Reproductive Investment of a Lacertid Lizard in Fragmented Habitat

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Abstract: *We studied the effect of habitat fragmentation on female reproductive investment in a widespread lacertid lizard (*Psammodromus algirus*) in a mixed-forest archipelago of deciduous and evergreen oak woods in northern Spain. We captured gravid females in fragments (≤10 ha) and forests (≥ 200 ha) and brought them to the laboratory, where they laid their eggs. We incubated the eggs and released the first cohort of juveniles into the wild to monitor their survival. Females from fragments produced a smaller clutch mass and laid fewer eggs (relative to mean egg mass) than females of similar body size from forests. Lizards did not trade larger clutches for larger offspring, however, because females from fragments did not lay larger eggs (relative to their number) than females from forests. Among the first cohort of juveniles, larger egg mass and body size increased the probability of recapture the next year. Thus, fragmentation decreased the relative fecundity of lizards without increasing the quality of their offspring. Reduced energy availability, increased predation risk, and demographic stochasticity could decrease the fitness of lizards in fragmented habitats, which could contribute to the regional scarcity of this species in agricultural areas sprinkled with small patches of otherwise suitable forest. Our results show that predictable reduction of reproductive output with decreasing size of habitat patches can be added to the already known processes that cause inverse density dependence at low population numbers.*

Key Words: clutch size, egg size, forest fragmentation, habitat quality, *Psammodromus*

Inversión Reproductiva de una Lagartija Lacértida en Hábitat Fragmentado

Resumen: *Estudiamos el efecto de la fragmentación sobre la inversión reproductiva de hembras en una lagartija lacértida (*Psammodromus algirus*) ampliamente distribuida en un archipiélago mixto de bosques deciduos y siempre verdes de roble en el norte de España. Capturamos hembras grávidas en fragmentos (≤ 10 ha) y en bosques (≥ 200 ha) y las trasladamos al laboratorio, donde pusieron sus huevos. Incubamos los huevos y liberamos a la primera cohorte de juveniles para monitorear su supervivencia. Las hembras de fragmentos produjeron una puesta de menor masa y pusieron menos huevos (en relación con la masa promedio de los huevos) que hembras con talla corporal similar provenientes de bosques. Sin embargo, las lagartijas no cambiaron puestas mayores por crías más grandes porque las hembras de fragmentos no pusieron huevos más grandes (en relación con su número) que las hembras de bosques. Entre las primeras cohortes de juveniles, la mayor masa de los huevos incrementó la probabilidad de recaptura en el siguiente año. Por lo tanto, la fragmentación redujo la fecundidad relativa de las lagartijas sin aumentar la calidad de sus crías. La disponibilidad reducida de energía, el incremento en el riesgo de depredación y la estocasticidad demográfica podrían disminuir la adaptabilidad de lagartijas en hábitats fragmentados, lo que podría contribuir a la escasez regional de esta especie en áreas agrícolas salpicadas de pequeños parches de bosque por lo demás*

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adecuado. Nuestros resultados muestran que la reducción predecible en la reproducción al disminuir el tamaño de los parches de hábitat se puede agregar a los procesos ya conocidos que causan la inversión de la denso dependencia en tamaños poblacionales pequeños.

Palabras Clave: calidad de hábitat, fragmentación de bosque, *Psammodromus,* tamaño de puesta, tamaño de huevo

Introduction

Understanding how the distribution and abundance of species are affected by habitat fragmentation is a central issue in conservation biology. The responses to fragmentation at a landscape level (e.g., low frequencies of patch occupancy or decreased species richness), however, are better known than the underlying processes of local decline or extinction (Wiens et al. 1993; Hokit et al. 1999). In addition, different species may show unique responses to fragmentation and associated changes in patch shape, matrix permeability, and dispersal capacity (Wiens 1989). Therefore, a detailed knowledge of the ecology of each species might be the best way to predict its responses to fragmentation (Simberloff 1988).

