

Variability of breeding resource partitioning in a lacertid lizard at field scale

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Abstract

Human activities cause increasingly deep alterations to natural environments. Yet, the effects on vertebrates with low dispersal capacity are still poorly investigated, especially at field scale. Life history variation represents one means by which species can adapt to a changing environment. Among vertebrates, lizards exhibit a high degree of variation in life-history traits, often associated with environmental variability. We examined the female breeding output of *Podarcis siculus* (Lacertidae) inside agricultural habitats, to test whether different cultivation and management influence the life-history traits of this species. Interestingly, we recorded variability of female breeding output at a very fine scale, namely among adjacent vineyards and olive orchards under different management levels. Lizards displayed the lowest breeding effort in the almost unmanaged sites, while clutch mass, relative fecundity and mean egg mass slightly increased in more intensively managed sites. However, in the most intensive cultivations we detected a life-history trade-off, where eggs from larger clutches tended to be relatively smaller than eggs from smaller clutches. This pattern suggests that agriculture can influence lizard reproductive output, partly favouring it in the presence of medium intensity cultivation but causing, in the most intensively managed sites, some environmental constraints that require a peculiar partitioning of the breeding resources. Even though further studies are needed to clarify the mechanisms driving the observed pattern, our results can be considered a starting point for evaluating the analysis of lizard breeding features as a tool to assess the impact of human activities, at least in agricultural environments.

Keywords

Agriculture; clutch size; egg size; life-history traits; lizard; *Podarcis siculus*; reproductive investment; trade-off

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Introduction

Human activities have always altered landscapes all over the world, with varying intensity through time and diverse consequences on a multitude of organisms. In the last century, land use changes represented the main direct driver of biodiversity loss and of change in terrestrial systems at both regional and global scale (Pereira et al., 2012). Hence, understanding how species respond to the new habitat matrixes in human-modified landscapes is an area of prime interest to evolutionary ecologists and conservation biologists. Animals with specific habitat requirements, but greater dispersal ability, may migrate to the remaining patches of natural and semi-natural habitats in an effort to cope with habitat changes. However, species with lower mobility must respond directly to the new environmental conditions, through selection and possible adaptation.

Because of their limited dispersal abilities, lizards are highly sensitive to environmental alterations even at local scale (Martin & Lopez, 2002). Despite this, their relatively low energetic requirements may enable them to survive and even reach high population densities under non-optimal conditions (Pough, 1980). This sometimes allows for the persistence of isolated populations in small fragments, or in environments with low resource availability (Regal, 1983), such as highly human disturbed habitats (i.e. intensive agricultural landscapes, urban areas). Moreover, squamates and lizards, in particular, exhibit a high degree of variation in life-history traits that is often associated with environmental variability (DeMarco, 1989; Ferguson et al., 1990; Schwarzkopf, 1992; Adolph & Porter, 1993; Olsson & Shine, 1997). For instance, clutch size and offspring size are known to vary in relation to temporal and spatial variation in food availability, thermal regimes and even predation pressure (Ballinger, 1983; Dunham et al., 1988; James & Whitford, 1994; Madsen & Shine, 1999; Angiletta, 2001; Bonnet et al., 2001; Du, 2006). For these reasons, the study of lizard reproductive output could turn out to be a useful tool to highlight and measure environmental alterations. However, few are the studies which have tested (and ascertained) the influence of human induced environmental changes, such as the ones provoked by habitat fragmentation and urbanization (Díaz et al., 2005; Lucas & French, 2012). Habitat alterations can influence lizard breeding features in complex ways, sometimes directly impairing the reproductive output (Díaz et al., 2005), sometimes apparently augmenting it, but just as a response to decreased survival in altered environments (Lucas & French, 2012), sometimes favouring a particular life stage but with unknown consequences on the following stages (Schlaepfer, 2003).

Nowadays, agriculture is among the main causes of landscape alteration, with dramatic consequences on a multitude of species.

