



## Research

**Cite this article:** Cotto O, Massot M, Ronce O, Clobert J. 2015 Dispersal as a source of variation in age-specific reproductive strategies in a wild population of lizards. *Proc. R. Soc. B* **282**: 20151741.

<http://dx.doi.org/10.1098/rspb.2015.1741>

Received: 21 July 2015

Accepted: 2 November 2015

**Subject Areas:**

ecology, evolution

**Keywords:**

dispersal syndrome, ageing, lizard, wild population

**Author for correspondence:**

Olivier Cotto

e-mail: [oliviercotto@hotmail.fr](mailto:oliviercotto@hotmail.fr)

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2015.1741> or via <http://rspb.royalsocietypublishing.org>.

# Dispersal as a source of variation in age-specific reproductive strategies in a wild population of lizards

Olivier Cotto<sup>1,4</sup>, Manuel Massot<sup>2</sup>, Ophélie Ronce<sup>1</sup> and Jean Clobert<sup>3</sup>

<sup>1</sup>Université Montpellier 2, CNRS, IRD, EPHE, Institut des Sciences de l'Evolution, CC65, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France

<sup>2</sup>UMPC, CNRS, Institut d'Ecologie et des Sciences de l'Environnement de Paris, 7 quai Saint Bernard, CC 237, 75252 Paris Cedex 05, France

<sup>3</sup>Station d'Ecologie Experimentale du CNRS, 09200 Moulis, France

<sup>4</sup>Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599, USA

Dispersal syndromes describe the patterns of covariation of morphological, behavioural, and life-history traits associated with dispersal. Studying dispersal syndromes is critical to understanding the demographic and genetic consequences of movements. Among studies describing the association of life-history traits with dispersal, there is anecdotal evidence suggesting that dispersal syndromes can vary with age. Recent theory also suggests that dispersive and philopatric individuals might have different age-specific reproductive efforts. In a wild population of the common lizard (*Zootoca vivipara*), we investigated whether dispersive and philopatric individuals have different age-specific reproductive effort, survival, offspring body condition, and offspring sex ratio. Consistent with theoretical predictions, we found that young dispersive females have a higher reproductive effort than young philopatric females. Our results also suggest that the early high investment in reproduction of dispersive females trades-off with an earlier onset of senescence than in philopatric females. We further found that young dispersive females produce smaller offspring in lower body condition than do young philopatric females. Overall, our results provide empirical evidence that dispersive and philopatric individuals have different age-specific life-history traits.

## 1. Introduction

Dispersal syndromes describe the patterns of covariation of morphological, behavioural, and life-history traits associated with dispersal. Dispersal syndromes impact the demographic and genetic consequences of dispersal and are thus of primary importance in the contexts of invasions and range shift in response to environmental variations such as climate warming [1]. Several proximate and ultimate factors have been identified to cause the association of dispersal with other traits and many studies have described differences in phenotypes between dispersive and philopatric individuals (see reviews in [2,3]). While there is evidence for a frequent association of dispersal with specific morphological or behavioural traits (e.g. [4] for offspring dispersal, [5] for aggressiveness, and less cooperation in dispersers), no clear evidence for a general consistent association of dispersal with life-history traits emerges ([3], but see [6]).

Interestingly, a few empirical studies suggest that life-history syndromes associated with dispersal can vary with age [7–10] which can be a source of discrepancies in the results from empirical studies investigating life-history dispersal syndromes. For example, Bouwhuis *et al.* [10] found that immigrant great tit (*Parus major*) females achieved a similar reproductive output to resident females but suffer higher rates of reproductive senescence. Hanski *et al.* [9] found that females of the butterfly *Melitea cinxia* born in recently colonized sites have higher fecundity when they are young and have a shorter lifespan than females born in old populations. However, these studies did not show a clear link between the dispersal status of individuals and their life history.

First, they had incomplete information about dispersal, either without information about the origin of immigrants [10] or because they infer dispersal status from the age of populations [9,11]. Second, they relied on measures of reproductive output and survival, which seldom provide information about the resource allocation between reproduction and survival [12,13]. There is, as yet, no study showing a direct link between the dispersal status of individuals and their age-specific life-history traits.

In this study, we conducted an investigation of the difference in age-specific life-history traits between dispersive and philopatric individuals in a population of the common lizard (*Zootoca vivipara*) with a particular focus on the energy expenditure for reproduction. The common lizard is a particularly appropriate species in which to investigate the relationship between dispersal and other life-history traits, because dispersal in this species occurs within a few dozen metres around the natal site, allowing it to be surveyed accurately. In contrast, in the survey of many other species such as birds, the natal population of immigrants is often unknown [8,14]. Moreover, both dispersal and age-specific traits are well documented in the studied population [1,15]. Massot *et al.* [15] in particular showed that in the common lizard, females investing a lot in their first reproduction suffer a decrease in survival with age compared with females investing little in their first reproduction. This suggests that, within the population studied, different life histories may coexist. Massot *et al.* [15], however, did not investigate what might be the origin of this heterogeneity in life-history traits. We hypothesize that this heterogeneity can be associated with the dispersal status of females.