Usually, high extinction rates in fragmented populations are assumed to be caused by random demographic or environmental fluctuations (Gilpin & Soulé 1986), but patch size can also impair fecundity in a deterministic way (Hokit & Branch 2003*b*; Luck 2003). For instance, small habitat patches generally house small populations, which may face Allee effects (when populations at low numbers are affected by a positive relationship between population growth rate and density; Courchamp et al. 1999) or inbreeding depression (Madsen et al. 1996; Madsen et al. 1999). Also, edge effects can increase predation rates in fragmented landscapes (e.g., Wilcove 1985; Tellería & Santos 1992; Robinson et al. 1995). In such a context, the probability of local extinction might increase more rapidly with decreasing patch size (Hokit & Branch 2003*a*).

Results of several studies, mostly of birds, show that fragmentation affects indirect indicators of demographic performance, such as mating success (Huhta et al. 1998; Dale 2001; Zanette 2001), density (Burke & Nol 1998; Zanette 2001), and local recruitment (Matthysen et al. 2001). Nevertheless, results have been less conclusive when demographic parameters were measured directly. Habitat fragmentation impaired breeding success in some studies (Luck 2003) but had no effect on reproductive success or population viability in others (Zanette 2000). These discrepancies could be because habitat fragmentation may elicit complex life-history responses. Breeding success may decrease in small fragments because of reduced food availability (Burke & Nol 1998; Zanette et al. 2000) or increased predation risk (Wilcove 1985; Tellería & Santos 1992). In these circumstances, life-history theory predicts either a variable reproductive investment, fitting resource availability, or a different allocation of resources, for example, trading larger clutches for larger offspring (Roff 1992; Stearns 1992). Thus if juveniles suffered from higher predation rates in small fragments, more but smaller offspring should be produced in these habitats. Alternatively, if large juveniles had a survival advantage that was accentuated in fragmented environments, offspring size should increase and clutch size should decrease with decreasing patch size (Sinervo 1990; Roff 1992; Stearns 1992).

We studied the effect of forest fragmentation on the breeding investment of female *Psammodromus algirus* lizards (Squamata: Lacertidae). This species is widespread in Iberian Mediterranean forests, but it is restricted to forest remnants and shows limited dispersal in areas that have been fragmented by agriculture (Santos & Tellería 1989; Díaz et al. 2000). Our goal was to document the effects of habitat fragmentation on the allocation of resources by female lizards in the context of the trade-off between clutch size and egg size. If fragmentation effects are significant and consistent, then predictable reduction of reproductive output with decreasing size of habitat patches can be added to the already known processes that cause inverse density dependence at low population numbers (Courchamp et al. 1999).

Methods

Study Area

We studied an agricultural landscape (approximately 70 km^2) in northern Spain (Lerma: 42°5′N, 3°45′W; elevation 850 m), where forests cover $\leq$ 10% of the total area and woodlots of variable size are interspersed among cereal fields. Forest remnants are deciduous woods (Pyrenean oaks [*Quercus pyrenaica* Willd.] in relatively moist soils) and evergreen woods (holm oaks [*Q. ilex* L.] in drier areas). Results of earlier studies suggest that deciduous Pyrenean oak woods are habitats of higher quality for lizards than are evergreen holm oak woods (Díaz 1997).

We studied lizards in forests (large unfragmented woodlots) and forest fragments that were either deciduous or evergreen woods. Fragments ranged between 0.6 and 6.8 ha (mean $\pm$ SE $= 2.6 \pm 0.7$ ha, $n = 9$; no significant differences between evergreen and deciduous wood

fragments: Mann-Whitney's U test $p > 0.4$). Forests were two deciduous woods of 227 and 317 ha and one evergreen wood of 567 ha.

Capture and Husbandry of Adults

We captured gravid females by hand or with a noose during two consecutive breeding seasons (2001 and 2002) in late May or early June and got them to the laboratory within 2 days of capture. Females ($n = 28$ in 2001 and 31 in 2002) did not differ significantly in snout-vent length (SVL), body mass, or body condition (body mass adjusted for SVL) between forests and fragments, wood types, or years (all $p > 0.05$). Thus, variation in body size or condition should not confound differences in reproductive investment.