In this study, we wanted to test whether the presence of different crops and managements can influence lizard life-history traits. In particular, we analyzed mean egg mass and clutch size from free-ranging gravid females of *Podarcis siculus* living in agricultural habitats subjected to different cultivations (olive orchards and vineyards) and management regimes (traditional and intensive). Previous studies

have shown that these anthropogenic pressures can influence *P. siculus* distribution and abundance, as well as diverse ecological aspects such as predation pressure, escape tactics, and parasite load (Biaggini et al., 2009; Biaggini & Corti, 2015). In addition, distinct crops and agricultural activities can deeply shape key habitat features and the availability of resources (i.e. prey, sites for egg laying and thermoregulating) potentially able to influence lizard reproductive variables. Given these considerations, we expected: i) to find differences in lizard female reproductive investment across different agricultural habitats; ii) that such differences could be recorded at field scale, comparing adjacent fields, thus stressing how deeply agricultural management can influence the life history traits of vertebrates with low dispersal ability; iii) that lizard reproductive features would be negatively affected by increasing management intensity, with females from the most exploited habitats displaying an impaired reproductive output as compared to females from less managed habitats.

Materials and methods

Study species and sites

Podarcis siculus (Rafinesque-Schmaltz, 1810) is a medium sized lacertid lizard mainly distributed in Italy, in most of the surrounding islands, and along the eastern coast of the Adriatic Sea (Corti, 2006). The study was performed in Central Italy, where *P. siculus* usually occurs at low altitude open habitats, which mostly include human disturbed areas in the study region. We surveyed an agricultural area (43°56'12"N, 10°59'59"E; 150 ha) including three vineyards (Vine, *Vitis vinifera*), two of which were intensively managed (Int-Vine) and one traditionally managed (Trad-Vine), and three olive orchards (Olive, *Olea europaea*), two of which were intensively managed (Int-Olive) and one traditionally managed (Trad-Olive). In general, olive orchards require less managing than vineyards, which are characterised by almost continuous farming activities (table 1). For both cultivations, the intensive management implies the use of chemicals and the predominance of mechanical practices, while the traditional management implies the scarce use of machinery, no chemicals and the maintenance of soil cover (table 1).

We collected 61 gravid females in two consecutive breeding seasons (2007, 2008), both by noosing and by hand; female reproductive state was determined by abdomen palpation. We avoided sampling on the edges of the study sites, starting collection from at least 6 m from the boundaries in vineyards, going much further inside in olive orchards where lizards were more uniformly distributed. Little information is available about *P. siculus*' daily movements: it is a territorial species (e.g. Henle & Klaver, 1986), with maximum home ranges of females ranging from 80 to 150 m² (Foà et al., 1990; Avery, 1993). This implies that most of their common activities are probably concentrated, at most, in a 7 m radius around the home range cores. Moreover, in lizards, gravid females tend to limit their movements due to impaired locomotor and escape capacities (e.g., Miles et al., 2000; Iraeta et al.,

Table 1.

Main management practices and main features of soil vegetation cover in the surveyed olive orchards and vineyards. Abbreviations: Int, intensively managed; Trad, traditionally managed.

Site	Main management practices	Soil cover
Trad-Olive	Mowing once a year, no ploughing, mechanical pruning less than once a year, harvest by hand.	Thick vegetation made up of bramble bushes and high weeds (15-60 cm high).
Int-Olive	Repeated ploughing across the year, pruning once a year, mechanical harvest.	Few sparse spots of herbaceous vegetation, mainly at the basis of the olive trees.
Trad-Vine	Repeated mowing in spring, no ploughing, pruning in spring by hand, harvest by hand.	Herbaceous vegetation among the rows (from few to 10 cm high).
Int-Vine	Repeated ploughing across the year, mechanical (and by hand) pruning in spring, mechanical harvest.	Absence of vegetation cover.

2008). These considerations gave us good reasons to assume that the collection site of females corresponded to their actual habitats.

