispersal costs often deeply modify model predictions. In our case, it has been shown that in a metapopulation system where all patches are ecologically identical, a cost to dispersal can generate complex evolutionary dynamics, and induce an evolutionary cycle in the phenotype space (Doebeli and Ruxton 1997). So it is likely that the introduction of a dispersal cost would not stabilize the system.

Evolution of the orange morph

Frequency-dependence and the interaction of the two morphs generate cyclic dynamics which destabilize the orange morph and increase its probability of extinction. Then the orange morph appears rather unstable and its persistence is tightly linked to its dispersal ability, which could explain the evolution of this morph despite its tendency to extinction. Indeed in a spatially structured and temporally variable environment, i.e. a multidimensional environment, evolution can favour the emergence of alternative phenotypes, and in particular of phenotypes displaying highly complex dynamics. These phenotypes can persist if they develop a high dispersal rate, and they typically coexist with low dispersing phenotypes showing stable dynamics when alone (Johst et al. 1999).

Here the orange morph exhibits frequency-dependence, which generates complex dynamics in coexistence with the “stable” yellow morph, stable meaning here density-dependent only and not subject to extinction when taken in isolation. Moreover the orange morph has a higher reproductive rate than the yellow morph. In small populations in a context of scramble competition, theoretical models predict that dispersal increases with the reproductive rate (Travis et al. 1999). The orange morph should then display a higher dispersal rate, and this has been verified in nature, for both male and female progeny (Sinervo et al. 2006).

In that context, the orange morph appears like a “disturbing” phenotype, which can evolve in populations by exploiting a precise part of the phenotype space that is not used by the yellow morph. In populations where the orange morph is not present, the yellow morph may have increased possibilities to explore the phenotype space and to adjust plastically its own strategy, and thereby become more persistent even in a variable environment. It would be interesting to follow demography in such monomorphic populations, and especially their potential for plasticity, to determine the degree to which the emergence of the orange morph can be considered as a destabilizing event on the yellow morph demography.

The invasion of the orange morph and the introduction of frequency-dependence made the social environment at least two-dimensional (Heino et al. 1997) and correspondingly increased the degree of non-linearity in the system. This increase in the dimensionality could have allowed the invasion and the evolution of a third strategy, the blue strategy, which is present in males and females. In this regard, the yellow morph could be seen as a ‘stable’ ancestral morph, and the two other morphs would have evolved secondarily by taking advantage of the increase in the complexity of the social system.

CONCLUSION

Our study demonstrates that the cyclic dynamics of *Uta stansburiana* populations are enhanced by frequency-dependent demographic processes, and that female morphs frequencies may not be at an equilibrium state. Even if the two morphs have the theoretical potential for being a Mixed Evolutionary Stable Strategy (Sinervo et al. 2000), the demographical constraints due to stochasticity could destabilize the system enough to lead to the extinction of one morph. Actually, the orange morph could be an unstable dispersing morph, maintained in the populations by extinction-recolonization events.

The model was built to describe the demography of a particular species, but most of its results can be extended to any species with similar characteristics. In particular, all dynamical properties as the emergence of cycles, the destabilizing effect of frequency-dependence, or the high extinction rate associated to cyclic dynamics should apply to any system close to the bifurcation point, or to species showing a natural tendency to cycle. In particular, semelparous or quasi-semelparous species are expected to be prone to strong population regulation, and therefore particularly sensitive to density- and frequency-dependent effects generating cyclic dynamics.

Moreover, we saw that even if frequency-dependence is necessary for the emergence of new strategies, it may increase their extinction rate if they are maintained at a low frequency in a closed population. The importance of connectivity and spatial structure for the maintenance of polymorphism that we highlighted in our study can be generalized to all populations with rare morphs or rare strategies.

Finally, the dynamics appeared highly sensitive to the model structure and parameters. All the qualitative results could be obtained by following the effects of the variation in either of the two most sensitive parameters of the model, but these results were strongly dependent of the position of the frequency-dependent function in the model. More theoretical work is needed on life-cycles and life-history parameters to identify precisely all the general effects of frequency-dependence on population dynamics.