The laboratory had natural light and dark conditions and ventilation. We housed lizards in terraria ($40 \times 60 \times 30$ cm) with white, opaque walls. The tops were covered with a green net (0.5-cm mesh) that prevented escape, let daylight enter the cages, and created a shrubby-like shelter. We filled the terraria with moistened soil about 10 cm deep and covered the soil with leaf litter. A lamp created a photothermal gradient (approximately 25–50° C) that allowed thermoregulation within the preferred temperature range (Belliure et al. 1996; Díaz 1997). An earthenware tile (approximately 10×15 cm) and thin sticks provided shade and shelter. We fed lizards crickets (*Acheta domestica*), mealworms (*Tenebrio mollitor*), and waxworms (*Galleria mellonella*) that had been dusted with a commercial diet supplement. All terraria contained water at all times.

Egg Laying

One advantage of our study species is that gravid females readily lay eggs in captivity, but their reproductive output still depends on the environmental conditions they experienced in the wild. In lizards, the hormonal and physiological coupling among clutch size, egg size, and clutch mass occurs during early vitellogenesis (Sinervo & Licht 1991; Sinervo 1994).

We detected egg laying by palpation or daily weighing of gravid females. The dates of capture and laying were similar in both years (mean values: 1 June and 12 June in 2001 and 27 May and 7 June in 2002), and fragmentation, wood type, and year did not have a significant effect on the time elapsed between the arrival of females in the laboratory and egg laying (analysis of variance [ANOVA], all $p > 0.2$).

Of 59 females, 3 (1 in 2001 and 2 in 2002) did not lay eggs, either because they had already laid in the field or because they were infertile. Two females laid clutches that were not viable in 2001. All these females were excluded from the analyses. Second clutches were laid by 11 females, with no significant differences in their frequency between forests and fragments, wood types, or years (all Fisher exact $p > 0.1$). We did not consider second clutches in our analyses because they were formed under artificial conditions. After the study, adult lizards were released at their sites of capture.

Husbandry of Eggs and Juveniles

Immediately after laying, we removed the female and carefully searched for the eggs, which were counted, wiped clean of sand, and weighed to the nearest 0.01 g. We placed each egg in an individually labeled, 150-mL plastic container filled with 10 g of vermiculite moistened with 8 g of water. Eggs were completely surrounded by the vermiculite, and we closed the containers hermetically to minimize evaporation. Eggs were incubated at a constant temperature of 30 ± 0.5° C, with weekly inspections to verify their normal gain of mass and their viability based on shell characteristics (shape, color, and texture). Moisture was kept constant by adding water to reach the initial mass of the moistened vermiculite.

Toward the end of incubation (45.2 ± 0.2 days, mean $\pm$ SE), we searched daily for newly hatched lizards. Hatchlings were weighed and given unique toe-clip marks before being transported to nursery terraria. These terraria were similar to those used for housing adults, except they received direct ultraviolet light 4 hours/day (F30 W/6500 K Reptistar terrarium lamp, SLI Sylvania, Madrid). Small crickets, dusted with commercial vitamins and calcium supplements, and water were provided ad libitum. We sorted juveniles from the same clutch among different terraria to separate environmental and familial effects.

Juvenile Survival

The juveniles reared in the laboratory during 2001 ($n = 178$; hatching success = 0.924 and hatchling survival = 0.913) were released into the wild in September 2001 in the context of an ongoing long-term study of survival in different habitats. Groups of five to six unrelated juveniles were released at each of 30 sites, distributed among two deciduous wood fragments (of 1.0 and 5.2 ha, separated by a distance of approximately 100 m) and two evergreen wood fragments (of 0.9 and 4.1 ha, separated by a distance of approximately 30 m) in the study area. Release sites, 15 in each wood type, were distributed among fragments according to their size. By design, half the offspring of each female were released in deciduous woods and the other half in evergreen woods so that offspring origin, but also egg or neonate mass, did not differ between forest types (ANOVA: $r^2 < 0.001$ and $p > 0.65$ in both cases). We measured all juveniles to the nearest 0.5 mm (SVL) before release. During the 2002 activity season we searched (286 person hours) for surviving juveniles.