We used data from the long-term monitoring of an area inhabited by the common lizard to investigate (i) age-specific variation in reproductive effort and survival in relation to dispersal status; (ii) whether the offspring body condition and morphology vary with the dispersal status and age of their mother; and (iii) whether the sex ratio of offspring varies with the dispersal status and age of their mother. Overall, our results show that dispersive and philopatric females have different age-specific life histories.

## 2. Methods

### (a) The species and studied population

The common lizard is a small live-bearing lacertid (adult snout-vent length (SVL) 50–70 mm) widely distributed across Europe. The average lifespan of this species is five years [16]. This species usually lives in open habitats such as peat bogs and heathland. The population studied is located on the Mont-Lozère (Southern France) and is divided into two continuous zones representing microhabitats with different levels of diversity: one zone with high structural diversity and high lizard density [ $Z+$ ; 4 300 m<sup>2</sup>], and one zone with low structural diversity and low density [ $Z-$ ; 4 700 m<sup>2</sup>] [17]. The structural diversity consists of rocks, trees, and grass [18]. Rocks and trees provide shelters and basking places, whereas grass is mostly used for foraging [18]. In this population, males first emerge from hibernation in mid-April followed by females and yearlings in early-May. Mating occurs as soon as females emerge and gestation lasts for approximately two months. Females start to reproduce at age two. Parturition starts in early-mid July and lasts for two to three weeks. Females lay an average litter of five offspring (range 1–12), which are immediately independent from their mother. Dispersal occurs within the

first 10 days of life, and there is no sex difference in dispersal propensity [17]. Hibernation starts in late September.

### (b) Population monitoring

We monitored the study population from 1989 to 2008 using capture-mark-recapture. This long-term survey was structured in two capture sessions each year. The first capture session occurred in June, the second occurred in September. During the first session, individuals were identified and, if new, were marked using toe-clipping. There is no effect of toe-clipping and handling on survival probabilities [19]. We recorded age, sex, SVL, and mass at each capture session. During the first capture session, all individuals, except pregnant females, were immediately released at the place where they were captured. Pregnant females were transferred and kept in standard laboratory conditions [20]. During captivity, each female was housed in an individual terrarium with a layer of soil and a shelter until parturition. Humidity was maintained by spraying water three times a day. Females were exposed to natural daylight and were allowed to thermoregulate for 6 h per day under a bulb (see [21] for more details). At parturition, offspring were sexed [22], weighed, and measured. Each female, together with her hatchlings, was then released at the female's last capture point. Capture points were located with a precision of 1 m. In the studied population, dispersal occurs within a few days after parturition [20]. A disperser was defined as an offspring that moved farther than 30 m from the initial point of release. This limit represents the upper 95% confidence limit of the home range [17]. Offspring defined as dispersers were never observed to return to their natal ground [20,23]. Philopatric offspring were defined as those that stayed within a 20 m range (average of the home-range diameter) of their initial release point. Individuals that moved between 20 and 30 m from their natal patch were not included in the analysis [20,23]. Dispersal occurs mostly within the area monitored [17]. The survival analysis included only juvenile females for which the dispersal status was inferred during the September capture session following their birth to detect any difference in survival during the first winter. The other analyses also included juveniles (males and females) for which the dispersal status was inferred the following year (i.e. not recaptured during the September session following their birth) to maximize our sample size.

### (c) Reproductive effort

We were interested in whether dispersive and philopatric individuals have different strategies of age-specific reproductive effort. In the common lizard, litter size correlates with the SVL of females ( $p < 0.0001$ ,  $R^2 = 0.53$ ) and the SVL of females increases as they age ( $p < 0.0001$ ,  $R^2 = 0.23$ ). To control these effects, we used a standardized value of female reproductive effort, calculated as the difference between her litter size and the expected litter size given her SVL, when linearly regressing litter size on SVL across all individuals (following [15]). Hence, a female with a litter size above the expected value has a high reproductive effort, whereas a female under the expected value has a low reproductive effort. We verified that, in our population, this standardized measure of reproductive effort had a Gaussian distribution (Shapiro test,  $p > 0.05$ ). We used linear-mixed models to investigate our hypotheses about age-specific reproductive effort [24]. Mixed modelling allows the disentangling of individual heterogeneity and ageing processes [25]. The most complex model includes (see electronic supplementary material, appendix A) as fixed effects, the effect of age, dispersal status, year of capture, density zone ( $Z-$ ,  $Z+$ ), and the first-order interaction between age and dispersal status. We modelled age as a factor and distinguished four age-classes (i.e. 2, 3, 4 years old and older). In our dataset, there were not enough females above 4 years old to distinguish further age-classes. A normally

