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# Contrasting size-dependent life history strategies of an insular lizard

Andreu ROTGER\*, José Manuel IGUAL, and Giacomo TAVECCHIA

Animal Demography and Ecology Unit, GEDA, IMEDEA (CSIC-UIB), c. M. Marques 21, 01790, Esporles, Spain

\*Address correspondence to Andreu Rotger. E-mail: andreurotger@gmail.com.

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## Abstract

In many species with continuous growth, body size is an important driver of life-history tactics and its relative importance is thought to reflect the spatio-temporal variability of selective pressures. We developed a deterministic size-dependent integral projection model for 3 insular neighboring lizard populations with contrasting adult body sizes to investigate how size-related selective pressures can influence lizard life-history tactics. For each population, we broke down differences in population growth rates into contributions from size-dependent body growth, survival, and fecundity. A life table response experiment (LTRE) was used to compare the population dynamics of the 3 populations and quantify the contributions of intrinsic demographic coefficients of each population to the population growth rate ( $\lambda$ ). Perturbation analyses revealed that the largest adults contributed the most to the population growth rate, but this was not true in the population with the smallest adults and size-independent fertility. Although we were not able to identify a single factor responsible for this difference, the combination of the demographic model on a continuous trait coupled with an LTRE analysis revealed how individuals from sister populations of the same species follow different life strategies and showed different compensatory mechanisms among survival, individual body growth, and fertility. Our results indicate that body size can play a contrasting role even in closely-related and closely-spaced populations.

**Key words:** body size, capture–recapture, integral projection model, Lilford's lizard, size-dependent mortality

Individual body size is an important determinant of life-history tactics in many taxa (Peters 1986). Owing to its pivotal role in multiple evolutionary tradeoffs, the dynamics of body size within and between populations can only be studied considering the whole life cycle of an organism (Roff 1992; Stearns 1992; Charnov 1993). Reptiles are good biological models to track the importance of body size in animal demography because, although it abates throughout an individual's lifespan, body growth is continuous (Schoener and Schoener 1978; Smith et al. 2010). In many reptile species, large individuals show social dominance over smaller ones generating asymmetric trophic and social interactions (Massot et al. 1992; Lecomte et al. 1994; Mugabo et al. 2010). However, realized body size at an early age or stage is mainly determined by environmental conditions and may thus constrain optimal decisions and individual

fitness (Rotger et al. 2016). For example, small breeding females may produce small eggs and have lower breeding or hatching success (Laurie and Brown 1990). Large sizes could also be constrained, for instance, with larger individuals more easily detected by predators than smaller ones (Stamps and Buechner 1985; Blanckenhorn 2000). Given this variability and the multiple factors involved, it is plausible to assume that body size plays a major role in individual strategy and is expected to reflect population-specific selective pressures.

Integral projection models (IPMs; Easterling et al. 2000) allow the characterization of the life cycle of an organism as a function of a continuous trait (Easterling et al. 2000; Ellner and Rees 2006; Rees and Ellner 2009; Coulson et al. 2010; Coulson 2012), providing an analytical framework to address hypotheses on eco-evolutionary dynamics (Rees and Ellner 2009; Chung et al. 2015) or

population management (Wallace et al. 2013). Besides the technical advantage, it has been shown that IPMs offer a more realistic model to investigate the role of body size in species with indeterminate growth (Bassar et al. 2013; Wallace et al. 2013). We use this approach to investigate the role of body size in shaping life-history tactics in 3 isolated populations of Balearic wall lizards *Podarcis lilfordi* (Günther 1874).

The Balearic wall lizard or Lilford's lizard is an endemic species of the Balearic archipelago (Spain). The species disappeared from the main islands of Mallorca and Menorca and is now confined to offshore islets and to the island of Cabrera (Alcover et al. 1999). Terrasa et al. (2009) described 4 main genetic clades based on mitochondrial DNA in agreement with the geographic distribution of the species. Males of the Lilford's lizard are ~10% larger than females, but body size and sexual size dimorphism can vary across populations (Salvador 1980, 1986). Newborn lizards measure ~30 mm long and laboratory data suggest that females begin to breed between the first and second year, at a snout-vent length (SVL) of ~50 mm (Castilla and Bauwens 2000).