Data Analyses

We analyzed clutch mass, clutch size, and mean egg mass with mixed, general linear models, with fragmentation and habitat type as fixed factors, year as a random factor, and females as replicates. We used mixed models because we were interested in applying the statistical inference about the effects of fragmentation and habitat quality to all years, rather than just to the 2 years of study. The mixed model requires leaving the random effects independent of the fixed effects (Searle et al. 1992) by constructing error terms that contain all the same sources of random variation except for the variation of the effect of interest. We formed ratios of suitable mean squares by using the variance components and mixed model ANOVA/ANCOVA (analysis of covariance) module of Statistica (version 6.1, StatSoft 2004). This program uses Satterthwaite's (1946) method of denominator synthesis to find the linear combinations of sources of random variation that serve as appropriate error terms for each effect. Thus, the degrees of freedom for the denominator mean square can be fractional rather than integer values, meaning fractions of sources of variation were used in synthesizing error terms for significance testing.

Females were not independent replicates of the effects of fragmentation or type of wood because we sometimes captured several lizards at the same particular woodlot. Obtaining independent replicates at the landscape level without changing other factors is one of the most difficult problems in landscape ecology (Wiens 1989), and averaging across fragments of a similar size could mask between-site variability in reproductive traits (Zanette 2000). Because of logistic restrictions, we had to choose between using a few individuals from several woodlots or many lizards from a few woodlots. We chose the former option, assuming that differences among sites were not important. To avoid estimating parameters and probabilities based on too small sample sizes (only 12 sites) and because 9 sites contributed females in both years, we decided not to use a nested approach. Nevertheless, among-site differences in a nested analysis were not significant for any of the life-history traits examined (all $p > 0.15$).

The effects of egg and juvenile traits on subsequent survivorship were examined using logistic regressions with presence and absence data in 2002 as the dependent binomial variable. We did not control for family effects (only six females contributed more than one recaptured offspring). When necessary, variables were log-transformed to meet the requirements of parametric tests. Estimates are given as mean ± 1 SE.

Results

Reproductive Investment

Multiple regressions showed that mean egg mass increased with maternal SVL ($\beta = 0.504$, $n = 54$, $p = 0.002$) and was negatively correlated with clutch size ($\beta = -0.675$, $p < 0.001$). To control for variation in maternal body size, we calculated the residuals from the linear regression of clutch size on female SVL ($r = 0.647$, $p < 0.001$). These residuals, which measure relative fecundity, were negatively correlated with mean egg mass ($r = -0.515$, $p < 0.001$), reflecting the trade-off between egg size and clutch size: eggs from smaller clutches tended to be larger. Thus, the detection of environmental effects on clutch size (or egg size) could require one to control for the effects of both female SVL and egg size (or clutch size).

Neither mean egg mass nor clutch size differed significantly between fragments and forests, wood types, or years (mixed-model ANOVA: $p > 0.4$ for all main effects). Although the overall breeding investment, measured as clutch mass adjusted for SVL, did not differ significantly between years or wood types, it was, however, smaller in fragments than in forests (2.74 ± 0.10 g, $n = 27$; and 3.04 ± 0.10 g, $n = 27$, respectively; Table 1 and Fig. 1). Furthermore, females from fragments laid fewer eggs than females from forests when controlling for the effects of

Table 1. Three-way mixed model analysis of covariance with the effects of fragmentation (fragments vs. forests), wood type (evergreen holm oak vs. deciduous Pyrenenan oak woods), and year on clutch mass of *P. algirus*, with log-maternal snout-vent length (SVL) as the covariate.

	Type of effect	*df effect*	*MS effect*	*DS error df**	*DS error MS**	F	p
Log-maternal SVL	fixed	1	11.69	45.00	0.26	45.24	<0.001
Fragmentation	fixed	1	1.09	3.31	0.02	55.86	0.004
Wood type	fixed	1	0.01	1.01	0.92	0.02	0.921
Year	random	1	0.22	0.88	0.88	0.24	0.717
Fragmentation × wood type	fixed	1	0.41	0.98	0.07	6.13	0.248
Fragmentation × year	random	1	0.01	0.98	0.07	0.17	0.754
Wood type × year	random	1	0.93	1.08	0.07	13.58	0.154
Year × fragmentation × wood type	random	1	0.07	45.00	0.26	0.26	0.614
Error		45	0.26				