distributed individual random effect was initially included to account for individual heterogeneity among mothers (see electronic supplementary material, appendix A for a full description of the model selection procedure). The individual random effect was, however, removed from the model if it did not improve the support of the model (i.e.  $\Delta\text{AICc} < 2$ ). In the latter case, we then used linear models to describe differences in reproductive effort among different female lizards. We used an information theoretic approach for model selection (see electronic supplementary material, appendix A). When the interaction between the dispersal status and the age of females was included in the model with the best support, we investigated the effect of dispersal in each age-class (see electronic supplementary material, appendix A).

#### (d) Offspring morphology and sex ratio

We investigated whether maternal dispersal and age affected offspring morphology and sex ratio. For morphology, we were interested in the body condition and body size (SVL) of offspring [26]. We defined body condition as the residual from the body mass/SVL relationship. We verified that this measure of body condition had a Gaussian distribution (Shapiro test,  $p > 0.05$ ). We constructed similar mixed linear models as described for reproductive effort, but added the sex of the offspring as a fixed effect for body condition and SVL. We replaced the explanatory factor year of capture (of females) by offspring year of birth, to take into account a possible cohort effect. We also investigated whether there was a trade-off between offspring morphology and litter size by adding litter size as a fixed effect in the above models. Models without and with litter size as a fixed effect address distinct questions: with the former, we ask whether mothers with a different history of dispersal produce offspring with a different morphology; with the latter model, we further investigate whether such a difference in morphology is entirely explained by different allocation strategies along the same trade-off between offspring condition and number. We defined the sex ratio as the number of males over the total number of offspring. We used generalized linear models to investigate our hypotheses regarding sex ratio, assuming a binomial distribution of the observations.

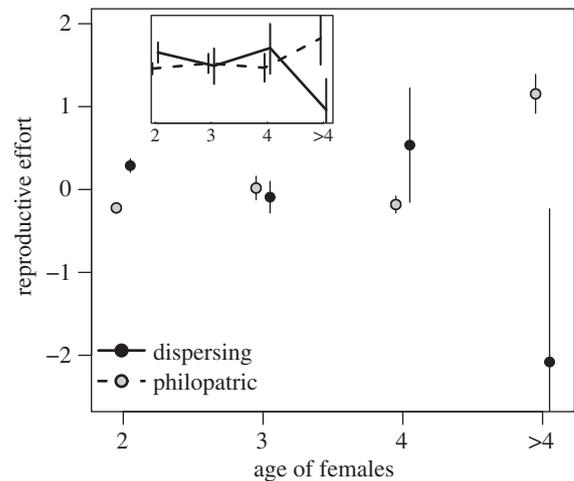
#### (e) Survival

We used the software MARK to estimate survival and capture probabilities in females. Emigration from the study population is uncommon [19], so that estimated survival can be assimilated to effective survival. The survival estimation at age one corresponds to the probability to survive the first winter (between September of the first year and June of the second year, see above). Subsequent survival estimates are defined on a yearly basis (between June capture sessions). We included age structure in the model [27] and the dispersal status of individuals as a covariate. We were especially interested in whether dispersive and philopatric mothers have different age-specific survival rates. Models were compared using the AIC corrected for small sample size (AICc, [28]). We tested the goodness of fit of the time-dependent Cormack–Joly–Seber model for philopatric and dispersive individuals [27] with the program RELEASE provided in MARK. We did not find significant heterogeneity in recapture and survival probabilities (test 2 + test 3,  $p > 0.9$ ).

### 3. Results

#### (a) Reproductive effort

The best model included the effect of age, dispersal, and the interaction of both (electronic supplementary material, appendix A). We then investigated the effect of dispersal within each age-class. Dispersal was included in the best models



**Figure 1.** Age-specific reproductive effort of philopatric and dispersive females. Main panel: observed values (mean  $\pm$  s.d.). The inset represents the predicted effect of dispersal by the best model (electronic supplementary material, appendix A, averaged over years) for each age-class with 95% confidence intervals (CIs). There were only three dispersive females (seven philopatric) in the oldest age-class explaining the decrease in precision.

explaining variation in reproductive effort in females of age two and older than four (electronic supplementary material, appendix A). Dispersive females of age two invested more in reproduction than philopatric females of the same age, but they invested less in reproduction when older than four (see figure 1 for the observed and predicted values).