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Appendix 1 : ULM program for the deterministic model

```
{ Uta stansburiana
{deterministic model
defmod uta(2)
mat : aoy
vec : voy
defvec voy(2)
no, ny
defmat aoy(2)
fo*soj + sa*sow, 0
0, fy*syj + sa*syw

defvar njo= fo*no
defvar njy = fy*ny
defvar nj = njo + njy
defvar nt = no + ny
defvar freqo = no/nt

{orange females fecundity
defvar fo = fomin + fabs*exp(-ho*no)
defvar fomin = 4.8
defvar fabs= 6.7
defvar ho = 0.008
```

```
{orange females survival during breeding season
defvar sa = 0.47

{orange females survival during winter
defvar sow=sawabs*exp(-ko*(a*nj + sa*nt ))
defvar a= 0.2
defvar ko = 0.015
defvar sawabs = 0.8

{orange juveniles survival
defvar soj=sjabs*exp(-ko*(sa*sow*no + sa*syw*ny + b*(njo+pio*njy)))

{frequency-dependent model
defvar pio = njo/(njo+njy)
{density-dependent model
{defvar pio=0.27
defvar b=0.9
defvar sjabs=0.84

{fecundity of yellow females
defvar fy = fymin + fabs*exp(-hy*nt)
defvar fymin = 3.94
defvar hy = 0.005

{yellow females survival during winter
```

```
defvar syw = sawabs*exp(-ky*(a*nj+ sa*nt))
defvar ky = 0.008


{yellow juveniles survival
defvar syj = sjabs*exp(-ky*(sa*sow*no + sa*syw*ny + b*(njy + c*njo)))
defvar c= 0.8


{initial population size
defvar no = 10
defvar ny = 50
```

Appendix 2 : Matlab program for the deterministic model

```
%Uta stansburiana
%deterministic model
%%%%
%initial populations

%orange initial population size ratio
no = 10

%initial yellow population size ratio
ny = 50

%total initial population
nt=no+ny;

%population and vector initialisation
pop=[];
voy=[no;ny];

%%%%
%max time
TMAX=1000;
```

```
%iteration start
for time=0:TMAX,


    %%%%
    % juveniles populations


    %%%%%%%%%%%%%%%%%%%%%%%%%%%%%
    %orange juveniles population


    %orange females fecundity
    fomin = 4.8;
    fabs = 6.7;
    ho = 0.008;
    fo = fomin + fabs*exp(-ho*no);


    %orange juveniles population at t+1
    njo = fo*no;


    %%%%%%%%%%%%%%%%%%%%%%%%%%%%%
    %yellow juveniles population


    %fecundity of yellow females
    fymin = 3.94;
    hy = 0.005;
```

```
fy = fymin + fabs*exp(-hy*nt);


%yellow juveniles population at t+1

njy = fy*ny;


%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

%total juveniles population

nj = njo + njy;


%%%%

% adults populations


%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

%adults survival


%females survival during breeding season

sa = 0.47;


%orange females survival during winter

a = 0.2;

ko = 0.015;

sawabs = 0.8;

sow = sawabs*exp(-ko*(a*nj + sa*nt ));
```

```
%yellow females survival during winter
ky = 0.008;
syw = sawabs*exp(-ky*(a*nj+ sa*nt));


%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%orange adults population


%frequency-dependent model
pio = njo/(njo+njy);


%density-dependent model
%pio=0.27;


%orange juveniles survival
b = 0.9;
sjabs = 0.84;
soj = sjabs*exp(-ko*(sa*sow*no + sa*syw*ny + b*(njo+pio*njy)));


%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%yellow adults population


%yellow juveniles survival
c = 0.8;
syj = sjabs*exp(-ky*(sa*sow*no + sa*syw*ny + b*(njy + c*njo)));
```

```
    %%%%%%%%%%%%%%%%%%%%%%%%%%%%%
    %filling matrix aoy
    aoy=[fo*soj+sa*sow, 0;
        0, fy*syj + syw*sa];

    %adult populations at t+1
    voy=aoy*voy;

 %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
    %needed variables

    %orange adults population at t+1
    no = voy(1);

    %yellow adults population at t+1
    ny = voy(2);

    %total adults population
    nt = no + ny;

    %save results in pop variable
    pop=[pop;[no njo ny njy nt nj]];

%iteration end
end;
```

