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Experimental study of dispersal behavior in the Common Wall Lizard, *Podarcis muralis* (LAURENTI, 1768)
(Squamata: Sauria: Lacertidae)

Experimente zum Ausbreitungsverhalten der Mauereidechse, *Podarcis muralis* (LAURENTI, 1768)
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Ökologische Aspekte des Ausbreitungsverhaltens der Mauereidechse, *Podarcis muralis* (LAURENTI, 1768), wurden unter den Kurzzeitbedingungen gegebener Populationsdichte und individueller Verfassung (BCI) untersucht. Die Beurteilung der individuellen Ausbreitungsbereitschaft erfolgte durch den Vergleich von Emigrationsraten in zwei alternativen Szenarien: (i) bei mäßiger Anfangsdichte (augmentation design) und (ii) hoher Anfangsdichte (colonization design). Die Versuchsanordnung bestand aus zwei durch Korridore miteinander verbundenen, seminatürlichen Enclosures, die zwei Vorkommensstellen simulierten.

Die Ausbreitungsaktivität der untersuchten Art war von der anfänglichen Populationsdichte in den Enclosures beeinflußt. Die Tiere zeigten kein Ausbreitungsverhalten im Versuchsaufbau 'Augmentation' und ein dichteabhängiges Ausbreitungsverhalten im Versuchsaufbau 'Colonization'. Allerdings wechselten Männchen häufiger zwischen den Enclosures als Weibchen, während weder das Geschlecht noch die Körperverfassung (BCI) die Ausbreitungsrate beeinflußten. Dabei zeigte *Podarcis muralis* Verhaltensähnlichkeiten mit *P. siculus* (RAFINESQUE-SCHMALTZ, 1810), obwohl bei letzterer Art eine höhere Dispersionsrate festgestellt wurde, und die Wechsel zwischen den Enclosures bei geringeren Populationsdichten einsetzten. Anders als *P. siculus* zeigte *P. muralis* einheitliches Dispersionsverhalten bei gegensätzlichen Dichtebedingungen: dabei verließen *P. muralis* stark bevölkerte Gebiete ebenso wie von Artgenossen unbewohnte Orte; sie vermieden es also, sich längere Zeit an ursprünglich von Artgenossen nicht bewohnten als an bewohnten Orten aufzuhalten.

ABSTRACT

Ecological aspects of the dispersal behavior of Common Wall Lizards, *Podarcis muralis* (LAURENTI, 1768), were studied under the short-term effects of population density and individual body condition. The individual dispersal attitude was assessed by comparing emigration rates between two alternative scenarios of (i) moderate starting density (augmentation design) and (ii) high starting density (colonization design). The study system consisted of two interconnected seminatural enclosures simulating two habitat patches linked by corridors.

The study revealed that the dispersal activity in the study species was influenced by the starting lizard density in the enclosures. The study species showed no dispersal behavior in the augmentation design and a density-dependent pattern in the colonization design. Moreover, males moved more frequently between enclosures than females, whereas neither sex nor body condition influenced the dispersal rate. *Podarcis muralis* showed behavioral similarity with *P. siculus* (RAFINESQUE-SCHMALTZ, 1810), although for this latter species dispersion rate was found to be higher and movements between enclosures to start at lower population densities. Unlike *P. siculus*, *P. muralis* exhibited different dispersal behavior at opposite density conditions: the lizards moved away from enclosures both highly crowded and unpopulated by conspecifics, i.e., avoided to stay longer in initially empty than in occupied enclosures.

KEY WORDS

Reptilia: Squamata: Sauria: Lacertidae, *Podarcis muralis*; European Wall Lizard; population ecology, population density; dispersal; Mediterranean maquis glade, Italy.

