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Experimental study of dispersal behaviour in a wall lizard species (*Podarcis sicula*) (Sauria Lacertidae)

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Movement behaviour and dispersal are key processes in biology because they represent a basic phase of the individual life-cycle with spin-offs for population dynamics, genetics and biogeography. Experimental studies have shown that the dispersal rate increases with density for a variety of taxa. Here we investigate the ecological aspects of animal movement and dispersal in a wall lizard species (*Podarcis sicula*), evaluating the short-term effects of increasing population density and individual conditions. The individual attitude on movement is assessed by comparing immigration between two alternative scenarios of augmentation (moderate starting density) and colonisation (high starting density) by using a connected semi-natural enclosure system. The main result of our study was that the patch density influenced the dispersal activity in the study species. Moreover, the movement rate between patches was sex-biased (higher in males), influenced by tail status, but not dependent upon body size and condition. The patch density drove the movement activity in the studied lizards (augmentation design), but there were also factors at individual level influencing the propensity to move (sex and tail status). In the studied lizard, individual decisions to leave a patch and settle in a new one are both condition-dependent – which means that individuals rely on a set of external cues to adjust their dispersal tactics – and phenotype-dependent – which means that dispersal propensity correlates with a suite of phenotypic traits.

KEY WORDS: dispersal, movements, wall lizards, density, Mediterranean glade.

INTRODUCTION

Movement behaviour and dispersal are key processes in biology because they represent a basic phase of individual life-cycle with spin-offs for population dynamics, genetics and biogeography. (BROWN & LOMOLINO 1998; CLOBERT et al. 2001; VAN DYCK & BAGUETTE 2005). According to some authors (see BROWN & LOMOLINO

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1998 for a synthesis), it is necessary to make a distinction between the ecological phenomenon and the biogeographical event of "dispersal". From an ecological point of view, dispersal is under the influence of multiple selective pressures (e.g. environmental, populational; PERRIN & GOUDET 2001). Therefore, the comprehension of the ecological and ethological factors determining and influencing dispersal is fundamental in order to predict the behavioural response of organisms to environmental and demographic changes (BOWLER & BENTON, 2005). Even in uniform landscapes, selection for dispersal can occur as a result of spatial and temporal variation in local population size and structure (CADET et al. 2003).

Experimental studies showed that the movement rate increases with density for a variety of taxa (insects: OTRONEN & HANSKI 1983; HURD & EISENBERG 1984; DOAK 2000; vertebrates: LÉNA et al. 1998; AARS & IMS 2000). Increasing population density can reduce individual fitness; hence it may become a driving force for dispersal. Population density is a prominent dispersal factor for most individuals as it can be seen either as an indication of intraspecific competition or as a sign of habitat quality. The nature of individuals themselves (age, size and relatedness) can influence the way density is perceived (CLOBERT et al. 2004). Moreover, dispersal is crucial to the persistence of small or fragmented populations, facilitating the invasion of new habitats and the maintenance of gene flow (EBENHARD 1991; HANSKI 1999). In local populations dispersal could result in either colonisation (empty patches – following on extinction) or augmentation (patches occupied by conspecifics) processes (LEVINS 1969; EBENHARD 1991; IMS & YOCCOZ 1997; LE GALLIARD et al. 2005). Colonisation allows dispersing individuals to minimise competition for limiting resources with those already present in the patch and subsequently with other immigrants ('beneficial colonisation' scenario – LAMBIN et al. 2001; LE GALLIARD et al. 2005). Moreover, immigrants may suffer from asymmetric competition due to a prior-resident advantage (e.g. social dominance: ANDERSON 1989; familiarity with the habitat: MASSOT et al. 1994). Conversely, an empty patch can be costly to immigrants if the absence of conspecific residents increases the costs of settlement in unfamiliar habitats ('costly colonisation' scenario – GREENE & STAMPS 2001).

The aim of this study is to investigate the ecological aspects of animal dispersal by comparing immigration between the two alternative scenarios of colonisation and augmentation. The short-term effects of increasing population density and individual conditions on dispersal are assessed in a wall lizard species of the genus *Podarcis* (*P. sicula*). In particular we aim to answer the following two key questions by using a similar experimental design (consisting of an augmentation and a colonisation design) developed for studies on common lizards (*Zootoca vivipara*) in France by LECOMTE & CLOBERT (1996): (i) Does enclosure density drive individual movement patterns between the patches in both the experimental designs? (ii) Do the individual's body condition, sex and tail status determine the individual pattern of dispersal, or could dispersal tendency be an intrinsic individual property?