* *Appropriate error terms for each effect were formed using Satterthwaite's (1946) method of denominator synthesis (DS).*

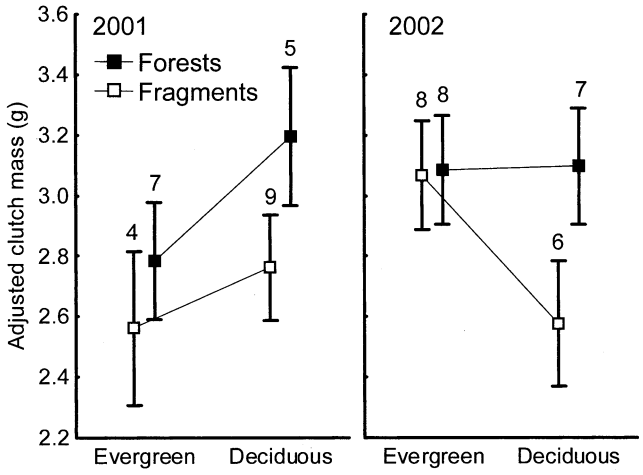

Figure 1. Mean (± 1 SE) clutch mass of female P. algirus *adjusted for snout-vent length in relation to fragmentation, habitat type (evergreen holm oak vs. deciduous Pyrenean oak woods), and year of capture. Sample sizes are shown on top of whiskers.*

female SVL and mean egg mass (Table 2, Fig. 2a). Despite the trade-off between relative fecundity and mean egg mass, females from fragments did not lay larger eggs than females from forests when controlling for the effects of SVL and clutch size. In fact, adjusted mean egg mass was larger, although not significantly so, in forests than in fragments (Table 2, Fig. 2b).

Juvenile Survival

Heavier eggs produced heavier hatchlings ($r = 0.876$, $n = 175$, $p < 0.001$) that led to larger juveniles, as shown by a positive correlation between hatchling mass and age-corrected body size (i.e., residuals of the regression of SVL on age; $r = 0.528$, $n = 178$, $p < 0.001$). In turn, egg and offspring size seemed to influence survivorship of lab-reared juveniles released into the wild because larger values for these traits increased their probability of recapture during the 2002 activity season (Table 3).

Discussion

Habitat fragmentation impaired the breeding success of lizards by affecting their total reproductive investment. Thus, females from fragments laid lighter clutches than females from forests of similar body size. They did not, however, lay a smaller number of larger eggs or vice versa. Instead, they laid fewer eggs (relative to their mass) than forest females of similar body size, but this lower relative fecundity was not counterbalanced by a larger size of the eggs and juveniles. Remarkably, this species seems to be able to adaptively adjust its partition of breeding resources into offspring size and number in other

Table 2. Three-way mixed model analyses of covariance with the effects of fragmentation (fragments vs. forests), wood type (evergreen holm oak vs. deciduous Pyrenenan oak woods), and year on clutch size and mean egg mass of *P. algirus*, with each of these variables used as a covariate for the analysis of the other one (sign of effect in parentheses).

		Clutch size						*Mean egg mass*					
	Type of effect	*df effect*	*MS effect*	*DS error df**	*DS error MS**	F	p	*df effect*	*MS effect*	*DS error df**	*DS error MS**	F	p
Log-maternal snout-vent length (+ in both cases)	fixed	1	77.70	44.00	1.39	56.03	< 0.001	1	0.0267	44.00	0.0019	14.33	< 0.001
Mean egg mass (-)/clutch size (-)	fixed	1	33.72	44.00	1.39	24.32	< 0.001	1	0.0454	44.00	0.0019	24.32	< 0.001
Fragmentation	fixed	1	6.39	7.50	0.09	70.96	< 0.001	1	0.0090	1.16	0.0014	6.20	0.215
Wood type	fixed	1	0.05	0.98	4.63	0.01	0.932	1	0.0001	1.01	0.0100	0.01	0.928
Year	random	1	0.59	0.82	4.36	0.14	0.785	1	0.0000	0.66	0.0086	0.00	0.971
Fragmentation × wood type	fixed	1	2.55	0.99	0.40	6.37	0.243	1	0.0058	1.00	0.0030	1.95	0.395
Fragmentation × year	random	1	0.03	0.92	0.39	0.08	0.823	1	0.0014	1.00	0.0030	0.48	0.614
Wood type × year	random	1	4.54	1.23	0.43	10.47	0.152	1	0.0101	1.02	0.0029	3.45	0.311
Year × fragmentation × wood type	random	1	0.40	44.00	1.39	0.29	0.593	1	0.0030	44.00	0.0019	1.58	0.215
Error		44	1.39					44	0.0019				