INTRODUCTION

The dispersal of an individual from one habitat patch to another has consequences not only for individual fitness, but also population dynamics, genetics, and biogeography (DUNNING et al. 1995; HANSKI 1999; CLOBERT et al. 2001). From an ecological point of view, dispersal is under the influence of multiple selective pressure (e.g., environmental, populational; PERRIN & GOUDET 2001). Ecological and experimental studies of dispersal have demonstrated that dispersal rate increases with population density for a variety of taxa (insects: DOAK 2000; vertebrates: LÉNA et al. 1998; AARS & IMS 2000). Dispersal is a process dependent on emigration of individuals from a habitat patch, successful inter-patch movement, and immigration into an other habitat patch (IMS & YOCCOZ 1997). Theory explains the potential benefits of dispersal (JOHNSON & GAINES 1990) which may reflect (i) the variation in environmental conditions between habitat patches (i. e., habitat quality and resource competition; MCPEEK & HOLT 1992), (ii) the avoidance of intraspecific competition or inbreeding in the natal habitat patch, (PERRIN & MAZALOV 1999) due to increasing population density (LÉNA et al. 1998) or low resource availability (KENNEDY & WARD 2003). Also, factors such as sex (BEIRINCKX et al. 2006; VIGNOLI et al. 2012) and age (ALTWEGG et al. 2000) can influence the individual's dispersal attitude. Indeed, the population density is a prominent factor controlling dispersal as it can be considered as an indication of both intraspecific competition and habitat quality. Moreover, characteristics of the individuals themselves (age, size, sex, and relatedness) can influence how the density is perceived (CLOBERT et al. 2004). In a local population, dispersal could result in either colonization of empty habitat patches (following local extinction) or augmentation (when habitat patches are already occupied by co-specifics) (LEVINS 1969; EBENHARD 1991; IMS & YOCCOZ 1997; LE GALLIARD et al. 2005). Immigrants may suffer from asymmetric competition due to a prior-resident's advantage (e.g., social dominance: ANDERSON 1989; familiarity with the habitat: MASSOT et al. 1994), as well as take advantage by reducing competition for limiting resources directly with those already present in the habitat patch and later with other immigrants ('beneficial colonization' scenario - LAMBIN et al. 2004; LE GALLIARD et al. 2005). Conversely, the colonization of an empty habitat patch can be costly to immigrants if the absence of resident conspecifics increases the costs of settlement in unfamiliar habitats ('costly colonization' scenario - GREENE & STAMPS 2001).

The aim of this study is to investigate the ecological aspects of animal dispersal comparing immigration between the two alternative scenarios of colonization and augmentation. The short-term effects of increasing population density and individual body condition on dispersal are assessed in the Common Wall Lizard *Podarcis muralis* (LAURENTI, 1768). The two key questions were: (i) does population density drive individual patterns of dispersal activity between the habitat patches in the two experimental designs, and (ii) do factors such as sex, size or body condition affect the individual pattern of dispersal?

MATERIALS AND METHODS

Study area.– The experiments took place in the World Wildlife Fund for Nature (WWF) oasis "Macchiagrande", a protected coastal area of Latium (central Italy) near Maccarese (Fiumicino municipality). The study plots were in a wide glade covered with the typical Mediterranean maquis shrubland (41°49'30.77" N, 12°13' 14.13" E) (VIGNOLI et al. 2012).

Study species.– The present research focused on a European lizard species, *Podarcis muralis* (LAURENTI, 1768), protected by the Berne Convention, and specifically, on a population belonging to the subspecies *nigriventris* BONAPARTE, 1836, endemic to the coastal Tyrrhenian area of Latium and Tuscany (Italy). The species shows a typical lacertid body shape with males larger than females. Although ecological habits may vary among locations, adult *P. muralis* are usually associated with shaded wooded or rocky habitats (GRUSCHWITZ & BÖHME 1986; BIAGGINI et al. 2010).

Protocol. – Specimens for the augmentation and colonization experiments were collected within the study area or in the immediate surroundings in April and July, 2006. The collecting periods were associated with two distinct reproductive peri-