Husbandry

Females were individually housed in terraria (60 × 30 × 30 cm) with white opaque walls, covered with a plastic net that prevented escape and let daylight enter. Terraria were exposed to natural light, ventilation and temperatures; roof tiles provided shade and shelter. Lizards were fed daily with mealworm (*Tenebrio molitor*) larvae and water was provided *ad libitum*. Terraria were checked twice a day for eggs. Upon egg deposition all eggs were weighed to the nearest 0.001 g using a digital balance, and total clutch mass was calculated. Mean egg mass was determined for each female, and the number of eggs per clutch was also recorded. In lizards, these reproductive features reflect the maternal environmental conditions and, as such, they can be used as measures of the reproductive output of females in their habitats even if the very last pre-laying phase occurs under controlled conditions (Sinervo & Licht, 1991; Sinervo, 1994; Díaz et al., 2005; Du et al., 2005a). After egg laying, each female was released at the site of capture. In the analyses we considered only females that laid eggs at most one week after their capture. The snout-vent length (SVL) of females was also recorded.

Statistical analysis

To explore the relationships among the main reproductive variables, we performed a stepwise regression (both backward and forward) in order to determine whether mean egg mass depended on clutch size and maternal SVL; the Akaike Informa-

tion Criterion (AIC) was used in model selection. A linear regression was also performed between clutch size and maternal SVL, and the residuals from this regression were used as a measure of relative fecundity (Díaz et al., 2005; Uller & Olsson, 2005). Then, a linear regression between residual clutch size and mean egg mass was performed to test for possible trade-offs in these life history traits.

Subsequently we focussed on the comparison among crops and managements. To see if maternal size could represent a possible confounding effect in the analyses of reproductive output, we performed a Mixed Model to determine whether SVL differed between cultivations and management practices (fixed factors); the sampling year was included in the model as random factor. We then used Mixed Models to determine the effects of cultivation type and management practice (fixed factors) on total clutch mass, mean egg mass, and relative fecundity, respectively; we included the sampling year as random factor. Total clutch mass was adjusted for SVL, while mean egg mass was adjusted for relative fecundity and vice versa. Female SVL, mean egg mass, and total clutch mass were log-transformed to conform to assumptions of normality.

Results

In table 2 the mean values of the main life history parameters are shown. The mean clutch size falls in the range 2-5, indicated as typical for *Podarcis siculus* (Corti & Lo Cascio, 2002); 7-8 eggs were laid by almost 10% of females, contradicting Henle (1988) that considered this clutch size exceptional.

The stepwise procedure selected clutch size as mean egg mass predictor (AIC = -427.1 vs AIC = -425.1 with maternal SVL included) and the two variables were negatively correlated ($N = 61$, $r = -0.378$, $P = 0.003$). Clutch size, in turn, was positively correlated with maternal SVL ($N = 61$, $r = 0.762$, $P < 0.001$). In addition, relative fecundity was negatively correlated with mean egg mass ($N = 61$, $r = -0.304$, $P = 0.017$). This revealed the presence of a life-history trade-off between egg number and egg size, where eggs from larger clutches tended to be smaller than eggs from smaller clutches (fig. 1). However, the same analysis per-

Table 2.

Sample size, mean values (\pm standard deviations) of maternal SVL, clutch size and egg mass considering the entire sample and the different habitat categories in olive orchards and vineyards. Abbreviations: Int, intensively managed; Trad, traditionally managed.

	<i>N</i> of females	Maternal SVL (mm)	<i>N</i> of eggs	Clutch size	Egg mass (g)
Total	61	61.65 \pm 4.38	258	4.23 \pm 1.53	0.2670 \pm 0.0946
Trad-Olive	12	59.17 \pm 1.73	34	3.09 \pm 1.22	0.2848 \pm 0.1102
Int-Olive	18	61.98 \pm 4.05	74	4.35 \pm 1.32	0.2564 \pm 0.1004
Trad-Vine	9	60.81 \pm 2.2	37	4.11 \pm 1.60	0.2756 \pm 0.0907
Int-Vine	22	62.88 \pm 5.52	113	4.71 \pm 1.60	0.2504 \pm 0.0876