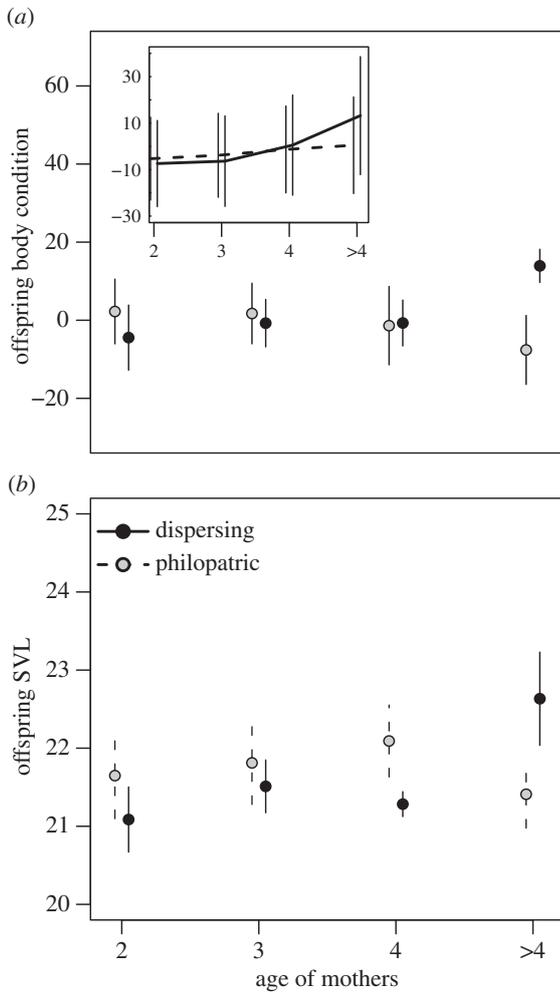
#### (b) Offspring morphology

For offspring body condition, we found strong support for an interaction between the dispersal status of mothers and their age. The best model always included this interaction independently of whether we included litter size as an explanatory factor in the model (electronic supplementary material, appendix A) suggesting that the difference in offspring body condition was not only the result of a shift along the trade-off between litter size and offspring body condition. Litter size had a negative effect on offspring body condition (regression coefficient:  $-3.55$ ; s.e.:  $0.88$ ). Furthermore, maternal dispersal was included in the best model within each age-class (see electronic supplementary material, appendix A). Dispersive females tended to improve the body condition of their offspring when they aged, whereas philopatric females did not change the body condition of their offspring throughout their life (figure 2a for observed and predicted values).

The best models explaining the variation in offspring SVL included an effect of dispersal, but not the interaction between the dispersal status of mothers and their age (electronic supplementary material, appendix A). Dispersive mothers produced, on average, shorter offspring than philopatric mothers (figure 2b for observed values, values predicted by the best model with 95% CI averaged over offspring sexes:  $21.1$  mm [ $20.52$ ,  $21.75$ ] for dispersive mothers versus  $21.8$  mm [ $21.24$ ,  $22.37$ ] for philopatric mothers). The litter size did not improve model support for the SVL (electronic supplementary material, appendix A).

#### (c) Sex ratio

The sex ratio in the population was slightly male-biased (figure 3, mean  $0.53$ ; s.e. =  $0.006$ ). We did not find strong

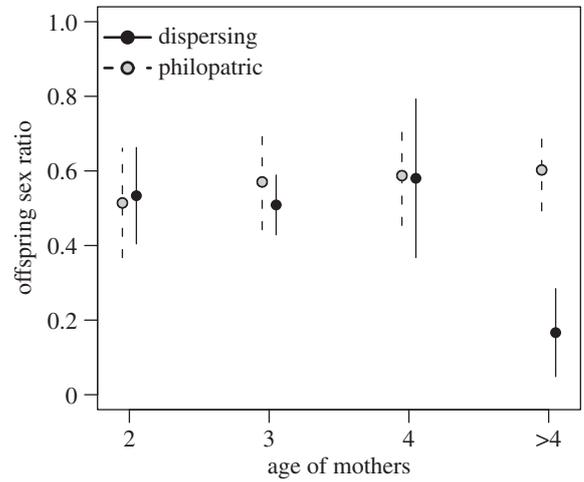


**Figure 2.** (a,b) Body condition and SVL of offspring as a function of the age of the mother. Main panel: observed values (mean  $\pm$  s.d.). The inset in the offspring body condition panel shows the predicted effect of dispersal by the best model for each age-class with 95% CIs (averaged over years). The interaction between age and dispersal did not improve model support for the SVL (see main text for predicted values about the effect of mother dispersal status).