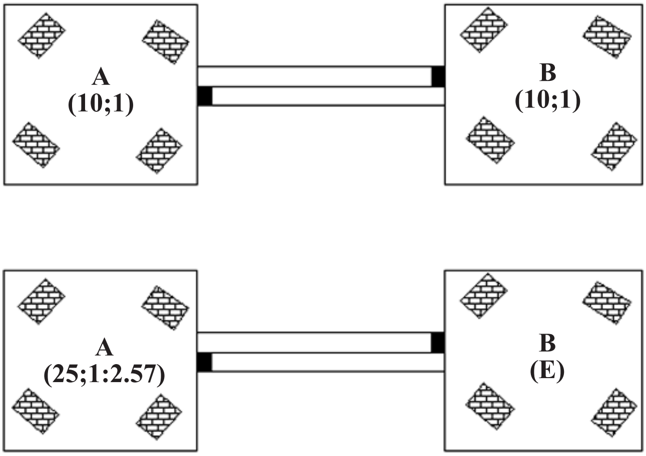

Figure 1: Both augmentation (above) and colonization (below) experimental designs consisted of interconnected enclosures (A and B). Individuals fallen in the pit at the end of the source enclosure corridors (black rectangles) were put in the target enclosures. Black rectangles – pit traps; bricked rectangles – refugia (see material and methods) (modified from VIGNOLI et al. 2012). Initial population size and sex ratio (m:f) are indicated. E – no lizards present.

Fig. 1: Beide Versuchsanordnungen - Augmentation Design (oben) und Colonization Design (unten) bestanden aus verbundenen Enclosures (A und B). Individuen, die in die Fallen (schwarze Rechtecke) an den Korridorenden der Quell-Enclosures gingen, wurden in die Ziel-Enclosures gesetzt. Schwarze Rechtecke – Fallen; gepflasterte Rechtecke – Refugien (siehe Material und Methoden) (verändert nach VIGNOLI et al. 2012). Populationsgrößen und Geschlechterverhältnisse (m:w) zu Versuchsbeginn sind angegeben. E – keine Eidechsen.

ods in late spring and summer, respectively. Thus, the reproductive status of females collected could have been slightly different between the two experiments and this might have caused a different behavior in female lizards. At the beginning of each treatment (for experimental design see below), specimens were sexed, measured (snout-vent-length, 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 (VIGNOLI et al. 2012). The measurements were not repeated during the experiment to avoid potential uncontrolled bias due to stress from individual collection and manipulation. Moreover, the tail status was recorded, as tail autotomy is known to affect different aspects of lizard ecology (social status, predation risk, home-range size, locomotory ability; OPPLIGER & CLOBERT 1997; CAPIZZI et al. 2007).

Experimental design.– The experimental system consisted of two enclosures representing two habitat patches each, connected by dispersal corridors used by lizards to move between enclosures (LECOMTE & CLOBERT 1996; CLOBERT et al. 2001; VIGNOLI et al. 2012) (Fig. 1). The experimental system has been used already for testing analogous hypotheses on a congeneric species (*P. siculus* [RAFINESQUE-SCHMALTZ, 1810]) (VIGNOLI et al. 2012). To exclude a potential bias distorting the results due to obvious deviation from natural conditions, the enclosures built try to mirror the size of the lizard's home range/territory in nature. The available data on territorial behavior reported the territory size of the study species to range from 6 to 52 m^2, not strongly different for males and females, with highly variable overlap of 8 - 60 % among home ranges (GRUSCHWITZ & BÖHME 1986). Each enclosure was composed of a pair of enclosed boxes (7 m × 7 m), connected by two independent one-way corridors (14 m × 1 m), each ending with a pit trap, allowing the capture and identification of dispersing individuals. All the enclosures and corridors were fenced by one meter high translucent polyethylene walls. The width of the corridors was large enough to allow lizards to disperse, but small and exposed enough to be unattractive, preventing any attempt of settlement (LECOMTE et al. 2004). Enclosures had a typical Mediterranean maquis shrubland habitat, providing lizards with refugia (rocks and wood branches) and sites for thermoregulation. Food (mostly grasshoppers and ants) and water were given *ad libitum*. Each individual caught in a pit trap was placed in the enclosure towards which it was moving.

Before being placed in the enclosures, the lizards were maintained in fauna boxes (50 cm × 40 cm) and fed with grasshoppers for one week for captivity acclimatization. Each lizard was individually marked by both temporary (color blotches on the dorsal body surface) and permanent (photographs of the gular pigmentation) methods (see VIGNOLI et al. 2012 for marking details). Lizards promptly acclimatized in the enclosures and showed natural behavior (territorialism, mating, etc.).