We focused our investigation on 3 geographically close populations belonging to the same genetic clade but showing a marked difference in the adult average SVL (Pérez-Mellado et al. 2008). In each population, we described the size-dependent variation in 4 different vital rates: the survival probability, the individual body growth rate, the number of eggs produced by females (recruitment), and the measure of inheritance (Coulson et al. 2010). Because size variation can affect life-history traits and population dynamics (Clutton-Brock et al. 1987; Rose et al. 1998), we expect to find differences in the life cycle and the realized population growth rate across populations. If a small body size is maintained by phenotypic selection, we expect to find a cost to being large on the island with the smallest average SVL (Blanckenhorn 2000). This phenotypic disadvantage may be expressed by a negative relationship between SVL and body growth, survival, and/or fecundity.

## Materials and Methods

### Study area and individual-based data

We focused on 3 neighboring islets inhabited by lizard populations belonging to the same genetic clade (Terrasa et al. 2009) and sharing the same climate (average distance of 2.2 km; Figure 1), namely Na Moltona (5.09 ha, "MO" hereafter), Na Guardis (1.98 ha, "NG" hereafter), and Es Curt (0.29 ha, "ES" hereafter). The 3 islets are predator-free, although occasional bird predation has been documented (Cooper et al. 2009). The islets host *P. lilfordi* as the unique lizard species. The smallest islet, ES, is space-limited with a poor, simplistic plant community, and food availability is stochastic and largely dependent on external inputs from the sea (see also Polis and Hurd 1996). In contrast, the largest islet, MO, has a complex plant community and constant food availability; mice *Mus musculus* and geckos *Tarentula mauritanica* are present as possible competitors but their population density is not comparable with that attained by lizards (Tenan et al. 2013). NG presents the same plant community as MO with comparable plant species that provide constant food as well (Santamaría et al. 2019). None of the islets are currently inhabited by humans, but the medium-sized islet (NG) is the closest to an urban area and harbor and seems to have experienced continuous anthropogenic disturbance because a small human settlement was established during the Punic era (4th century BC) that lasted ~300–400 years (Guerrero 2000). This includes the occasional presence of rats *Rattus rattus*, recorded only once during the 6 years of the

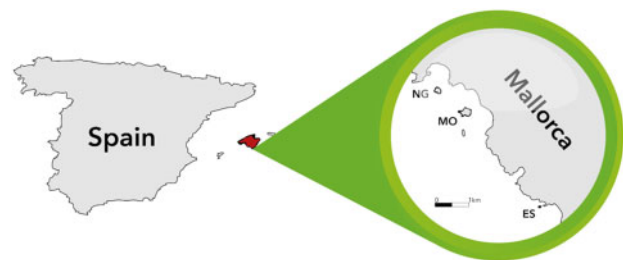
study. Data on individual size were collected at MO from 2009 to 2015 whereas, at NG and ES, data collection began in 2010. In each islet, lizards were captured in pitfall traps during 3-day capture–recapture sessions in October and April (Ruiz de Infante et al. 2013). Each captured lizard was sexed, weighed, and measured SVL to the nearest millimeter and photographed using a digital camera for individual identification (Sacchi et al. 2010; Moya et al. 2015). Individuals were released near the trap of capture to maintain the spatial structure of the population. We assessed the effect of body size on survival, growth rate, and recruitment using a likelihood ratio test (LRT; Lebreton et al. 1992). In logistic regression, the LRT the difference in model deviance follows a  $\chi^2$ -statistic whereas it follows an  $F$ -statistic in Poisson regressions and with normally distributed errors. All analyses described below were conducted in the program R (R Core Team 2017).

### Size-dependent survival and growth rate

Size-dependent annual survival,  $S_r$ , of females was estimated from October to October using capture-mark-recapture models (Williams et al. 2002). In these models, however, time-dependent individual covariates, such as weight or body size, cannot be easily accommodated because covariate values are unknown when individuals are not caught (see Bonner and Schwarz 2009). As in Fernández-Chacón et al. (2015), we considered size-classes and accommodated body growth as transitions between classes using a multisite capture–mark–recapture framework (Schwarz et al. 1993). In this case, missing values would not affect the estimate of survival according to size classes. We stratified observations in 5 state classes identified by combining age at maturity with the length-by-age growth curve estimate for each population using all data available (see Supplementary data). The 5 state classes considered were individuals born in the previous spring ("newborn," hereafter), "juvenile" ~1-year old but under the size of sexual maturation, individuals in their first reproductive season ("subadult," hereafter), adults between the size of first reproduction and the maximum asymptotic size estimated by the growth curve ("adult"), and females that have reached or exceeded the maximum asymptotic size ("senior"). Each population reached the 5 state classes at different body sizes (see results in Supplementary data). The probability to move from a size-class  $r$  to a class  $s$ ,  $\Psi^{rs}$ , relates to the speed of growth. Finally, to obtain a linear function between survival probability and body size, we considered the observed average body size in size-class  $j$ ,  $B_j$ , with  $j = 1, 2, \dots, 5$ , and constrained the 5 size-class survivals as:

$$\text{Logit}(S^r) = a + bB_j$$

where  $S^r$  is the survival of females in size class  $r$ ,  $a$  and  $b$  are the linear predictors of the size-dependent survival (see a similar approach in Fernández-Chacón et al. 2015). Models were built in the program



**Figure 1.** Location of the 3 insular populations. NG, Na Guardis population; MO, Na Moltona population; ES, Curt population.

MARK (White and Burnham 1999) and the goodness-of-fit test was assessed with the program U\_CARE (Choquet et al. 2009).

Annual observed growth rate was estimated for each islet using data from consecutive recaptures only. That is, October  $i$  to October  $i + 1$ . The change in size at islet  $j$  between year  $t$  and  $t + 1$  was modeled as:

$$E(y)_{j,t+1} = a_{j,t} + b_{j,t}x_t$$

where  $y$  is the SVL measure of a given individual at islet  $j$  at time  $t + 1$  and  $x$  is the same measure the year before. This analysis was carried out using a generalized linear mixed model with “year” as a fixed explanatory factor and considering the individual identity as a random term to avoid pseudo-replications. Finally, we estimated the conditional variance ( $\text{var}(y)$ ) of the best model using the squared residuals of the regression on size at time  $t$ .

### Size-dependent recruitment and inheritance function

We used the number of total eggs laid by females as a proxy of recruitment. The number of total eggs produced by  $x$ -sized females was estimated using experimental data. In April 2014 and 2015, 5–8 gravid females from each island were kept in individual terraria until laying. We replicated the same conditions of substrate, food, light conditions, and basking sites for oviposition following Castilla and Bauwens (2000). All females were released in August at the same site of capture. We investigated the relationship between female body size and number of eggs laid using Poisson regressions. The inheritance function, describing the probability that hatchling size correlates with mother’s size, was formulated by a regression between mother and offspring size. For this, we used data from 15 eggs hatched in 2015 after being placed in an egg-incubator with stable temperature (27°C–29°C) and humidity (80–90%) and from the information reported by the experimental study of *P. lilfordi* by Castilla and Bauwens (2000).

### IPM and elasticity analyses

We parameterized a deterministic post-breeding IPM based on the estimated relationship between vital rate and SVL. As above, we note SVL at year  $t$  as “ $x$ ” and SVL at year  $t + 1$  as “ $y$ ” in the formulae. We refer to the size domain of  $x$  as  $\Omega$ :

$$n(y, t + 1) = \int_{\Omega} P(y, x) + F(y, x)n(x, t)dx$$

where the function  $P(y, x)$  represents the size-dependent survival for individuals of size  $x$  as:

$$P(y, x) = s(x)G(y, x)$$

where,  $G(y, x)$  is the probability of growing from size  $x$  to size  $y$  in 1 year. Similarly,  $F(y, x)$  represents the production of  $y$ -sized offspring from  $x$ -sized parents at time  $t$ . The fertility function is represented by:

$$F(y, x) = r(x)p\text{HSD}(y, x)$$

with  $r(x)$  being the recruitment function describing the number of total eggs produced by a  $x$ -sized female and  $D(y, x)$  the inheritance function describing the probability that a reproducing female of size  $x$  at year  $t$  produces a recruit of size  $y$  at year  $t + 1$ . The 2 functions are multiplied by  $p_{\text{HS}}$ , the size-independent probability of hatching in Castilla and Bauwens (2000). In addition, the recruitment function was fixed to 0 in individuals  $<50$  mm because they are not sexually mature. These demographic functions constitute the kernel

of the IPM, which describes all possible transitions between sizes in a single time-step, for example, year (Rees et al. 2014). The  $F$  function is multiplied by 0.5 to account for females only, assuming equal sex ratio. Our final kernel equation is:

$$K(y, x) = s(x)G(y, x) + s(x)r(x)p\text{HSD}(y, x)/2$$

The IPM projection kernel for each population was discretized into a matrix with 300 size classes and analyzed as in matrix population models (Easterling et al. 2000; Ellner and Rees 2006). IPMs were built in the software R version 3.4 (R Core Team 2017). Elasticities were used to measure the proportional change in the population growth rate,  $\lambda$  (de Kroon et al. 1986), caused by proportional changes in  $P(y, x)$  and  $F(y, x)$  (Tuljapurkar 1990). We computed the elasticities of  $\lambda$  in each islet and partitioned them into contributions from survival-growth and fecundity components of the kernel (Ellner and Rees 2006). Note that for the survival and growth functions we only consider time-independent models as the final integral model is time-independent. However, models including a year effect in survival or growth rate were not supported or equally supported than constant models (see also Supplementary Table S2).

### Life table response experiment

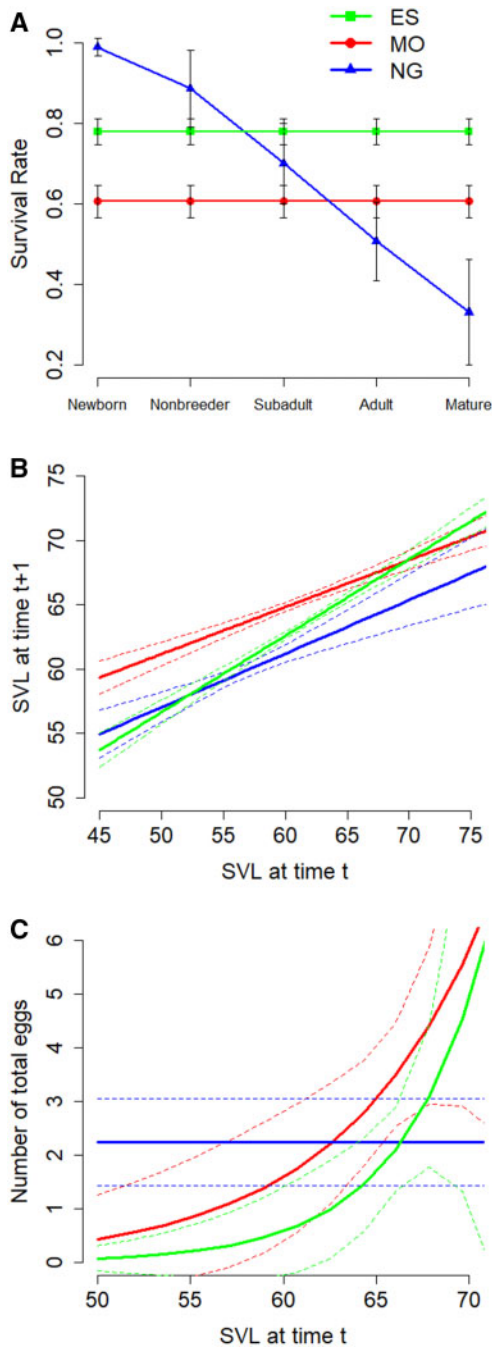
To quantify the contributions of each vital rate to the observed difference in the intrinsic population growth rate,  $\lambda$ , we designed 3 between-population life table response experiments (LTREs; Caswell 2001). The LTRE broke down the total difference in  $\lambda$  into the contributions of survival, growth, and fertility coefficients. The total difference in  $\lambda$  between populations reflected the difference in parameter values multiplied by the parameter sensitivity and summed over all parameters that differed first between MO and NG populations (MO-NG), followed by MO and ES populations (MO-ES) and finally NG and ES populations (NG-ES). We calculated the midpoint sensitivities of intrinsic demography using the mean matrix of the paired populations above-mentioned (MO-NG, MO-ES, and NG-ES) as the reference model (Caswell 2001) including the sum of coefficients. Sensitivities were estimated numerically by applying the sensitivity formula (Ellner and Rees 2006).