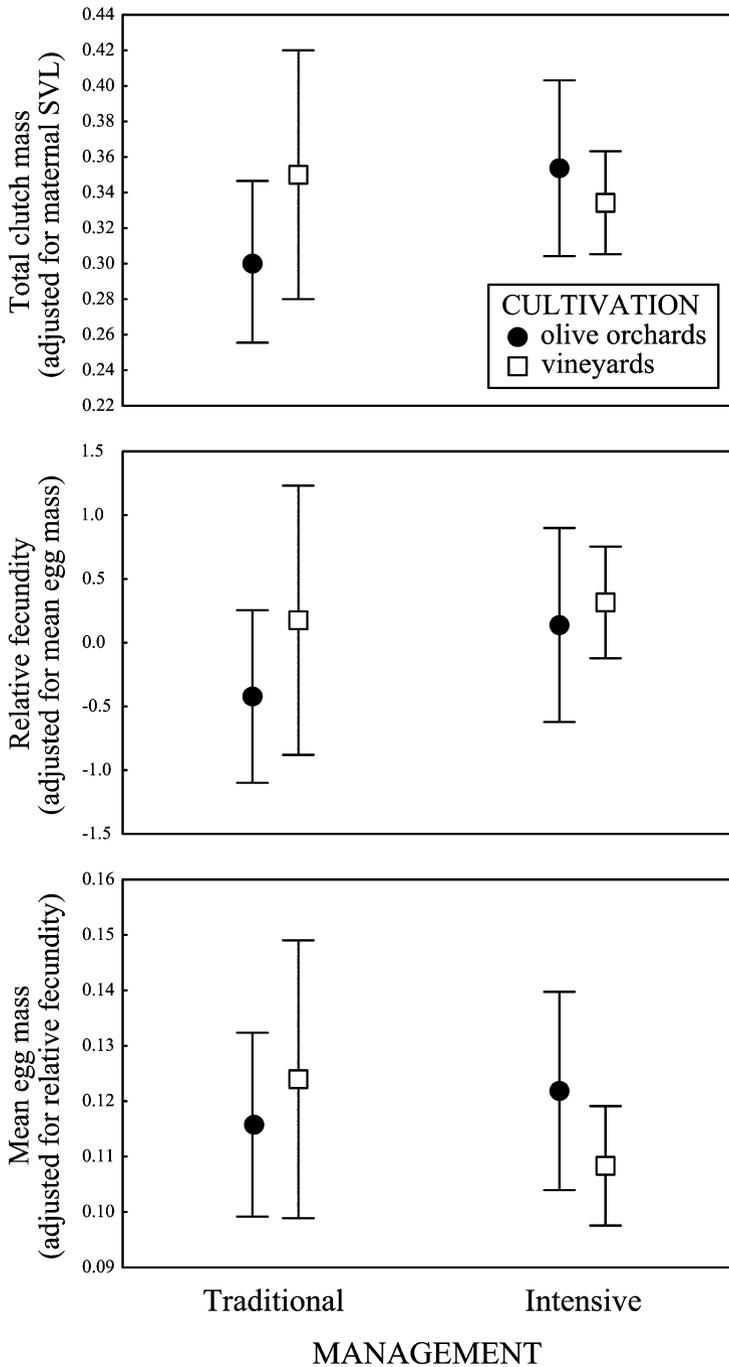


Figure 1. Total clutch mass, relative fecundity and mean egg mass in relation to cultivations (olive orchards and vineyards, black dots and white squares, respectively) and management (traditional and intensive, on the left and on the right, respectively; see table 2 for sample sizes).

Table 3.

Mixed Models results showing the effects of cultivation and management on total clutch mass, relative fecundity and mean egg mass, respectively ($N = 61$; cultivation: $N_{\text{Olive}} = 28$, $N_{\text{Vine}} = 33$; management: $N_{\text{Trad}} = 20$, $N_{\text{Int}} = 41$; year: $N_1 = 48$, $N_2 = 13$).