Two experimental designs simulated different density starting conditions (EBENHARD 1991; IMS & YOCCOZ 1997):

(i) Augmentation design – (April 28 - May 28, 2006). Both enclosures of a pair started with an experimental population of 10 lizards each, and the individuals attempting to disperse found the reached enclosure already colonized (LECOMTE & CLOBERT 1996; VIGNOLI et al. 2012). The experimental starting density of 10 lizards per enclosure (sex ratio m/f: enclosures A = 1.0, B = 1.0) (Fig. 1, above) was slightly higher than that estimated under natural conditions (VERBEEK 1972; BOAG 1973; BARBAULT & MOU 1988; BROWN et al. 1995). Sex ratio was assessed similar to that found at the collection site. The experiment ended after 30 days.

(ii) Colonization design – (May 18 - July 12, 2006). One enclosure (A) of a pair started with a population of 25 lizards (18 males, 7 females), simulating an overpopulated condition, whereas, the other was free from lizards (Fig. 1, below). Based on the available literature data on sex ratio under natural conditions (e.g., BARBAULT & MOU 1988), sex ratio was biased towards males (m/f: 2.57) that are expected to be more prone to move than females (VIGNOLI et al. 2012). The experiment ended after 56 days when the system entered a balanced dynamic equilibrium in terms of movements between enclosures (see below).

Two 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, p = 0.41). Observations on the experimental system were made daily and at two levels (VIGNOLI et al. 2012): (a) individual level: the number of individual between-enclosure movements was recorded; and (b) enclosure level: the lizard density within each enclosure and the dispersal rate (number of dispersal events divided by the number of individuals in each enclosure) were computed at the beginning and at the end of each experimental day. As evidenced in VIGNOLI et al. (2012), this protocol of analysis might generate data pseudoreplication, i.e., the number of daily movements between enclosures would be non-independent from each other if an individual moved between enclosures more than once per day. This type of behavior was however, not observed (see Results); hence, the possible bias due to this aspect is irrelevant. Experimental observations lasted until movements between enclosures ended or entered a balanced dynamic equilibrium (VIGNOLI et al. 2012). Individuals were grouped into three classes based on their dispersal activity: the residents (individuals that never leave their initial enclosure), the emigrants (dispersers that settled in the arrival enclosure), and the transients (dispersers that moved at least twice between enclosures) (LE GALLIARD et al. 2005; VIGNOLI et al. 2012).

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 the Generalized Linear Models procedure (MCCULLAGH & NELDER 1989). Two models were built, respectively, selecting as dependent variables the number of individual movements (Poisson distribution and log link function) and classes of dispersal activity (multinomial distribution and cumulative log link function) as dependent variables. 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 2-way interactions between the three factors and the covariate (fractional factorial design) (MCCULLAGH & NELDER 1989). Univariate tests were used to analyze the size and the body condition of the lizards (normal distribution, t-test and ANCOVA on log-weight and log-SVL as covariate) and the number of dispersal events (Poisson distribution, non-parametric tests) and the classes of dispersal activity (multinomial distribution; non-parametric tests). The observed movement pattern between enclosures was estimated by nonlinear regression models with both sides of the equation log-transformed (VIGNOLI et al. 2012). At enclosure level, the influence of population density on the total number of between-enclosure dispersal events and dispersal rate was tested 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

Statistically, male (m) and female (f) individuals [N = 43] did not differ in SVL [mm] ($\bar{x}_{m,\,29} = 62.23$; $SD_m = 7.357$; $\bar{x}_{f,\,16} = 59.26$; $SD_f = 5.38$; $t = -1.43$; $p = 0.161$; t-test), and body condition ($\bar{x}_{m,\,29} = 0.014$; $SD_m = 0.072$; $\bar{x}_{f,\,16} = -0.025$; $SD_f = 0.076$; $F_{1,42} = 2.847$; $p = 0.099$; ANCOVA), but varied in body mass [g] ($\bar{x}_{m,\,29} = 5.96$; $SD_m = 2.71$; $\bar{x}_{f,\,16} = -4.39$; $SD_f = 1.15$; $t = -2.20$; $p = 0.033$), the males being heavier than females. Tail status did not differ between sexes ($\chi^2 = 0.15$; $df = 1$; $p = 0.703$; Chi-square test).

The experimental design clearly influenced the lizard dispersal behavior: the augmentation design did not produce any between-enclosure movement, whereas in the colonization design, 39 attempts to move between the enclosures occurred. As for the number of dispersal attempts, most individuals (36/43) were classified as residents ($\chi^2 = 19.56$; $df = 1$; $p < 0.001$), this pattern was true also for males and females analyzed separately.