MATERIALS AND METHODS

Study area

The experiments took place in the Macchia Grande WWF Oasis, a protected coastal area of Latium (central Italy) near Maccarese (Fiumicino municipality). The study plots were sited in a wide glade within the typical Mediterranean maquis (41°49′30.77″N, 12°13′14.13″E).

Study species

The present research focused on a lacertid lizard, *Podarcis sicula campestris* (De Betta 1857) protected by the Berne Convention, endemic to most of the peninsular and Northern Italy and Corsica. The study species has a typical lacertid body shape with males bigger in size than females. Although ecological habits may vary among locations, adult *P. sicula* are generally dwellers of open areas (BÖHME 1986).

Protocol

Specimens of the study species were collected within the study area in April 2006 and in July 2006 respectively for augmentation and for colonisation experiments. Because the experiments were conducted during the lizard reproduction season, we have to take in account that especially males could have shown a marked territorial behaviour and more agonistic inter-individual inter-actions could be expected. At the beginning of each treatment all specimens were sexed, snout-vent measured (SVL) and weighed, and the individual body condition index (BCI) was estimated as the residuals from the log-log regression between body mass and SVL. We use log-transformed data in order to avoid a spurious quadratic effect of SVL on BCI that may arise as a consequence of allometry (MEIRI 2010). We did not repeat the individual BCI estimate throughout the whole experiment period in order to avoid a potential uncontrolled bias due to the stress from individual collection and manipulation for measurements. The tail status was also recorded, as tail autotomy is known to affect different aspects of lizard ecology (social status, predation risk, home-range size, locomotor ability; OPPLIGER & CLOBERT 1997; CAPIZZI et al. 2007). The tail was categorised as complete or lost respectively when it was undamaged or completely regenerated, and when it was broken or at the beginning of the regeneration process. A tail damaged in proximity to its end was considered as complete.

Experimental design

The experimental system consisted of two units of two patches each connected by dispersal corridors used by lizards to move between patches (LECOMTE & CLOBERT 1996; CLOBERT et al. 2001; LE GALLIARD et al. 2005) (Fig. 1). Each unit is composed of a pair of enclosed boxes (7 × 7 m) connected by two independent one-way corridors (14 × 1 m), each ending with a pitfall trap, allowing the capture and identification of dispersing individuals (Fig. 1). All the enclosures and corridors were delimited and hermetically closed by 1 m high polyethylene walls. The width of corridors was chosen to be large enough to allow lizard to disperse and small enough and without refugia to be unattractive, preventing any attempt at settlement (LECOMTE et al. 2004). Enclosures had a Mediterranean open maquis standardised habitat, providing lizards with refugia and sites for thermoregulation. Food (mostly grasshoppers and ants) and water were given ad libitum. Each individual caught in the pitfall trap was placed in the patch towards which it was going.