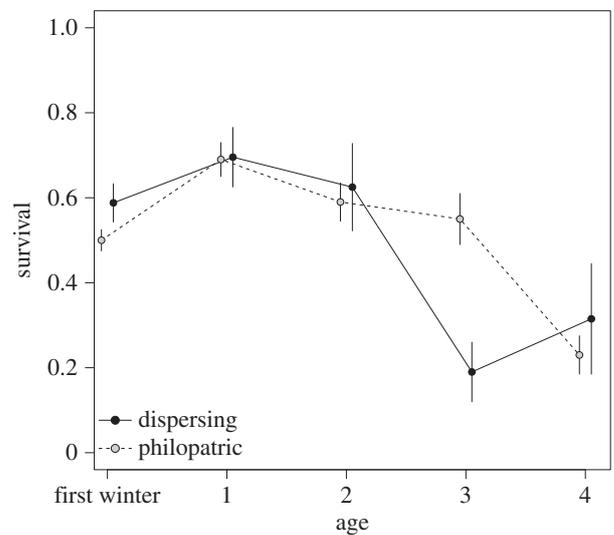
support for any of our explanatory factors (see electronic supplementary material, appendix A). The dispersal status of mothers and the density zone were the most (but weakly) supported ones. Dispersive females had a slightly less male-biased sex ratio in their progeny than philopatric females (figure 3 for observed values by age-classes, predicted value with 95% CI for the model, including dispersal alone: 0.54 [0.47, 0.62] for dispersive mothers versus 0.56 [0.51, 0.61] for philopatric mothers). In addition, females from the low-density zone tended to have a less male-biased sex ratio than females from the high-density zone (predicted value with 95% CI for the model, including the density zone alone: females living in Z<sup>-</sup>: 0.50 [0.42, 0.58], females living in Z<sup>+</sup>: 0.57 [0.43, 0.62]).

#### (d) Survival

The best models describing the variation in survival with age in females included the dispersal status as a covariate and were dependent on year for recapture probabilities (see electronic supplementary material, appendix B). No difference of support was found between models with and without a global interaction between age and dispersal ( $\Delta$ AICc < 2, see electronic supplementary material, appendix B). Survival



**Figure 3.** Sex ratio of offspring as a function of the age of the mother. Observed values (mean  $\pm$  s.d.).



**Figure 4.** Estimated age-specific survival rate for dispersive (solid line) and philopatric females (dotted line). Age-specific survival rates are estimated using MARK, for each type of female independently, with year-dependent recapture probabilities (see electronic supplementary material, appendix B). The first survival estimate (first winter) is between the September capture session following birth and the following June capture session. The following estimates are between June capture sessions. Vertical bars represent standard errors.

slightly improved after the first winter, and then decreased with age (figure 4). During the first three years of life, dispersive and philopatric females had similar age-specific survival rates. The survival of dispersive females dropped at age three, whereas the survival of philopatric females dropped at age four (figure 4). To investigate if dispersal had an age-dependent effect on survival, we performed models with the effect of dispersal on survival restricted to a single age-class. We found that the best model included an interaction between dispersal and survival only at age three (electronic supplementary material, appendix B), in accordance with the previous observation.

## 4. Discussion

The causes of intraspecific variation in life-history traits with age are still poorly understood [29]. Such variation has been

shown to be influenced by natal conditions (maternal age, birth date, environmental quality, or natal density, see [10,30]) and early investment in reproduction [15,29,31]. In our study, we show that age-specific life-history traits can also vary depending on the dispersal status of individuals. Our study contrasts with previous investigations by assessing the dispersal status of individuals directly and measuring several life-history traits. In particular, we measured the reproductive effort that is indicative of a strategy of resource allocation.

We found that young dispersive females invested more in reproduction than young philopatric individuals. Conversely, old philopatric females invested more in reproduction than old dispersive females. In addition, we found that survival declines sooner in life in dispersers than in philopatric females, suggesting a cost of early reproduction on survival. This last result is in agreement with previous findings in the same species, where the decline in survival probabilities with age was found to be specific to females investing more in their first reproduction [15]. We found that the cost of early reproductive effort on dispersive female survival occurs one year after their first reproduction (figure 4). Massot *et al.* [15] found that the cost of early reproduction on survival, regardless of the dispersal status, occurs two years after reproduction. This suggests a greater cost of early reproduction in dispersive females. Moreover, our results are consistent with findings in other species, which indirectly showed an association of dispersal with early high reproductive effort and low survival ([9] in the butterfly *Melitea cinxia*, [32] for early reproduction in the invasive ladybird *Harmonia axyridis*).