## Results

### Size-dependent survival and growth rate

Survival probability was estimated using a total of 767 females (MO = 324, NG = 197, ES = 246). The goodness-of-fit suggested that the general model fit the data adequately in all populations (MO:  $\chi^2 = 17.70$ ,  $df = 36$ ,  $P = 0.99$ ; NG:  $\chi^2 = 7.84$ ,  $df = 14$ ,  $P = 0.90$ ; ES:  $\chi^2 = 26.61$ ,  $df = 39$ ,  $P = 0.86$ ; see Supplementary data for GOF details). Individual SVL influenced survival only in NG ( $\chi^2 = 5.11$ ,  $df = 1$ ,  $P = 0.02$ ) whereas in MO ( $\chi^2 = 2.73$ ,  $df = 1$ ,  $P = 0.10$ ) and ES ( $\chi^2 = 2.69$ ,  $df = 1$ ,  $P = 0.10$ ), a model assuming a size-independent survival was retained (Table 1 and Supplementary Table S2). The relationship between SVL and survival in NG was negative and indicated a pronounced senescence (Table 2 and Figure 2A).

The growth rate function between consecutive Octobers ( $G(y, x)$ ; Table 2 and Figure 2B) was estimated based on data from 304 females (MO = 129, NG = 40, ES = 135). Growth rate was higher in MO compared with the other 2 islets (Table 2). Variation among years was not an important parameter; there seemed to be some effect only in MO but it was not sufficiently significant to be



**Figure 2.** Size-dependent demographic parameters in 3 populations of *P. lilfordi*. MO red lines, NG blue lines, and ES green lines. Dashed lines correspond to confidence intervals. (A) Survival, (B) growth, and (C) number of total eggs per female.

considered in the model ( $F=2.20$ ,  $df=5$ ,  $P=0.07$ ; and [Supplementary Table S2](#)).

#### Size-dependent recruitment and inheritance function

We obtained a total of 105 eggs (MO:  $n=49$ , NG:  $n=27$ , ES:  $n=29$ ) from 38 females captured (MO:  $n=14$ , NG:  $n=12$ , ES:

$n=12$ ). The average number of eggs laid by female in each population was small (see [Table 1](#)). We found a positive relationship between female size and number of total eggs laid in MO ( $F=5.52$ ,  $df=1$ ,  $P=0.02$ ) and ES ( $F=4.62$ ,  $df=1$ ,  $P=0.03$ ; [Table 2](#) and [Figure 2C](#)). In contrast, the number of total eggs in NG ( $F=0.39$ ,  $df=1$ ,  $P=0.53$ ) was independent from female size ([Supplementary Table S2](#)). After the incubation period, only 15 eggs hatched, 13 from MO, and 2 from ES. We did not find a positive association between mother and offspring sizes. It is possible that females trade egg size, and consequently the size at hatching, with egg, and/or clutch numbers and the inheritance function was expressed by the average value ( $29.3 \pm 2.6$  mm;  $n=15$ ) for all 3 populations ([Table 2](#)).

#### Size-dependent population structure and population growth rate

The population size-dependent structure appeared similar in all 3 islets but not identical due to the difference in growth rate ([Figure 3](#)). Size structure in MO was characterized by a high proportion of small (newborns) and large lizards, whereas intermediate sizes were poorly represented compared with the other 2 islets. All populations had a large proportion of new recruits and mature individuals. The reproductive value of NG remained constant until reaching large sizes and decreased afterwards. Populations with large-sized females had similar growth rates ( $\lambda_{MO}=0.97$ ,  $\lambda_{ES}=1.03$ ) whereas in NG, where females were smaller, it was higher ( $\lambda_{NG}=1.15$ ).

#### Elasticity analysis

We calculated the relative contribution of demographic parameters to population growth rate ( $\lambda$ ). The survival-growth component had the largest elasticity value in MO and ES (80% and 87%, respectively) compared with the reproduction component (20% and 13%, respectively). However, in NG the contribution of reproduction accounted for nearly one-third of the population growth (29%). In NG, large (old) individuals had low reproductive value due to the low survival probability and the population seemed to focus the productivity on medium-sized lizards ([Figure 4](#)). In contrast, in MO and ES the contribution of medium-size females to population growth was very small. However, ES showed a small peak around 50 mm, on medium-sized individuals mainly explained by their slightly higher survival rate compared with the other populations ([Figure 4](#)).