REFERENCES

Bellows, T.S., 1981. Models for Density Dependence. Journal of Animal Ecology, 50: 157-180.

Boukal, D.S., Berec, L., 2002. Single species models of the Allee effect : extinction boundaries, sex ratios and mate encounters. Journal of Theoretical Biology, 218: 375-394.

Brown, J.S., Vincent, T.L., 1987. Coevolution as an Evolutionary Game. Evolution, 41: 66-79.

Calsbeek, R., Sinervo, B., 2003. Uncoupling direct and indirect components of female choice in the wild. Proceedings of the National Academy of Sciences of the USA 99: 14897-14902.

Calsbeek, R., Alonzo, S.H., Zamudio, K., Sinervo, B., 2001. Sexual selection and alternative mating behaviours generate demographic stochasticity in small populations. Proceeding of the Royal Society Biological Sciences Series B 269: 157-164.

Caswell, H., 2000. Matrix Population Models (second edition). Sinauer Associates, Sunderland, 727 pp.

Caswell, H., Weeks, D.E., 1986. Two-sex models : Chaos, extinction, and other dynamic consequences of sex. The American Naturalist, 128: 707-735.

Comendant, T., Sinervo, B., Svensson, E., Wingfield, J., 2003. Social competition, corticosterone and survival in female lizard morphs. Journal of Evolutionary Biology, 16: 948-955.

Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D. (Editors), 2001. Dispersal. Oxford University Press, Oxford, 452 pp.

Dennis, B., Desharnais, R.A., Cushing, J.M., Henson, S.M., Costantino R.F., 2001. Estimating chaos and complex dynamics in an insect population. Ecological Monographs, 71: 277-303.

Doebeli, M., 1995. Dispersal and Dynamics. Theoretical Population Biology, 47: 82-106.

Doebeli, M., Koella, J.C., 1994. Sex and population dynamics. Proceedings of the Royal Society London Biological Sciences Series B, 257: 17-23.

Doebeli, M., Ruxton, G.D., 1997. Evolution of Dispersal Rates in Metapopulation Models : Branching and Cyclic Dynamics in Phenotype Space. Evolution, 51: 1730-1741.

Doebeli, M., Dieckmann, U., 2000. Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions. The American Naturalist, 156: S77-S100.

Eadie, J.M., Fryxell, J.M., 1992. Density Dependence, Frequency Dependence, and Alternative Nesting Strategies in Goldeneyes. The American Naturalist, 14: 621-641.

Ferrière, R., Clobert, J., 1992. Evolutionary stable age at first reproduction in a density-dependent model. Journal of Theoretical Biology, 157: 253-267.

Ferrière, R., Sarrazin, F., Legendre, S., Baron, J.-P., 1996. Matrix population models applied to viability analysis and conservation: Theory and practice with ULM software. Acta Oecologica, 17: 629-656.

Frank, A.S., 1986. Dispersal polymorphisms in subdivided populations. Journal of Theoretical Biology, 122: 303-309.

Guckenheimer, J., Oster, G., Ipaktchi, A., 1977. The dynamics of density dependent population models. Journal of Mathematical Biology, 4: 101-107.

Hansell, R.I.C., Brown, D.B., 1987. Convergence to an evolutionary stable strategy in the two-policy game. The American Naturalist, 130: 929-940.

Hassell, M.P., 1975. Density-dependence in single-species models. Journal of Animal Ecology, 44: 283-296.