Before putting the lizards in the enclosures, they were maintained in terraria (50 × 40 cm) and fed with grasshoppers for 1 week for captivity acclimatisation. Each lizard was individually marked by means of both temporary and permanent methods: (a) for a prompt recognition of the individuals in the enclosures and when they were found in the pitfalls, we marked them by using non-toxic paint producing a combination of two colour blotches on the dorsal body surface (mark held out for a maximum of 15–20 days because of shedding); (b) in order to recognise individuals throughout the study period we marked them permanently by means of photographs of the dorsal pigmentation. Lizards promptly acclimatised in the enclosures and showed natural behaviour (territorialism, mating, etc.). At the end of each experiment we found newborn individuals in all the enclosures, evidence of occurring and repeated oviposition and hatchling.
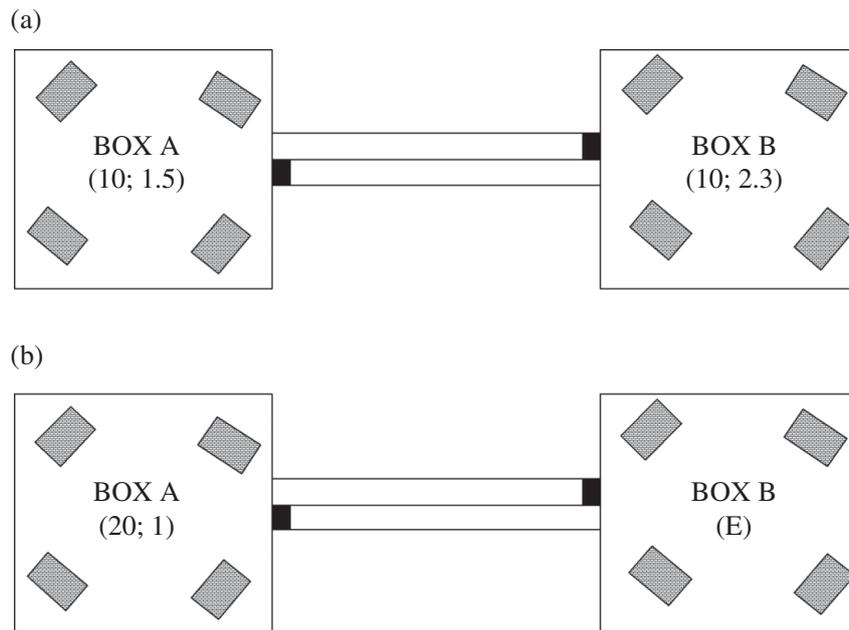
(a)

(b)

Fig. 1. — Spatial organisation of the enclosures used in both the experimental designs. The experimental enclosures were built as connected (disperser individuals fallen in the pitfall are put in the other enclosure). Numbers in brackets indicate population size and sex ratio. E, empty. a: Augmentation design. b: Colonisation design. Black rectangles, pitfall traps; bricked rectangles, *refugia* (see Materials and Methods for the specifications).

We made up two experimental designs that simulated different density starting conditions (EBENHARD 1991; IMS & YOCCOZ 1997):

(i) *Augmentation design (28 April – 17 July 2006)*. Both patches of a pair started with an experimental population of 10 lizards and the individuals attempting to disperse found the reached patch already colonised (LECOMTE & CLOBERT 1996; LE GALLIARD et al. 2005). We tested the same starting density in both the enclosures of 10 lizards (sex ratio M/F: box A = 6/4, box B = 7/3) (Fig. 1a), slightly higher than that estimated under natural conditions (VERBEEK 1972; BOAG 1973; BARBAULT & MOU 1988; BROWN et al. 1995), and lower in number but comparable in terms of biomass to other experimental studies on *Zootoca vivipara*, a lacertid species smaller in size (15–27 ind/50 m^2; LECOMTE & CLOBERT 1996; BOUDJEMADI et al. 1999; CLOBERT et al. 2004; LECOMTE et al. 2004). The sex ratio was different between the enclosures but lay within the range observed in the collection site. The experiment ended after 81 days.

(ii) *Colonisation design (20 July – 4 October 2006)*. One patch (box A) of a pair started with a population of 20 lizards (sex ratio M/F: 1.0), whereas the other patch was empty (Fig. 1b). The colonisation design made it possible to test how high (box A at starting condition) and low (box B after the first movements) density levels influence individual movement rate. The experiment ended after 71 days.

Two different lizard populations were tested in the two experimental designs. Lizard body size and body condition did not differ between treatments at the start of the experiments (ANOVAs of treatment effect, all $P > 0.41$).

Observations on the experimental system were made daily and at two levels: (a) individual level: the number of individual movements between patches was recorded; and (b) enclosure level:

the lizard density within each patch and the dispersal rate (number of movements divided by the number of individuals in each patch) were estimated respectively at the beginning and at the end of each experimental day. For the analyses both the number of movements and the dispersal rate were used. This analysis protocol generates a risk of data pseudoreplication because the same individuals are moving through the entire dispersal period. This means that the different daily numbers of movements are not independent because the same individuals are at the origin of these movements. This sort of pseudoreplication can occur, for example, if there are individuals that move a lot, increasing the number of movements for each day. Actually, we observed just one individual per experiment that showed this type of behaviour (see Results); hence the associated bias should be irrelevant. Experimental observations lasted until movements between patches ended or consistently compensated each other. The observed movement pattern between enclosures was estimated by nonlinear regression models with both sides of the equation log-transformed (we supposed that the net movements between enclosures as time went by could probably best be expressed in terms of some negative exponential function). Individuals were grouped into three classes based on their dispersal activity: the residents (individuals that never leave their initial patch), the immigrants (dispersers that settled in the arrival patch), and the transients (dispersers that moved at least twice between patches) (LE GALLIARD et al. 2005).