**Appropriate error terms for each effect were formed using Satterthwaite's (1946) method of denominator synthesis (DS).*

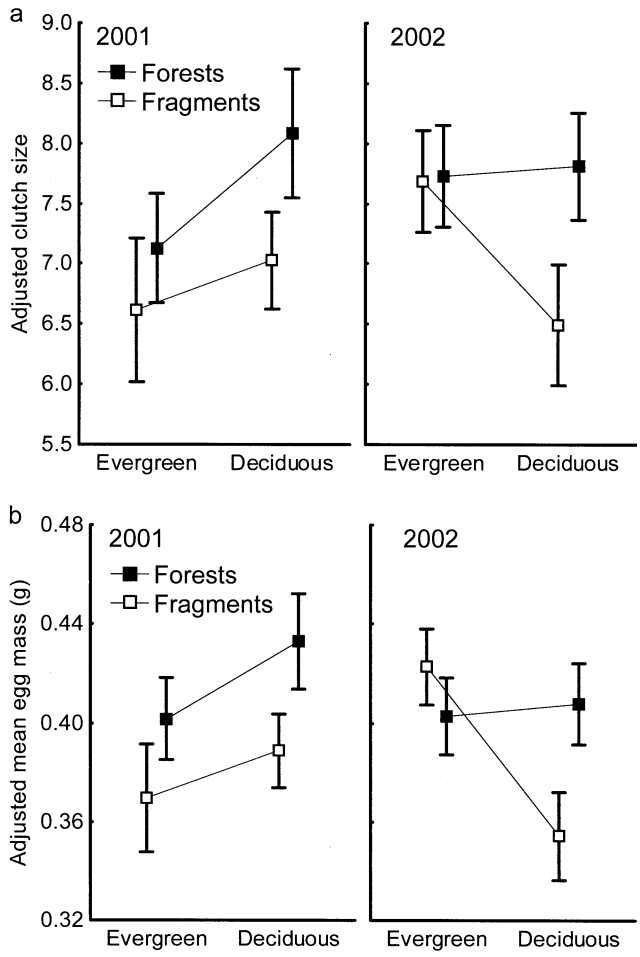

Figure 2. (a) Mean (± 1 SE) clutch size of female P. algirus *adjusted for snout-vent length and mean egg mass and (b) mean egg mass adjusted for snout-vent length and clutch size in relation to fragmentation, habitat type (evergreen holm oak vs. deciduous Pyrenean oak woods), and year of capture. Sample sizes as in Fig. 1.*

environmental contexts, for example, across its geographical range (clutches in our population were larger and eggs were smaller than those in a population in central Spain [authors, unpublished data]; see Sinervo [1990] for a similar example in *Sceloporus occidentalis*).

This pattern suggests two possible interpretations. Lizards would be maladapted in small fragments if fragmentation accentuated either the fecundity advantage of laying many small eggs or the survival advantage of large eggs (Sinervo et al. 1992; Sinervo 1994; Civantos et al. 1999). Alternatively, similar life-history outcomes could be favored throughout the patchy landscape (Roff 1992; Stearns 1992), despite females from fragments producing fewer but not larger eggs than females from forests of similar body size (Table 2 & Fig. 2). In either case, our results indicate that habitat fragmentation impaired lizard reproduction.

In our population, being large seemed to favor first-year survival. Results of previous studies specifically designed to unravel the determinants of hatchling or juvenile survival in this species show that body size is the phenotypic trait that best predicts survival (Civantos et al. 1999; Civantos & Forsman 2000). The reduced relative fecundity of females from fragments, however, was not counterbalanced by a larger size, and hence quality, of their offspring, perhaps because reduced energy availability distorts the physiological coupling between clutch and egg size projected at the onset of vitellogenesis (Sinervo & Licht 1991). Because both fecundity and offspring survival are major components of fitness (Roff 1992; Stearns 1992), our results show that fragmentation can deterministically hamper population viability.