Hassell, M.P., Lawton, J.H., May, R.M., 1976. Patterns of dynamical behaviour in single-species populations. Journal of Animal Ecology, 42: 495-507.

Heino, M., Metz, J.A.J., Kaitala, V., 1997. Evolution of mixed maturation strategies in semelparous life histories: The crucial role of dimensionality of feedback environment. Philosophical Transactions of the Royal Society of London B, 352:1647-1655.

Heino, M., Metz, J.A.J., Kaitala, V., 1998. The enigma of frequency-dependent selection. Trends in Ecology and Evolution, 13: 367-370.

Holt, R.D., McPeek, M.A., 1996. Chaotic population dynamics favors the evolution of dispersal. The American Naturalist, 148: 709-718.

Johst, K., Doebeli, M., Brandl, R., 1999. Evolution of complex dynamics in spatially structured populations. Proceedings of the Royal Society London Biological Sciences Series B, 266: 1147-1154.

Legendre, S., 2000. ULM software. http://www.snv.jussieu.fr/Bio/ulm/ulm.html

Legendre, S., Clobert, J., 1995. ULM, a software for conservation and evolutionary biologists. Journal of Applied Statistics, 22: 817-834.

Legendre, S., Clobert, J., Møller, A.P., Sorci, G., 1999. Demographic stochasticity and social mating system in the process of extinction of small populations : the case of passerines introduced to New Zealand. The American Naturalist, 153: 449-463.

May, R.M., Oster, G.F., 1976. Bifurcations and dynamic complexity in simple ecological models. The American Naturalist, 110: 573-599.

Møller, A.P., Legendre, S., 2001. Allee effect, sexual selection and demographic stochasticity. Oikos, 92: 27-34.

Namkoong, G., Selgrade, J.F., 1986. Frequency-dependent selection in logistic growth models. Theoretical Population Biology, 29: 64-86.

Sinervo, B., 2001. Runaway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. Genetica, 112-113: 417-434.

Sinervo, B., Lively, C.M. 1996. The rock-paper-scissors game and the evolution of alternative male reproductive strategies. Nature, 380: 240-243.

Sinervo, B., Clobert, J., 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. Science, 300: 1949-1951.

Sinervo, B., Doughty, P., Huey, R.B., Zamudio, K. 1992. Allometric engineering : a causal analysis of natural selection on offspring size. Science, 258: 1927-1930.

Sinervo, B., Svensson, E., Comendant, T., 2000. Density Cycles and an offspring quantity and quality game driven by natural selection. Nature, 406: 985-988.

Sinervo, B., Bleay, C., Adamopoulou, C., 2001. Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. Evolution, 55: 2040-2052.

Sinervo, B., Calsbeek, R., Comendant, T., Both, C., Adamopoulou, C., Clobert, J., 2006. Genetic and maternal determinants of effective dispersal: the effect of sire genotype and size at birth in side-blotched lizards. The American Naturalist, 168: 88-99.

Smith, R.H., Meade, R., 1980. The dynamics of dicrete-time stochastic models of population growth. Journal of Theoretical Biology, 86: 607-627.

Stoer, J., Burlisch, R., 2002. Introduction to Numerical Analysis (third edition). Springer, New York, 768 pp.

Svensson, E.I., Sinervo, B., Comendant, T., 2001. Condition, genotype-by-environment interaction, and correlational selection in lizard life-history morphs. Evolution, 55: 2053-2069.

Svensson, E.I., Sinervo, B., Comendant, T., 2002. Mechanistic and experimental analysis of condition and reproduction in a polymorphic lizard. Journal of Evolutionary Biology, 15: 1034-1047.

Travis, J.M., Murrell, D.J., Dytham, C., 1999. The evolution of density-dependent dispersal. Proceedings of the Royal Society London Biological Sciences Series B, 266: 1837-1842.

Yoshimura, J., Clark, C.W., 1991. Individual adaptations in stochastic environments. Evolutionary Ecology, 5: 253-267.