Statistical analyses

The pattern of dispersal at individual level (i.e. number of individual movements and classes of dispersal activity) was modelled by means of Generalized Linear Models procedure. Two models were built respectively selecting as dependent variables the number of individual movements (Poissonian distribution and log link function) and classes of dispersal activity (multinomial distribution and cumulative log link function). The sex, the tail status and the experimental design (binary variables) were included in the model as factors (categorical predictors), and SVL as covariate (scale predictor); the model design included the main effects for each variable, and all two-way interactions between the three factors and the covariate (fractional factorial design) (MCCULLAGH & NELDER 1989). We also used univariate tests for analysing the number of movements (normal distribution after log transformation; parametric tests) and the classes of dispersal activity (multinomial distribution; non-parametric tests). At patch level, the influence of patch density on the total number of movements and dispersal rate was tested by using Spearman rank correlations. All statistical analyses were performed by Statistica (Statsoft, version 7.0), with two tails and alpha set at 5%.

RESULTS

Overall analyses

Males and females differed in terms of body size (SVL) ($n = 41$; mean$_{M(23)}$ = 72.02 mm; SD$_M$ = 4.45 mm; mean$_{F(18)}$ = 66.58 mm; SD$_F$ = 5.95 mm; dof = 39; $t = -3.36$; $P < 0.01$; t-test) and body mass ($n = 41$; mean$_{M(23)}$ = 9.07 g; SD$_M$ = 1.75 g; mean$_{F(18)}$ = 6.08 g; SD$_F$ = 2.00 g; dof = 39; $t = -5.10$; $P < 0.001$). Body condition index (BCI) differed between sexes, males showing higher values ($n = 41$; mean$_{M(23)}$ = 0.031; SD$_M$ = 0.033 ; mean$_{F(18)}$ = -0.038; SD$_F$ = 0.061; dof = 39; $t = -4.69$; $P < 0.001$), whereas the tail status did not ($n = 41$; χ^2 = 0.37; df = 1; $P > 0.05$; Chi-square test).

The overall movements between enclosures in each experimental design for each sex category are summarised in Table 1. The individual propensity to move from each patch was influenced by the experimental design (i.e. the starting patch density and the

Table 1.

Descriptive statistics of the number of movements in each enclosure (both directions) for each design and sex category.

Design	Enclosure				Number of movements					
	Box A		Box B		Total		Males		Females	
	Initial n	Final n	Initial n	Final n	A-B	B-A	A-B	B-A	A-B	B-A
Augmentation	10	16	10	4	22	28	17	21	5	7
Colonisation	20	5	0	14	57	44	42	35	10	4

Initial n, number of individuals at the beginning of the experiment; Final n, number of individuals at the end of the experiment; A-B, movements from box A to box B; B-A, movements from box B to box A.

Table 2.

Synopsis of the Generalized Linear Model (fractional factorial design) results, showing which parameters (including the between effects) significantly influence the individual movements in the study species through the experimental design.

Model	Wald statistic	df	Sig.
(Intercept)	0.429	1	0.512
Sex	12.246	1	0.0001
Tail	4.748	1	0.029
Design	9.136	1	0.003
SVL	0.015	1	0.903
Sex × Design	1.337	1	0.248
Tail × Design	5.098	1	0.024
Sex × Tail	4.158	1	0.041

SVL, snout-vent length; Tail, tail status.

presence/absence of individuals in the arrival patch), sex and tail status (Table 2). The colonisation design produced an overall higher number of between-patches movements than the augmentation did.

As regards overall movements made by the individuals in both the experimental designs, the sexes behaved differently, males displaying a higher propensity to disperse, this pattern being consistent throughout the two experiments (Table 2). The tail status affected individual movements and its effect was also design-dependent (Table 2): the individuals with a broken tail showed a higher dispersal propensity than the others in the colonisation design.