Fixed effects	Value	Std. error	df	<i>t</i>	<i>P</i>
Response variable: Maternal SVL					
Intercept	1.778	0.014	56	128.107	0.000
Management	0.016	0.011	56	1.537	0.130
Cultivation	0.005	0.012	56	0.448	0.656
Manag*Cultiv	0.000	0.015	56	0.010	0.992
Random effect (year): Std. Dev. Intercept = 0.016; Std. Dev. Residuals = 0.027					
Response variable: Total clutch mass					
Intercept	-0.167	0.634	56	-0.264	0.793
Management	0.755	0.341	56	2.217	0.031
Cultivation	0.757	0.395	56	1.916	0.060
Manag × Cultiv	-1.095	0.489	56	-2.238	0.029
Random effect (year): Std. Dev. Intercept = 0.811; Std. Dev. Residuals = 0.874					
Response variable: Relative fecundity					
Intercept	-0.621	0.293	56	-2.125	0.038
Management	0.685	0.375	56	1.825	0.073
Cultivation	0.779	0.436	56	1.785	0.080
Manag × Cultiv	-0.661	0.534	56	-1.239	0.220
Random effect (year): Std. Dev. Intercept = 0.000; Std. Dev. Residuals = 0.970					
Response variable: Mean egg mass					
Intercept	0.377	0.852	56	0.443	0.660
Management	0.333	0.929	56	1.138	0.260
Cultivation	0.390	0.339	56	1.151	0.255
Manag × Cultiv	-0.881	0.420	56	-2.099	0.040
Random effect (year): Std. Dev. Intercept = 1.159; Std. Dev. Residuals = 0.750					

formed for the two kinds of management separately, confirmed the existence of the trade-off only in intensively managed sites (Int: $N = 41$, $r = -0.335$, $P = 0.032$; Trad: $N = 20$, $r = -0.252$, $P = 0.283$). In contrast, we did not find significant results by performing the same analysis for the two cultivations separately (Olive: $N = 28$, $r = -0.321$, $P = 0.096$; Vine: $N = 33$, $r = -0.269$, $P = 0.130$).

We found no significant differences in maternal SVL between cultivations or between managements (table 3), so maternal size did not represent a possible confounding effect in the reproductive output analyses. The Mixed Model exploring the variation pattern of total clutch mass (adjusted for SVL) showed no significant differences among cultivation types, but it revealed that lizards laid significantly heavier clutches in intensive crops than in traditionally managed ones, and that there was a significant interaction between the two effects, cultivation and management (table 3, fig. 1). The relative fecundity (adjusted for mean egg mass) did not

change in relation to cultivations and managements (table 3, fig. 1). On the contrary, analyzing the mean egg mass (adjusted for relative fecundity) revealed a significant interaction between cultivation and management: in olive orchards lizards laid heavier eggs in intensive managed sites when compared to traditionally managed ones, while in vineyards the opposite pattern occurred (table 3, fig. 1).

Discussion

Human alteration of natural environments has been extensive, yet the effects on vertebrates with lower dispersal capacity, like reptiles, are largely unexplored. Life history variation represents one means by which species can adapt to a changing environment (Caughley, 1994; Caughley & Sinclair, 1994; Roff, 2002). Interestingly, we recorded variability of *Podarcis siculus* breeding output at a very fine scale, namely among females from adjacent sites with differing cultivations and managements. In intensively managed areas we also detected a life-history trade-off, where eggs from larger clutches tended to be relatively smaller than eggs from smaller clutches. This suggests that such habitats might have some environmental constraints that require a different partitioning of lizard breeding effort.