Life-history differences between dispersing and philopatric individuals can be explained because dispersal is a costly behaviour (reviewed in [33]) and/or because dispersers experience different selective pressures than philopatric individuals. For example, dispersive females can express different life-history traits than philopatric females because they are in lower body condition. The fact that life-history differences are reversed with increasing age is, however, difficult to reconcile with a simple cost argument, or with initial heterogeneity in the quality of dispersers and non-dispersers, as the sole explanation for the observed syndromes. Furthermore, we estimated post-dispersal fitness for each type of female without finding a difference (electronic supplementary material, appendix C), suggesting that dispersive and philopatric females instead have different life-history strategies. Interestingly, theory provides hypotheses about how divergent selection on dispersive and philopatric individuals may shape their age-specific life-history traits.

The associations between the age-specific reproductive effort, age-specific survival, and dispersal that we found is consistent with the prediction of a recent model [34]. Cotto *et al.* [34] predicted that if pre-reproductive individuals disperse and settle, on average, in sites with low competition, these individuals, when starting to breed, suffer less from competition than young philopatric individuals. In contrast, both philopatric and old dispersive individuals are predicted to live in sites with high competition. This, in turn, induces different age-specific selection between dispersive and philopatric individuals. In particular, young dispersive individuals are predicted to invest more in reproduction than young philopatric individuals [34]. The energy allocated to reproduction early in life should further trade-off with a shorter lifespan in dispersive individuals. In the common lizard, dispersal occurs mainly during the first 10 days of

life [17], and yearlings suffer competition from adults [18,19], as assumed in the model of Cotto *et al.* [34]. This model thus provides an interesting hypothesis to explain the pattern that we have described in the common lizard. Exploring this hypothesis further would entail investigating the intraspecific competition encountered by dispersive and philopatric individuals along their lifetime.

We found that the above difference in age-specific reproductive effort between dispersal statuses was associated with differences in offspring body condition. The body condition of offspring from dispersive mothers tended to increase as the mother aged. Similarly, Massot *et al.* [15] found that offspring body condition increased with age in females displaying a high first reproductive effort. Moreover, we found that the body condition of offspring was negatively correlated with the litter size. This is suggestive of a trade-off between reproductive effort and offspring body condition and that, depending on their age, dispersive and philopatric females have different strategies along this trade-off. Increasing offspring body condition can be a strategy of mothers to face intraspecific competition [35]. Our results further suggest that other factors related to maternal dispersal and age might affect offspring body condition, regardless of the strategy of mothers along this trade-off.

In the studied population, the heritability of dispersal is not yet known, but juvenile dispersal has been shown to be influenced by the post-natal environment and by maternal effects [20,23]. Moreover, several previous studies have found that offspring with a better body condition in the common lizard were better dispersers or dispersed under different motivations (e.g. patch density, kin competition) than did thinner offspring [20,36]. It would therefore be interesting to test whether the variation of offspring dispersal depends on maternal age (as reported by [37]) and dispersal history. This would allow the investigation of whether mothers, depending on their dispersal status and age, adjust the dispersal rate of offspring via their body condition. Such a test would require information about the age and dispersal status of both mothers and offspring, which we unfortunately did not have for enough individuals in the present dataset.

We did not find that the interaction between maternal age and dispersal status explained variations in offspring sex ratio. However, we found some, albeit ambiguous, evidence that dispersive females had a less male-biased sex ratio than philopatric females. Conversely, Taylor & Crespi [38] predicted that philopatric females should produce less male-biased sex ratios than dispersive females, because local competition for mates among related males is more intense in offspring from philopatric females than in offspring from dispersive females. Such predictions might not hold in our study area where relatedness could be strong among offspring from dispersive females. Our data also suggest that offspring sex ratio is less male-biased in the area with low density. Further theoretical and empirical investigation of variation in relatedness of locally competing males in relation with density and maternal dispersal status would be necessary to make conclusions about the potential adaptive value of sex ratio variation in our study.

Whatever the causes of the life-history syndromes that we described, the association of dispersal with high early reproductive rates has both demographic and evolutionary consequences. The described syndrome will affect in particular the age structure and demographic dynamics in the

context of colonization of new habitats and range shifts. The high fecundity of young immigrants could increase the effective gene flow through space [39]. Life-history differences between dispersers and non-dispersers may also impact the evolutionary forces that mould ageing patterns in populations [34]. Our results emphasize the need to take into account the age of individuals when investigating variation in life-history traits associated with dispersal. We thus hope that our study will stimulate further research in age-specific dispersal syndromes in a wider range of species.

**Ethics.** The study was carried out in accordance with institutional guidelines under licence from the French Ministry of the Environment, and under a permit from the Seine-et-Marne Veterinary department (permit no.77-02).