As regards classes of dispersal activity (Fig. 2; Table 3), the experimental design did not affect the individual distribution pattern among classes, whereas the sexes displayed different dispersal patterns, females not showing a specific pattern ($\chi^2 = 0.333$, df $= 2$, $P = 0.846$), and most males being transients (16/23) ($\chi^2 = 13.664$, df $= 2$, $P = 0.001$; Chi-square test).
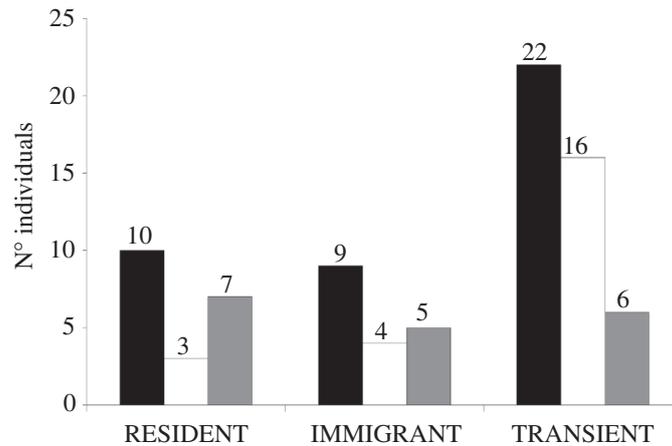
Fig. 2. — Number of cumulated movements performed by the lizards during the two experimental designs. Black bars, total individuals; white bars, males; grey bars, females. See the methods for movement categories.

Table 3.

Synopsis of the Generalized Linear Model (fractional factorial design) results, showing which measured parameters (including the between effects) significantly influence the dispersal categories in the study species through the experimental designs.

Model	Wald Chi-square	df	Sig.
Sex	4.007	1	0.045
Tail	1.079	1	0.299
Design	3.050	1	0.081
SVL	0.688	1	0.407
Sex × Design	0.106	1	0.745
Tail × Design	3.146	1	0.076
Sex × Tail	0.001	1	0.982

SVL, snout-vent length; Tail, tail status.

Augmentation design

At the beginning of the experiment, the density in both enclosures was 0.20 ind/m^2 and the sex ratio was 1.5 (box A) and 2.33 (box B) male-biased (Fig. 1a). After 81 days, the density in box A reached 0.31 ind/m^2 (12 males and four females) with a sex ratio of 3 (Table 1), whereas box B was inhabited by four individuals only (0.08 ind/m^2), one male (SVL = 67.45 mm; BCI = 0.02) and three females (sex ratio: 0.33) (Table 1). Overall, lizards performed 50 movements (0.62 per day); although we observed a decrease in terms of net movements between boxes as time went by, this was not statistically significant ($r = -0.085$; $n = 81$; $P = 0.451$; nonlinear regression), and at the end of the experiment the enclosure system was still not stable due to the persistence of movements of one transient male. Sex ($t = -1.21430$, df = 18, $P = 0.240$) did

not influence individual dispersion propensity. The patch density did not affect lizard dispersal activity (number of movements: $r = 0.014$, $n = 162$, $P = 0.854$; dispersal rate: $r = -0.040$, $n = 162$, $P = 0.550$).

Colonisation design

After 101 individual movements (1.42 per day), from the initial density of 0.41 ind/m^2 (10 males and 10 females, box A, Fig. 1b), the enclosures reached the final densities of 0.10 ind/m^2 (five individuals box A) and 0.29 ind/m^2 (14 individuals in box B) with a sex ratio of 0.25 (one male and four females) and 1.8 (nine males and five females) respectively (one male died after 54 days) (Table 1). Overall movement rates progressively decreased over time with a statistically significant trend ($r = -0.589$; $n = 71$; $P = 0.0001$; nonlinear regression). Males dispersed significantly more than females ($t = -2.822$, df = 19, $P = 0.011$). It should be noted that the only resident male (SVL = 72.04 mm; BCI = 0.066) in box A displayed a highly aggressive behaviour towards other males, preventing them from exploiting the basking substrates. Lizard density in box A was positively correlated to both the daily total number of movements ($r = 0.682$, $n = 71$, $P = 0.00001$) and the movement rate ($r = 0.549$, $n = 71$, $P = 0.000001$). Regarding box B, the daily total number of movements did not correlate with patch density ($r = -0.134$; $n = 71$, $P = 0.26$), whilst the dispersion rate showed a high correlation with the number of individuals in the patch ($r = 0.981$, $n = 71$, $P = 0.0000001$).