Table 1: Numerical values for the parameters used in the deterministic model (the range of possible values considering the constraints imposed by parameters estimated in the field is indicated for competition parameters), sensitivity and elasticity of model growth rate to variation of each parameter

Parameter	Value	Sensitivity	Elasticity
S_a	0.47	-0.035	-0.027
Φ_w	0.8	-0.014	-0.017
φ_w	0.84	0.687	0.925
F	6.7	-0.083	-0.891
f_o	4.8	-0.076	-1.337
f_y	3.9	-0.017	-0.248
a	0.2	-0.117	-0.037
b	0.9	-1.713	-2.47
c	0.8	0	0
k_o	0.015 [0.012 ; 0.04]	-112.56	-2.7
k_y	0.008 [0.007 ; 0.011]	7.438	0.095
h_o	0.008 [0 ; 0.01]	4.694	0.06
h_y	0.005 [0 ; 0.007]	5.172	0.041

Table 2: Coefficient of temporal correlation (R_o) between orange populations for different dispersal rates

Dispersal rate	Null	Fixed	Density-dependent	Orange-density dependent	Orange-frequency dependent
R_o	0.69	0.4	0.3	0.23	0.35

Table 3: Total (P_t) probability of extinction for the orange morph in a model, and mean number of local extinction events per population (L_e) with or without environmental stochasticity

Dispersal rates	No environmental stochasticity	Strong environmental stochasticity
Null	P_t= 0.87	P_t= 0.99
	L_e= 0.81	L_e= 0.99
Fixed	P_t= 0.005	P_t= 0.085
	L_e = 4.61	L_e = 12.5
Density-dependent	P_t= 0.005	P_t= 0.094
	L_e = 8.26	L_e = 19.99
Orange-density	P_t= 0.006	P_t= 0.085
dependent	L_e =8.1	L_e = 26.17
Orange-frequency	P_t= 0.006	P_t= 0.081
dependent	L_e = 8.98	L_e = 17.89