## References

- Clobert J, Massot M, Le Galliard J-F, Clobert J, Baguette M, Benton T, Bullock J. 2012 Multi-determinism in natal dispersal: the common lizard as a model system. In *Dispersal ecology and evolution* (eds J Clobert, M Baguette, TG Benton, JM Bullock, S Ducatez). Oxford, UK: Oxford University Press.
- Bélíchon S, Clobert J, Massot M. 1996 Are there differences in fitness components between philopatric and dispersive individuals? *Acta Oecol. Int. J. Ecol.* **17**, 503–517.
- Ronce O, Clobert J. 2012 Dispersal syndromes. In *Dispersal ecology and evolution* (eds J Clobert, M Baguette, TG Benton, JM Bullock, S Ducatez), pp. 119–138. Oxford, UK: Oxford University Press.
- MacKay PA, Wellington WG. 1977 Maternal age as a source of variation in the ability of an aphid to produce dispersive forms. *Res. Popul. Ecol.* **18**, 195–209. (doi:10.1007/BF02510847)
- Duckworth RA. 2008 Adaptive dispersal strategies and the dynamics of a range expansion. *Am. Nat.* **172**, S4–S17. (doi:10.1086/588289)
- Stevens VM, Whitmee S, Galliard L, Clobert J, Böhning-Gaese K, Bonte D, Baguette M. 2014 A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecol. Lett.* **17**, 1039–1052. (doi:10.1111/ele.12303)
- 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. *J. Anim. Ecol.* **57**, 287–306. (doi:10.2307/4779)
- Tully T, Clobert J, McCleery RH, Perrins CM. 2004 *Parent-offspring competition and natal dispersal at several spatial scales in the great tit*, *Parus major*. Oxford, UK: Oxford University Research Archive.
- Hanski I, Saastamoinen M, Ovaskainen O. 2006 Dispersal-related life history trade-offs in a butterfly metapopulation. *J. Anim. Ecol.* **75**, 91–100. (doi:10.1111/j.1365-2656.2005.01024.x)
- Bouwwhuis S, Charmantier A, Verhulst S, Sheldon BC. 2010b Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. *J. Anim. Ecol.* **79**, 1251–1261. (doi:10.1111/j.1365-2656.2010.01730.x)
- Haag CR, Saastamoinen M, Marden JH, Hanski I. 2005 A candidate locus for variation in dispersal rate in a butterfly metapopulation. *Proc. R. Soc. B* **272**, 2449–2456. (doi:10.1098/rspb.2005.3235)
- Clutton-Brock TH. 1984 Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* **123**, 212–229. (doi:10.1086/284198)
- Descamps S, Boutin S, Berteaux D, Gaillard JM. 2007 Female red squirrels fit Williams' hypothesis of increasing reproductive effort with increasing age. *J. Anim. Ecol.* **76**, 1192–1201. (doi:10.1111/j.1365-2656.2007.01301.x)
- Auld JR, Charmantier A. 2011 Life history of breeding partners alters age-related changes of reproductive traits in a natural population of blue tits. *Oikos* **120**, 1129–1138. (doi:10.1111/j.1600-0706.2010.19161.x)
- Massot M, Clobert J, Montes-Poloni L, Haussy C, Cubo J, Meylan S. 2011 An integrative study of ageing in a wild population of common lizards. *Funct. Ecol.* **25**, 848–858. (doi:10.1111/j.1365-2435.2011.01837.x)
- Sorci G, Clobert J, Michalakis Y. 1996 Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*. *Oikos* **76**, 121–130. (doi:10.2307/3545754)
- 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. *Lizard Ecol. Hist. Exp. Perspect.* **183**, 206. (doi:10.1515/9781400863945.183)
- 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.
- 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. (doi:10.2307/1940026)
- Massot M, Clobert J. 2000 Processes at the origin of similarities in dispersal behaviour among siblings. *J. Evol. Biol.* **13**, 707–719. (doi:10.1046/j.1420-9101.2000.00202.x)
- Lepetz V, Massot M, Chainé AS, Clobert J. 2009 Climate warming and the evolution of morphotypes in a reptile. *Glob. Change Biol.* **15**, 454–466. (doi:10.1111/j.1365-2486.2008.01761.x)
- Lecomte J, Clobert J, Massot M. 1992 Sex identification in juveniles of *Lacerta vivipara*. *Amphibia-Reptilia* **13**, 21–25. (doi:10.1163/156853892X00193)
- Massot M, Clobert J, Lorenzon P, Rossi JM. 2002 Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *J. Anim. Ecol.* **71**, 253–261. (doi:10.1046/j.1365-2656.2002.00592.x)
- Pinheiro J, Bates D, DebRoy S, Sarkar D. 2014 *R Core Team (2013) nlme: linear and nonlinear mixed effects models R package version 3.1–117*. (<http://CRAN.R-project.org/package=nlme>)
- Nussey D, Coulson T, Festa-Bianchet M, Gaillard JM. 2008 Measuring senescence in wild animal populations: towards a longitudinal approach. *Funct. Ecol.* **22**, 393–406. (doi:10.1111/j.1365-2435.2008.01408.x)
- Cote J, Clobert J. 2010 Risky dispersal: avoiding kin competition despite uncertainty. *Ecology* **91**, 1485–1493. (doi:10.1890/09-0387.1)
- Clobert J, Lebreton JD, Allaine D. 1987 A general approach to survival rate estimation by recaptures or resightings of marked birds. *Ardea* **75**, 133–142.
- Hurvich CM, Tsai C-L. 1989 Regression and time series model selection in small samples. *Biometrika* **76**, 297–307. (doi:10.1093/biomet/76.2.297)
- Bouwwhuis S, Charmantier A, Verhulst S, Sheldon B. 2010 Trans-generational effects on ageing in a wild bird population. *J. Evol. Biol.* **23**, 636–642. (doi:10.1111/j.1420-9101.2009.01929.x)
- Cartwright SJ, Nicoll MA, Jones CG, Tatayah V, Norris K. 2014 Anthropogenic natal environmental effects on life histories in a wild bird population. *Curr. Biol.* **24**, 536–540. (doi:10.1016/j.cub.2014.01.040)
- Hayward A, Mar K, Lahdenperä M, Lummaa V. 2014 Early reproductive investment, senescence and lifetime reproductive success in female Asian elephants. *J. Evol. Biol.* **27**, 772–783. (doi:10.1111/jeb.12350)
- Laugier GJ, Le Moguédec G, Tayeh A, Loiseau A, Osawa N, Estoup A, Facon B. 2013 Increase in male