#### LTRE

The LTRE analysis showed which vital rates contributed differently to the population growth rate ( $\lambda$ ) in each population. The difference in  $\lambda$  between MO-NG and NG-ES was greater than we observed between MO and ES ([Figure 5](#)). Intrinsic body size growth ( $g(x)$ ) in the MO population was the most important contributor to the total difference in  $\lambda$  between MO and NG and between MO and ES. In contrast, fertility showed an important contribution in NG. However, the vital rate that contributed the most to the difference between NG and MO was survival. The high fertility and slow body growth of individuals in NG compensated for the low survival of large sizes. Note that average annual survival regardless of body size was higher in NG than in MO ([Figure 5](#)). In the 2 populations with the largest individuals (i.e., MO and ES), the fertility contribution was similar and close to zero. In contrast, the contribution of the survival-growth function was high and similar in both populations, but the

**Table 1.** Number of individuals ( $n_i$ ), number of eggs ( $n_e$ ), survival of each class, mean SVL at time  $t$  (SVL1), and  $t + 1$  (SVL2) of females of each population, and number of total eggs with the mean number of eggs laid per female and their mean SVL

Islet	Survival						Growth			Total eggs		
	$n_i$	Newborn	Nonbreeder	Subadult	Adult	Mature	$n_i$	SVL $t$ (mm)	SVL $t + 1$ (mm)	$n_e$	Eggs/female <sup>a</sup>	SVL females
MO	324	–	–	0.61 (0.04)	–	–	129	61.33 (4.57)	65.30 (2.58)	49	3.50 (1.56)	65.28 (2.46)
NG	197	0.99 (0.02)	0.89 (0.10)	0.70 (0.10)	0.51 (0.10)	0.33 (0.14)	40	57.07 (3.65)	59.97 (2.25)	27	2.25 (1.05)	59.25 (3.39)
ES	246	–	–	0.79 (0.03)	–	–	135	61.55 (3.56)	63.51 (2.65)	29	2.42 (1.16)	64.50 (3.63)

Values in parentheses are standard errors.,

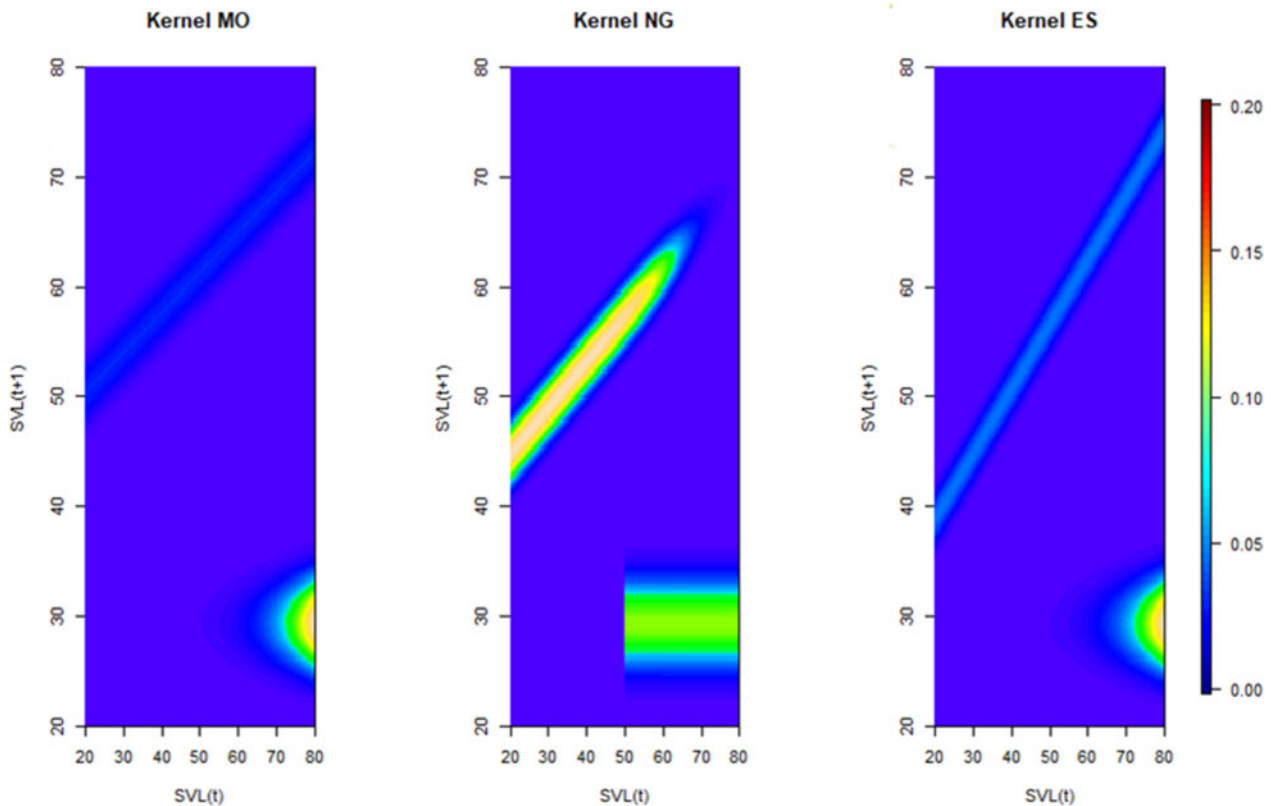
<sup>a</sup>Mean number of total eggs laid by female.