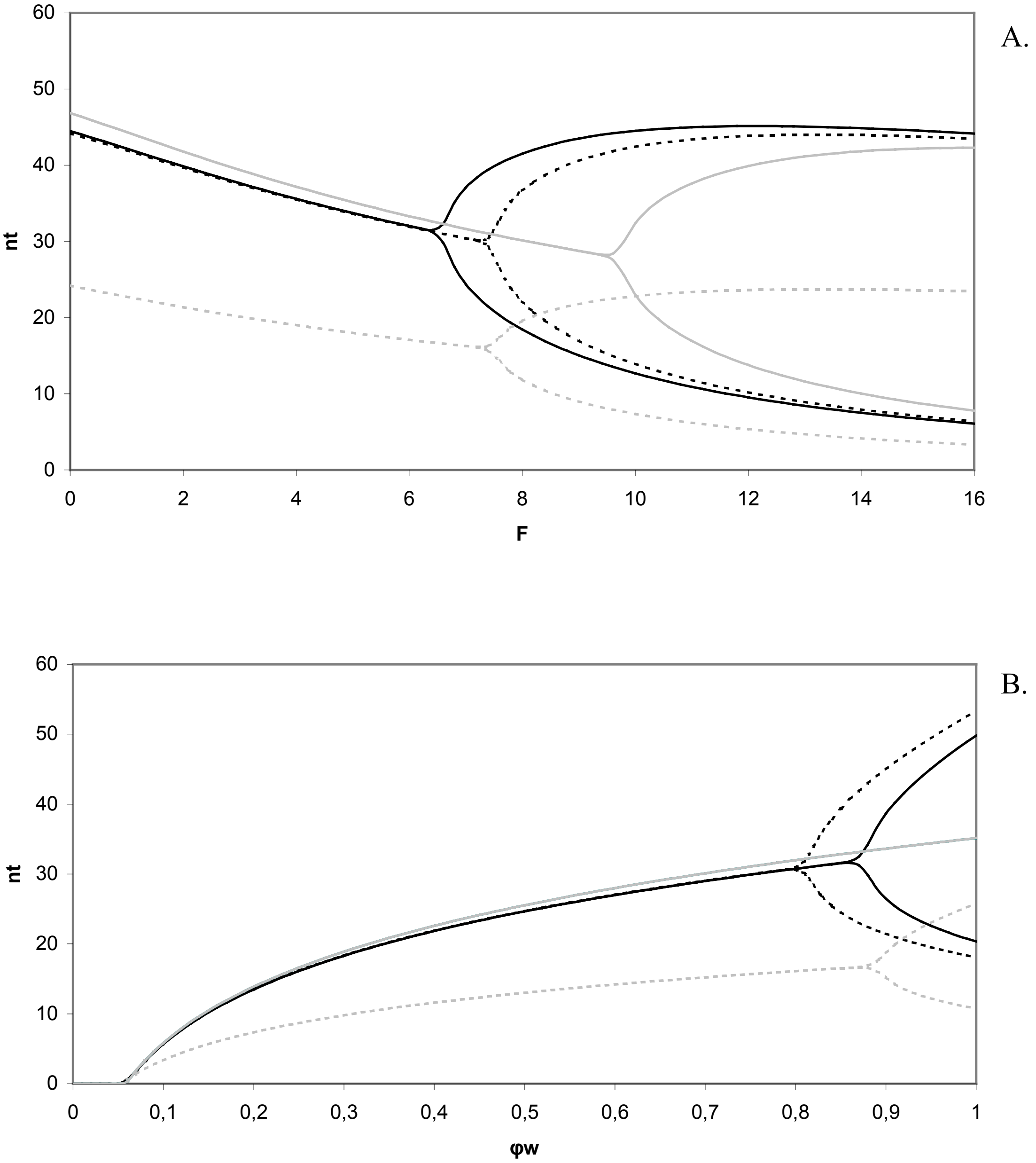


Figure 1 : Bifurcation diagrams of a yellow population (-----), an orange population (——), or a mixed population in the density-dependent (-----) or in the frequency-dependent model (——). A. For different values of maximal fecundity. B. For different values of maximal juvenile survival. All other parameters are fixed and their values correspond to those used in the deterministic model.