Augmentation design

The experiment started with equal numbers (10), densities (0.20 individuals/m^2) and sex ratios (1:1) in both enclosures

Table 1: The number of individuals and dispersal events between enclosures A and B (both directions) for the experimental designs ‘Augmentation’ and ‘Colonization’. Initial N – number of individuals at the beginning of the experiment; Final N – number of individuals at the end of the experiment; A-B – dispersal events from enclosure A to enclosure B; B-A – dispersal events from enclosure B to enclosure A.

Tab. 1: Anzahl der Individuen in und Ortswechsel (in beiden Richtungen) zwischen den Enclosures A und B für die Versuchsanordnungen ‘Augmentation’ und ‘Colonization’. Initial N – Anzahl Individuen zu Beginn des Experiments; Final N - Anzahl Individuen zu Ende des Experiments; A-B – Ortswechsel von Enclosure A zu Enclosure B; B-A – Ortswechsel von Enclosure B zu Enclosure A.

Design / Experiment	Enclosure				Number of dispersal events / Anzahl Ortswechsel					
	A		B		Total		Males / Männchen		Females / Weibchen	
	Initial N	Final N	Initial N	Final N	A-B	B-A	A-B	B-A	A-B	B-A
Augmentation	10	10	10	10	---	---	---	---	---	---
Colonization	25	14	0	11	25	14	22	13	3	1

(Fig. 1, above). The experiment was stopped after 30 days because no movement was observed between enclosures. All the individuals behaved as residents.

Colonization design

The experiment started with 25 (18 m, 7 f) lizards at a density of 0.51 individuals/m^2 and a sex ratio of 2.57 (m/f) (enclosure A; Fig. 1, below). The final numbers, densities and sex ratios in the two enclosures after a total of 39 between-enclosure dispersal events (0.70 per day) were 14 (9 m, 5 f), 0.29 individuals/m^2 and 1.8 (m/f) (enclosure A) and 11 (9 m, 2 f), 0.22 individuals/m^2 and 4.5 (m/f) (Table 1). The number of dispersal events per day decreased significantly with time (r = -0.378; N = 56; $p < 0.01$). As for overall dispersal attempts made by the individuals, the sexes behaved differently, males displaying a higher propensity to disperse. Neither size nor body condition influenced the individual tendency to disperse (Table 2). Overall, dispersal types did not show differences in terms of number of individuals (χ^2 = 2.24; df = 2; p = 0.326). Although there was a higher tendency to relocate among males, no statistically significant differences were found between male and female dispersal types (χ^2 = 3.08; df = 2; p = 0.205) (Fig. 2). Moreover, any of the considered parameters (BCI, SVL, and tail status) had an effect on dispersal types (Table 3). In the starting enclosure (A), a significant effect of the population density on the dispersal rate (r = 0.452; N = 56; p = 0.0004) and on the daily number of dispersal events towards enclosure B (r = 0.481; N = 56; p = 0.0001) was found, whereas in enclosure B, lizard dispersal behavior was not related to density (dispersal rate: r = -0.133; N = 56; p = 0.329; number of dispersal events per day r = -0.104; N = 56; p = 0.445). Although lizards in enclosure B did not show an overall density-related tendency to move, a closer inspection of this pattern revealed that: (i) individuals that emigrated to the empty enclosure B returned to the enclosure of origin (A) as long as the density in enclosure B was below a threshold of 0.18 individuals/m^2 (11 movements/26 days); (ii) at higher densities (0.20-0.24 individuals/m^2), movements from enclosure B to A largely ended (3 movements/28 days); these differences were statistically significant (χ^2 = 4.571; df = 1; p = 0.032).