DISCUSSION

The dispersal process is basically influenced by environmental (habitat quality and size, trophic resource availability), populational (density and demography) and individual (morpho-physiological conditions) parameters (CLOBERT et al. 2001; IMS & HJERMANN 2001). Experimental studies demonstrated a primary role of population density in regulating the pattern of dispersal processes (LAMBIN et al. 2001), showing that emigration tended to increase with density for a variety of taxa (see BOWLER & BENTON 2005 for a review).

How animals perform dispersal processes is an interesting question, widely studied in several taxa but rarely tested in reptile species (CLOBERT et al. 2001). Movement behaviour has never been studied in *Podarcis* lizards, so one of the aims of this study has been to provide data on this aspect. The main result of our study was that both populational (density, intraspecific relationships) and individual (sex, tail status) parameters influenced the dispersal activity in the study lizard species at the adult stage, as also previously revealed by early studies on other animals (TRAVIS et al. 1999; IMS & HJERMANN 2001; CADET et al. 2003).

The experimental design (i.e. initial patch density and condition in arrival patch) influenced the individual propensity to move from each patch. The colonisation design produced an overall higher number of between-patches movements than the augmentation did. Lizards did not show a clear dispersal pattern in the augmentation design (any significant effect of the tested factors was found), whereas in the colonisation design a density-dependent pattern was observed. Moreover the sex and tail status conditioned individual movement behaviour, whereas lizard size (SVL) and body condition index

(BCI), although differing among sexes (males being bigger and showing higher BCI values than females), did not show any effect. The males displayed a higher propensity to disperse than females did in both the experimental conditions. The tail status affected individual movements independently of body size and sex. This effect was also design-dependent, the individuals with broken tail showing a higher dispersal propensity than the others in the colonisation design. Regarding classes of dispersal activity the experimental design did not affect individual distribution among classes, whereas only sex showed significant differences, since males were characterised by transient behaviour (LE GALLIARD et al. 2005).

We analysed the relationships between density and lizard movement behaviour using the number of movements and the dispersal rate. If we consider density and number of movements per patch, the positive relationship found in the colonisation design (Box A) is probably due to a simple equation, i.e. more individuals = more potential dispersers. On the other hand, the positive relationship found between dispersal rate and density in the colonised habitat in both the boxes in the same experimental design cannot be explained so easily and could be interpreted as a clear effect of the number of individuals in a patch (density) on their own movement behaviour. Thus, the more crowded the patch (empty or already occupied) gets, the more the dispersal rate rises due to an increasing number of dispersers. Indeed, other density-independent settlement costs could play a role in the dispersal process (e.g. in unfamiliar habitats new arrivals could require time and effort before being able to use the new sites efficiently; STAMPS 1995). It is also possible that the arrival of unfamiliar immigrants could play a significant role in the movement behaviour of different individuals, inducing inter-individual interactions within a given patch. Moreover, the density variations inside each patch can affect lizard behaviour in various ways. Indeed, it is known that an increased patch density may provoke changes in time budget, lizards devoting more time to basking, altering the inter-individual interactions (DIEGO-RASILLA & PÉREZ-MELLADO 2000).

Regarding the effect of sex on individual propensity to move between patches, sex-biased dispersal has been demonstrated to occur in several taxa (reviewed in LOMNICKI 1988; LAMBIN et al. 2001), and this pattern is often linked with reproductive strategy: if males are phylopatric (mammals, GREENWOOD 1980; amphibians, SINSCH 1992) then females disperse further; conversely, if site fidelity is female-biased (birds, GREENWOOD 1980; amphibians, DELLA ROCCA et al. 2005; reptiles, TUCKER et al. 1998) then males are the sex more prone to disperse (LOMNICKI 1988). Moreover, an inter-sexual difference in home range size could also affect dispersal behaviour because the overlap degree among the home ranges is likely to affect territorial behaviour (BROWN & ORIANS 1970). Actually, there are nearly no published data on home range size for the studied species. In the only known study on *P. sicula*, BEARZI (1989) found that home ranges were positively related to body length (SVL) and differed between sexes, males having bigger home ranges than females. Although in lizards there are also examples that corroborate GREENWOOD'S (1980) mating system hypothesis for sex differences in dispersal (DOUGHTY et al. 1994), very few data are available on this topic. In the absence of further investigations, our observed male-biased propensity to move could be explained as an asymmetric intra-sexual competition (stronger between males) due to territorial behaviour (HUEY et al. 1983) that generates the observed dispersal pattern (LAMBIN et al. 2001).