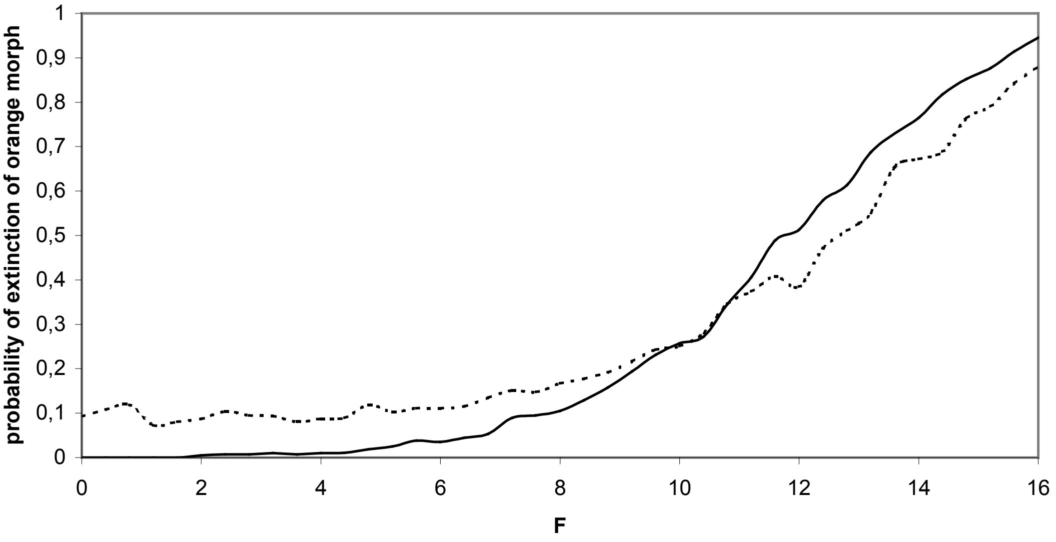
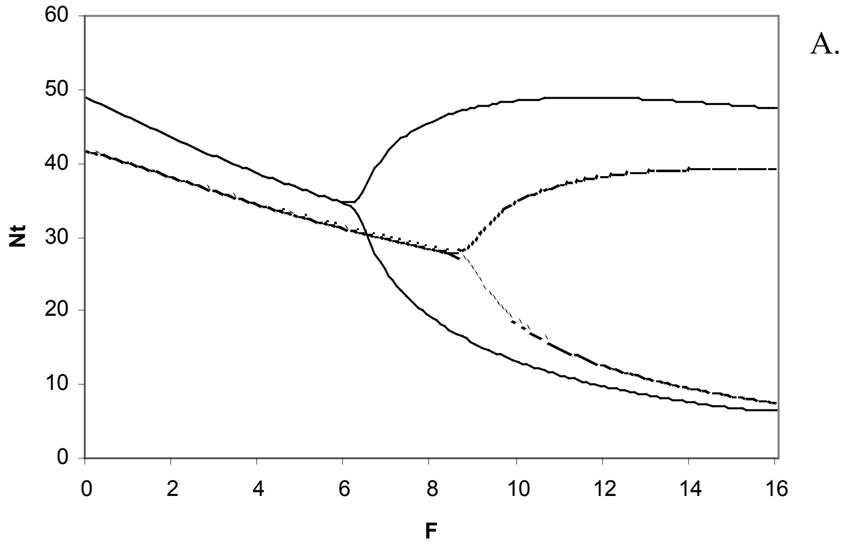


Figure 2 : Probability of extinction for the orange morph for different values of maximal fecundity in the frequency-dependent model (—) and in the density-dependent model (---)



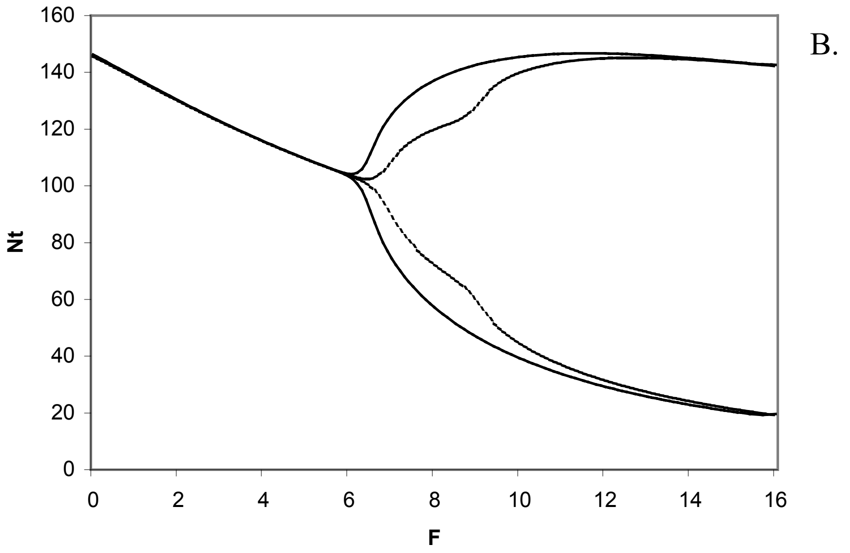


Figure 3: Bifurcation diagram for a mixed population for different values of maximal fecundity in the single population model (——) and in a metapopulation model with a fixed dispersal rate of 0.2 (----). All other parameters are fixed and their values correspond to those used in the deterministic model. A. At the population scale. B. At the metapopulation scale.