**Table 2.** Statistical models of demographic parameters of *P. lilfordi* in MO, NG, and ES used to construct the IPMs

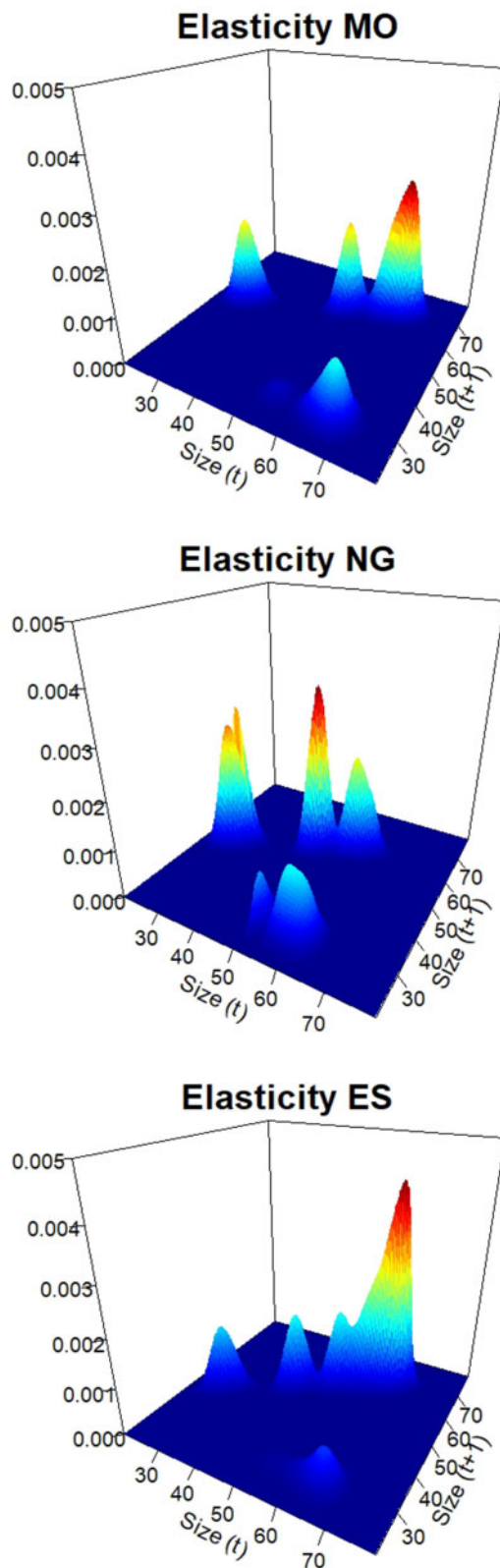
Equation	Model notation	MO	NG	ES
Survival				
$\text{logit}(s) = a + b \cdot \text{SVL}$	S ~ NULL	0.43 (0.16)	–	1.261 (0.18)
	S ~ SVL	–	15.66 (7.45) – 0.26 (0.12) · SVL	–
Growth				
$y = a + b \cdot \text{SVL}$	G ~ NULL	–	–	–
	G ~ SVL	42.89 (2.35) + 0.36 (0.04) · SVL	36.18 (4.19) + 0.42 (0.07) · SVL	26.89 (2.40) + 0.59 (0.04) · SVL
SD		1.97	1.65	1.6
Recruitment				
$\Psi = a + b \cdot \text{SVL}$	R ~ NULL	–	0.81 (0.19)	–
	R ~ SVL	–8.10 (4.05) + 0.14 (0.06) · SVL	–	–8.27 (4.71) + 0.14 (0.07) · SVL
Inheritance				
$y = a + b \cdot \text{SVL}^a$	I ~ NULL	29.33 (2.57)	29.33 (2.57)	29.33 (2.57)
	I ~ SVL	–	–	–

It is shown the parameters values of the models selected on basis AIC values (see Supplementary Table S2).  $a$  and  $b$  values represent model parameters and standard errors are given in brackets. SD is the standard deviation of the residuals of the growth model. Model notation: NULL, no effect; SVL, effect of female body size (SVL),

<sup>a</sup> Same value for all populations.