**Data accessibility.** The data used in this paper are published on Dryad: <http://dx.doi.org/10.5061/dryad.425gv>.

**Authors' contribution.** O.C., M.M., O.R., and J.C. designed the study. O.C. analysed and interpreted data with M.M., O.R., and J.C.; O.C. wrote the manuscript and M.M., O.R., and J.C. helped to edit the manuscript.

**Competing interests.** We declare we have no competing interests.

**Funding.** We received no funding for this study.

**Acknowledgements.** We thank Timothée Bonnet, David Claessen, Thierry Chambert, Patrice David, Courtney Fitzpatrick, Matthieu Paquet, Daniel Promislow, Maria Servedio, Haven Wiley, and four anonymous reviewers for constructive comments on an earlier version of this paper. We also thank everyone that helped in collecting the data over the years. O.C. acknowledges support from the Ministry of Research through a PhD scholarship. This is publication ISEM 2015-213.

- reproductive success and female reproductive investment in invasive populations of the harlequin ladybird *Harmonia axyridis*. *PLoS ONE* **8**, e77083. (doi:10.1371/journal.pone.0077083)
33. Bonte D *et al.* 2012 Costs of dispersal. *Biol. Rev.* **87**, 290–312. (doi:10.1111/j.1469-185X.2011.00201.x)
34. Cotto O, Kubisch A, Ronce O. 2014 Optimal life history strategy differs between philopatric and dispersive individuals in a metapopulation. *Am. Nat.* **183**, 384–393. (doi:10.1086/675064)
35. Leips J, Richardson JM, Rodd FH, Travis J. 2009 Adaptive maternal adjustments of offspring size in response to conspecific density in two populations of the least killifish, *Heterandria formosa*. *Evolution* **63**, 1341–1347. (doi:10.1111/j.1558-5646.2009.00631.x)
36. Le Galliard J, Clobert J. 2003 Mother–offspring interactions affect natal dispersal in a lizard. *Proc. R. Soc. Lond. B* **270**, 1163–1169. (doi:10.1098/rspb.2003.2360)
37. Ronce O, Clobert J, Massot M. 1998 Natal dispersal and senescence. *Proc. Natl Acad. Sci. USA* **95**, 600–605. (doi:10.1073/pnas.95.2.600)
38. Taylor PD, Crespi BJ. 1994 Evolutionarily stable strategy sex ratios when correlates of relatedness can be assessed. *Am. Nat.* **143**, 297–316. (doi:10.1086/285605)
39. Ingvarsson PK, Whitlock MC. 2000 Heterosis increases the effective migration rate. *Proc. R. Soc. Lond. B* **267**, 1321–1326. (doi:10.1098/rspb.2000.1145)