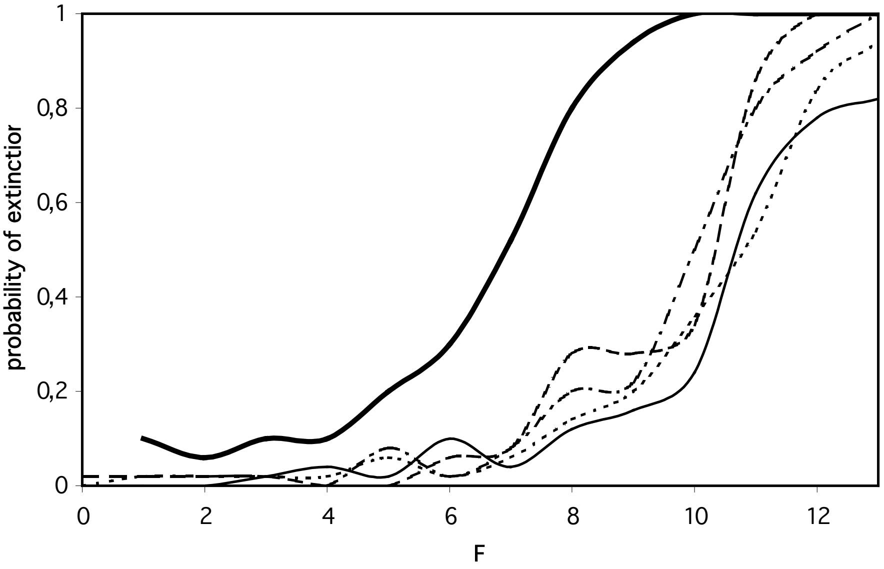


Figure 4: Probabilities of extinction of orange populations for different values of maximal fecundity with no dispersal (——), or with a fixed (----), density-dependent (— - —), orange-density dependent (— —), or frequency dependent (——) dispersal rate.

Résumé

Un polymorphisme est défini par la coexistence au sein d'une population de variants phénotypiques discrets pour un caractère donné. Dans la plupart des cas, de nombreux traits morphologiques, physiologiques ou comportementaux sont corrélés au caractère polymorphe, qui devient alors le marqueur d'un syndrome phénotypique particulier, ou stratégie alternative. Chez le lézard vivipare, les femelles montrent un polymorphisme de couleur ventrale, celle-ci pouvant être jaune, orange ou mixte (mélange de jaune et d'orange). Chez cette espèce, les conditions écologiques sont favorables à l'évolution de stratégies alternatives, qui pourraient être signalées par le polymorphisme de couleur ventrale. Au cours de cette thèse, j'ai cherché à tester cette hypothèse, en caractérisant les différences morphologiques, comportementales, et d'histoire de vie entre les morphes de couleur. Il semble que les couleurs ventrales soient corrélées à des syndromes phénotypiques complexes, définissant des stratégies alternatives. J'ai également cherché à identifier le mécanisme sélectif permettant le maintien de ce polymorphisme dans les populations naturelles, en étudiant les effets d'une manipulation de la fréquence des morphes sur la fitness des individus. Sous l'hypothèse d'un déterminisme génétique simple de la couleur ventrale, les femelles hétérozygotes (couleur mixte) bénéficieraient d'un avantage sélectif dans certains contextes sociaux, ce qui permettrait le maintien du polymorphisme dans un environnement spatialement hétérogène. Les exemples de stratégies alternatives chez les femelles restent rares, et cette étude confirme l'importance de la compétition sociale dans l'évolution de ces stratégies. Dans un contexte phylogénétique, la similarité des résultats obtenus chez le lézard vivipare avec le système du lézard à flancs tachetés, *Uta stansburiana*, souligne également la généralité des processus à l'origine de l'évolution des stratégies alternatives, aussi bien chez les femelles que chez les mâles, et ouvre des perspectives à plus large échelle sur les conséquences des polymorphismes de stratégies sur la dynamique des populations.

Mots-clés : polymorphisme de couleur ; stratégies alternatives ; compétition sociale ; overdominance ; fréquence-dépendance.