In particular, we observed that in the almost unmanaged site, the traditionally managed olive orchard, lizards displayed a relatively low breeding effort, with fewer and rather small eggs in comparison to the other sites (fig. 1). Clutch mass, relative fecundity and mean egg mass slightly increased in the intensively managed olive orchards and in the traditional vineyard (fig. 1), thus suggesting that agricultural managing might partly favour *P. siculus* breeding output inside agricultural lands. Indeed, the creation of open habitats, which often follows agricultural managing, can be favourable for thermophilous vertebrates. However, in the most intensively managed sites, the intensive vineyards, lizards exhibited a peculiar pattern in the allocation of the reproductive effort. In these habitats females laid a high total clutch mass, comparable to that recorded in intensive olive orchards and traditional vineyards but, interestingly, the high number of eggs (in relation to maternal size) was combined with the minimum recorded mean egg mass (in relation to relative fecundity; fig. 1). This indicates that in intensively managed vineyards, differently from the other crops, the production of many eggs had to be counterbalanced by a reduction in their size.

The identification of the proximate causes of a trade-off between offspring size and number in *Podarcis siculus* was not among the aims of this study and future investigations are needed to clarify them. In other vertebrates, there exists a complex relationship between the proximate and the ultimate forces responsible for changes in life-history traits, with such traits typically being influenced by a number of environmental variables (Ballinger, 1983; Berven & Gill, 1983).

In lizards, two main proximate factors are usually implicated in such life-history shifts: space limitation of maternal body size (Vitt & Congdon, 1978; Congdon & Gibbons, 1987; Shine, 1988, 1992; Du et al., 2005a) and resource availability

(DeMarco, 1989; Schwarzkopf, 1992; James & Whitford, 1994; Olsson & Shine, 1997; Bonnet et al., 2001; Jordan & Snell, 2002; Olsson et al., 2002; Uller & Olsson, 2005; Oufiero et al., 2007). In our study, female lizards did not significantly differ in SVL among sampling sites, suggesting that maternal body size constraints may be less likely in this system. As an alternative, we can hypothesize that the observed life-history differences may be linked to environmental variability. Focusing on intensively managed vineyards, the use of chemicals and machineries can affect the availability and quality of food resources, altering the arthropod communities on both soil and grapevines (James et al., 2002; Thorbek & Bilde, 2004; Prischmann et al., 2005).

The complete absence of grass soil cover could affect factors such as soil temperature and moisture and, consequently, the quality of nesting sites, which are known to influence the life-history traits of many lizard species (Packard & Packard, 1988; Van Damme et al., 1992; Shine et al., 1997; Braña & Ji, 2000, 2007; Du et al., 2005b). Soil temperatures can also influence hatchling survival, as it happens in the congeneric *P. muralis*, for which higher incubation temperatures provoke negative effects on hatchling size, growth rates, and sprint speeds (independently from the size; Van Damme et al., 1992). Moreover, ploughing can cause a reduction of lizard refuges (Benson, 1999), impairing their possibility of escaping predators. Indeed, ecological aspects, such as predation and environmental stress, can influence lizard reproductive traits too (Lucas & French, 2012). From this perspective, the production of a high number of eggs in the intensive vineyards, even if at the expense of body size, might represent a strategy to balance enhanced mortality rates (if mortality is size-independent), as it happens in other species (Sinervo et al., 2000). Previous investigations indicated that, in the same study area, juvenile lizards experienced a higher predation pressure in vineyards than in olive orchards (Biaggini et al., 2009). However, whether hatchlings did actually face a decreased survival in intensively managed vineyards is not yet known and future investigations are required to clarify the extent to which the abovementioned mechanisms drive *P. siculus* breeding output in the surveyed localities.

The detection of variability in lizard breeding output among adjacent sites that are under different managements, suggests that agriculture can influence lizard reproductive output. Interestingly, if the recorded pattern is a response to an increased mortality in intensively managed vineyards, this could indicate a threshold of ecological and environmental factors beyond which the advantages of landscape transformation due to agricultural managing start decreasing for *P. siculus*. Taking into account the high capacities of this species to occupy habitats and sites poor in resources, where other vertebrates often fail to settle, the arising of a trade-off in this species could indicate a threshold for management practice sustainability. In this perspective, similar studies could have useful implications for conservation strategies in agro-ecosystems. Hence, these results could represent a starting point to deepen the use of lizard reproductive features as a tool to assess the impact of human activities, at least in agricultural environments.

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