With regard to tail condition effects on individual dispersion propensity, it is hypothesised that tail loss may alter movement behaviour and the escape tactics of

lizards (see BATEMAN & FLEMING 2009 for a review). Actually, the effect of tail loss on the behaviour of lizards, which run on all four limbs, is controversial (ARNOLD 1988), because the tail plays no obvious role in locomotion and locomotor performance may be enhanced by tail loss (DANIELS 1983). Moreover, it is not clear whether the condition of a regenerated tail has to be considered as intact or broken tail status as regards its effect on lizard locomotor activity. Most studies on this topic have concentrated mainly on escape tactics and predator avoidance rather than on the 'normal' movement patterns (i.e. walking speed) of tailless lizards (DIAL & FITZPATRICK 1984; BELLAIRS & BRYANT 1985; but see FORMANOWICZ et al. 1990; MARTÍN & AVERY 1998). Indeed, the effect on tail loss on locomotory activity could be species-specific (CAPIZZI et al. 2007), being considered a disadvantage for a lizard as it decreases its sprint performance (BALLINGER et al., 1979; PUNZO 1982; DIAL & FITZPATRICK 1984), an advantage as it enhances locomotor performance (DANIELS 1983), or not producing any effect (RUGIERO 1997). Thus tailless individuals could unpredictably change their dispersion behaviour. Moreover, the subsequent costs associated with tail regeneration might decrease the fitness of individuals (reviewed in Arnold, 1988), as well as reducing an individual's social status (FOX et al. 1990) and mating access in males (MARTÍN & SALVADOR 1993). Moreover, energetic regeneration costs in tailless lizards may produce increasing feeding rates (DIAL & FITZPATRICK 1981), diversion of energy from somatic growth (BALLINGER & TINKLE 1979; ALTHOFF & THOMPSON 1994) or reproductive effort (DIAL & FITZPATRICK 1981; MARTÍN & SALVADOR 1993) to compensate tail regeneration. Our data on *P. sicula* showed that tailless lizards had a higher propensity to move among patches than did tailed individuals. Thus without further studies specifically addressed to this topic it is not easy to correctly interpret the observed pattern. A possible explanation could concern a behavioural shift made by our lizards in response to tail loss in ways that may compensate for potential altered locomotor performance and inability to further employ autotomy as defensive strategy (FORMANOWICZ et al. 1990). Moreover, if the tail status affects individual social status in the study species, tailless individuals with reduced social status may be forced by dominants to move from one patch to another; alternatively, we can assume that their increased feeding needs for tail regeneration energy allocation induces them to actively search for food across patches. Indeed, tailless individuals could be more prone than tailed ones to move because they need to compensate for the costs of tail loss by altering their behaviour in various ways, i.e. foraging only on abundant and easily captured prey (MARTÍN & SALVADOR 1997), modifying their use of microhabitats, and avoiding competition with individuals of higher social status (FOX & ROSTKER 1982).

Moreover, we observed that single specimens had a significantly higher movement rate independently of population density, sex, tail status and BCI. Thus, in the studied lizards, individual decisions to leave a patch and disperse in a new one are both condition-dependent, which means that individuals rely on a set of external cues to adjust their dispersal tactics (e.g. DENNO & RODERICK 1992; MATTHYSEN 2005; CLOBERT et al. 2009), and phenotype-dependent, dispersal propensity being correlated with a suite of phenotypic traits (HUYGUE et al. 2007; VERCKEN et al. 2007). No dispersal type characterising the overall phenotypic attributes of dispersers compared to residents was found (e.g. dispersers are bigger or display a more aggressive behaviour than residents; dispersal syndrome; CLOBERT et al. 2009).

Dispersal behaviour in the study lizards proved to be in some aspects species-specific and was influenced by several external (e.g. density, dominance, intraspecific competition, habitat quality) and internal (e.g. sex, tail status) factors, as well as an individual tendency to dispersal.

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