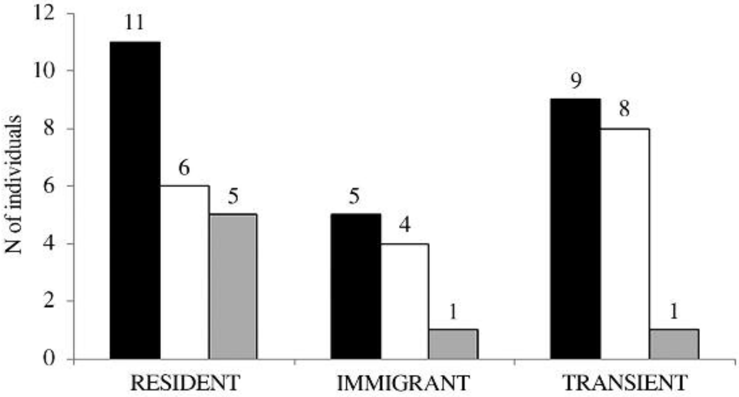

Figure 2: Number of dispersal events between enclosures performed by lizard individuals during the colonization design. Black bars – total individuals; white bars – males; grey bars – females. The individuals are categorized into three types of disperser: Resident – no dispersal event; Immigrant – one dispersal event; Transient – more than one dispersal event.

Abb 2: Anzahl der Ortswechsel zwischen Enclosures, die von den Untersuchungsindividuen im Colonization Design Experiment durchgeführt wurden. Schwarz – Männchen + Weibchen, weiß – Männchen; grau – Weibchen. Die Individuen sind drei Ausbreitungstypen zugeordnet: Resident – Kein Ortswechsel; Immigrant – ein Ortswechsel; Transient – mehr als ein Ortswechsel.

Table 2: Synopsis of the Generalized Linear Model (fractional factorial design) results, showing that only 'Sex' among the studied parameters (including between-effects) significantly influenced the individual dispersal movements between enclosures. BCI – body condition index; SVL – snout-vent-length; Tail – tail status.

Tab. 2: Die Übersicht der Ergebnisse der Generalized Linear Model Statistik (Teilfaktorenplan) zeigt, daß der Einfluß der untersuchten Variablen (einschließlich ihrer Interaktionen) auf die Häufigkeit individueller Ortwechsel zwischen den Enclosures nur für den Parameter Geschlecht signifikant war. BCI – Body Condition Index; SVL – Kopf-Rumpf-Länge; Tail – Schwanzstatus.

Model	Wald Chi-Square	*df*	*p*
(Intercept)	2.815	1	0.093
Sex	**5.441**	**1**	**0.020**
Tail	2.305	1	0.129
SVL	1.399	1	0.237
BCI	1.047	1	0.306
Sex * Tail	0.031	1	0.861

Table 3: Synopsis of the Generalized Linear Model (fractional factorial design) results, showing the influence of the studied parameters (including between-effects) on the dispersal types (residents, immigrants, transients). BCI – body condition index; SVL – snout-vent-length; Tail – tail status.

Tab. 3: Die Zusammenfassung der Generalized Linear Model Statistik (Teilfaktorenplan) zeigt den Einfluß der untersuchten Variablen (einschließlich ihrer Interaktionen) auf die Dispersionstypen resident, immigrant und transient. BCI – Body Condition Index; SVL – Kopf-Rumpf-Länge; Tail – Schwanzstatus.

Model	Wald Chi-Square	*df*	*p*
(Intercept)	0.849	1	0.357
Sex	2.422	1	0.120
Tail	1.341	1	0.247
SVL	0.105	1	0.746
BCI	0.397	1	0.528
Sex * Tail	0.353	1	0.553

DISCUSSION

Although animal dispersal patterns are widely studied in several taxa, reptiles were rather neglected in this respect (CLOBERT et al. 2001), *Podarcis* lizards in particular (VIGNOLI et al. 2012). The present study showed that the dispersal of adult *P. muralis* was influenced by both population (density, intraspecific relationships) and individual (sex) parameters, as previously revealed for *P. siculus* (VIGNOLI et al. 2012) and other animals (TRAVIS et al. 1999; IMS & HJERMANN 2001; CADET et al. 2003).