The reproductive success of lizards, although clearly impaired by forest fragmentation, will be difficult to understand because of a complex variation in habitat suitability between breeding seasons. The reproductive output of females from deciduous woods was relatively constant between years and (at least in large forest tracts) higher than that of females from evergreen woods (Figs. 1 & 2). Perhaps the way in which phenology and structure of each wood type favor (or hinder) lizard activity depends on changes in weather conditions between years, particularly at the start of the breeding season (when most vegetation sprouting takes place), making the amount of energy locally available for maintenance, growth, and reproduction unpredictable (Olsson & Shine 1997). Environmental stochasticity of this kind is likely to be common, which means controlling for the effects of putative differences in habitat quality and conducting studies

Table 3. Traits of laboratory-reared juvenile *P. algirus* released in 2001 that were or were not recaptured the next activity season (n= 28 and 150, respectively), and results of the corresponding logistic regressions.

	Survivors	*Not recaptured*	*Wald statistic*	p
Egg mass[a] (g)	0.42 ± 0.01	0.39 ± 0.01	2.97	0.085
Hatchling mass (g)	0.57 ± 0.02	0.52 ± 0.01	5.02	0.025
Age-corrected SVL[b] (mm)	1.35 ± 0.56	−0.25 ± 0.23	6.90	0.009

[a] *For egg mass,* n = *27 and 148 because three isolated eggs were encountered and weighed 4–5 days after laying, when they had already absorbed much water from the wet sand.*
[b] *Residuals of the regression of snout-vent length (SVL) on age measured immediately before release.*

in different years will be important to understanding the long-term fitness consequences of habitat fragmentation.

The body condition of females from fragments was not worse than that of females from forests, but their reproductive output was reduced, perhaps because there was less energy available for egg production in fragments than in forests. Food abundance for ground-foraging insectivores could be reduced in small forest remnants (Burke & Nol 1998; Zanette et al. 2000; Luck 2003). Lizards, with their limited dispersal capacities, could be obliged to cope with food shortages by investing less energy in reproduction. On the other hand, predation risk could also be higher in small fragments, for example, because of the increased incidence of generalist predators from the surrounding open fields (Wilcove 1985; Andrén 1992; Tellería et al. 2001). Lizards can respond to increased predation risk by reducing activity, at the expense of an impaired resource acquisition (Martín & López 1999; Downes 2001; Pérez-Tris et al. 2004). An experiment carried out with the same females we used in this study showed that lizards exposed to high predation risk decrease activity, feed at lower rates, and consequently lose body mass (Pérez-Tris et al. 2004). Should predation risk be higher in small fragments, females would probably access fewer resources at the cost of an impaired breeding success.

Fragmentation might also hamper reproduction through processes associated with small population size. Isolation of fragments can prevent gene flow among populations (Clark et al. 1999; Hutchison & Templeton 1999; Templeton et al. 2001), decreasing genetic diversity and causing inbreeding depression at small population sizes (e.g., Madsen et al. 1996, 1999). Marked individuals in our study area seldom moved among fragments separated by just 30–100 m, but we cannot evaluate the plausibility of these hypotheses without analyzing population genetic structure and diversity.

Whatever its proximate causes, the negative effect of fragmentation on the reproductive output of lizards, added to possible genetic erosion and unpredictable hazards, can lead to much local extinction without compensatory recolonization (Templeton et al. 2001). We have other data (authors, unpublished) showing that fragment size predicts the presence of lizards in our study area better than habitat type or structure, and results from an earlier study show that the species is absent from fragments of < 90 ha in more isolated holm oak remnants located nearby (Díaz et al. 2000). These conservation problems, common to fragmented populations of many species of terrestrial ectotherms, would be better understood by considering the role of deterministically impaired reproduction when modeling the demographic consequences of habitat fragmentation (Hokit & Branch 2003*a*).

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