The augmentation design did not lead to any dispersal. The lack of dispersal activity was probably due to the habitat features in the corridors connecting the enclosures. The corridor physical environment was left completely exposed, not to make dispersal particularly attractive to lizards. Indeed, the Common Wall Lizard is typically a wood and shrub dweller (GRUSCHWITZ & BÖHME 1986; BIAGGINI et al. 2010). For the dispersal pattern comparison with another *Podarcis* species (*P. siculus*) studied in the same experimental system (VIGNOLI et al. 2012), one has, however, to take into account that the threshold between the "cost to stay" and the "benefit to move" can be different in different species confronted with the same habitat type. Expecting population density to be among the main factors driving the dispersal processes, the authors suppose that the effect of the starting density in the experimental design was too weak to compensate the costs of moving through the unattractive and potentially unsafe corridor landscape connecting the enclosures. Due to the lack of any attempt to move between enclosures by individuals (= no between-enclosure interaction), one can consider the experimental setting of two enclosures as two replicates of the same starting density condition, corroborating the outcome of this experiment.

The colonization design evidenced that settlement probability was influenced by the presence of conspecifics: lizards avoided staying longer in initially empty rather than in occupied patches. The present short-term study did not allow for measuring real fitness variation in relation to dispersal benefits/costs (LECOMTE & CLOBERT 1996; LE GAILLARD et al. 2005). However, the observed pattern could be explained by the expected fitness increase at low to moderate population densities, and decrease at moderate to high densities due to the Allee effect (ALLEE 1951). Moreover, immigrants can benefit from the presence of resident conspecifics, i. e., profiting from their selection of suitable refugia and reducing settlement costs (SAETHER et al. 1996; but see DANIELSON & GAINES 1987 for an opposite trend). Thus, newcomers may use conspecifics to assess the relative quality of the new habitats (STAMPS 1987, 1991, 2001; BOULINIER et al. 1996; DANCHIN & WAGNER 1997). Indeed, the settlement benefits/costs are expected to follow an Allee effect pattern as a function of density, because for latecomers: (i) the effort required to assess habitat quality is smaller than for the first arrivals at low to moderate densities (STAMPS 1987, 1988, 1995), and (ii) the chance to find a suitable unoccupied site is reduced compared with the first arrivals at high densities (STAMPS, 1994; GREENE & STAMPS, 2001; CLOBERT et al. 2009). Density-independent handicaps such as increased effort for efficiently using the new habitat patches (STAMPS 1995) may add to the settlement costs in unfamiliar habitats. The observed behavioral pattern of hesitant colonization can decrease the costs of settlement in unfamiliar habitats (STAMPS 1988; GREENE & STAMPS 2001).

Sex was found to influence the dispersal behavior in the studied lizard species as previously evidenced in *P. siculus* (VIGNOLI et al. 2012). This occurs in several taxa (reviewed in LOMNICKI 1988), often in relation to reproductive strategy. In some mammals (GREENWOOD 1980) and amphibians (SINSCH 1992), males are less prone to disperse than females; conversely, in many other species the females show higher site fidelity than males (LOMNICKI 1988; birds - GREENWOOD 1980; amphibians - DELLA ROCCA et al. 2005; reptiles - TUCKER 1998). Although little data is available, *Podarcis* lizards seem to develop sex-dependant differences in home range size which is larger in males (BEARZI 1989), whereas other authors found the territorial conditions to be highly variable and not strongly different among sexes (GRUSCHWITZ & BÖHME 1986). That could affect dispersal behavior. In general, territoriality is affected by the degree of overlap between home ranges (BROWN & ORIANS 1970). Lack of information on sex-specific differences in site fidelity of lizards, makes the authors speculate that the finally observed male-biased distribution could be the result of stronger competition between males due to their territorial behavior (HUEY et al. 1983; VIGNOLI et al. 2012). The observed dispersal pattern could also be a matter of scale given that dispersing *Podarcis* females made long distance (long term) dispersals (between abandoned and new home ranges) whereas males performed short distance dispersals within their bigger home ranges (BROWN 1995; DIEGO-RASILLA & PÉREZ-MELLADO 2003).

Individual efforts to leave a habitat patch and settle in a new one are doubtlessly species-specific and likely to depend on habitat conditions, i. e., external cues such as density, habitat quality and phenotype, dispersal propensity, thereby correlating with a suite of phenotypic traits (e.g., DENNO & RODERICK 1992; MATTHYSEN 2005; CLOBERT et al. 2009; VIGNOLI et al. 2012). No phenotypic attributes were found globally characterizing dispersers compared to residents (e.g., dispersers are larger or display a more aggressive behavior than residents - CLOBERT et al. 2009), but most dispersers were males.

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