**Figure 3.** The transition surface of the IPM for the 3 islets. The x- and y-axes represent the SVL of individuals at time  $t$  and time  $t + 1$ , respectively; the diagonal indicates the survival and growth of individuals from hatchlings (on the left) to mature individuals (on the right). The half circle along the bottom of the diagonal indicates the number of hatchlings produced by females of increasing size.



**Figure 4.** Elasticity surfaces for the IPM fitted by each population.

rapid growth in MO seemed to be compensated for by the lower survival compared to ES (Figure 5). The greatest fertility difference was observed between NG and ES.

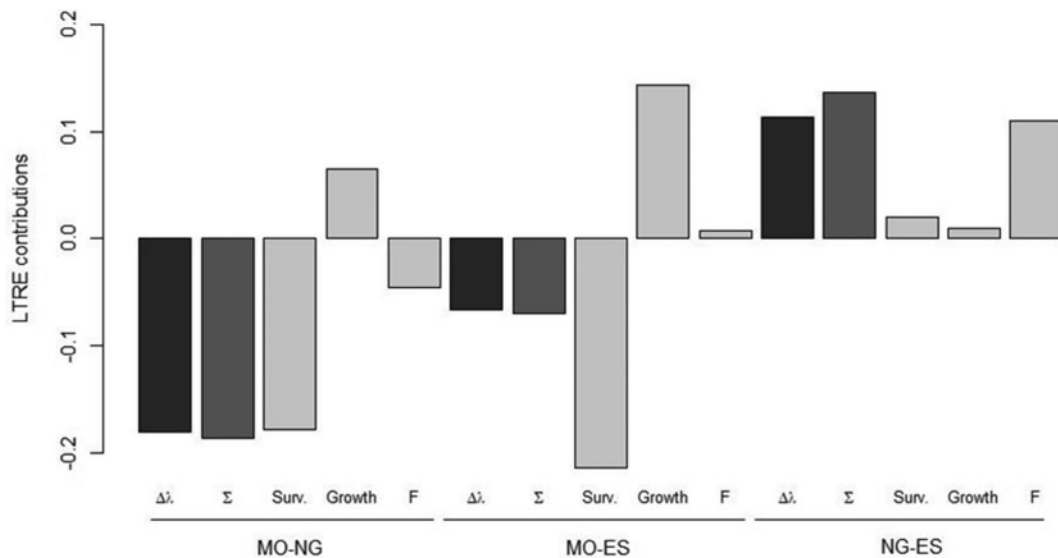
## Discussion

IPMs model population dynamics by considering a population structure based on continuous characters rather than using the classical discretization into stage- or age-classes (Easterling et al. 2000). We used individual-based information collected >6 years and an experimental estimate of female fertility to track the role of body size in the life-history tactics of Lilford's lizard in 3 isolated and neighboring populations. We aimed to quantify how each size-dependent vital rate contributed to the population growth rate of each population. We did so by combining the size-dependent demography (IPM) with a LTRE analysis.

We found that survival probability showed a different pattern according to the islet considered. Survival was size-independent in the islands with the largest females (MO and ES), whereas it was negatively associated with SVL in the islet with the smallest females (NG). On the contrary, the body growth rate was similar in MO and NG but different in ES where animals attained a similar adult size as in MO. The difference in growth in ES was probably due to a difference in resource availability in agreement with what found in other reptiles (Andrews 1976; Blanckenhorn 2000). For example, Kubička and Kratochvíl (2009) examined the hierarchical allocation of energy in the Madagascar ground gecko *Paroedura picta* and found that energies are first allocated to body growth as opposed to reproduction.

Per female fertility was positively associated with female SVL in MO and ES, but not in NG where the egg number was independent from female size. The lack of relationship between mother and the offspring size contrasted with the general pattern described in reptiles by Bauwens and Diaz-Uriarte (1997). However, despite the small sample size ( $n = 15$ ), the number of eggs laid by female was similar to the figure for the species (Speybroeck et al. 2016). This result agrees with the experimental work of Castilla and Bauwens (2000) on the reproductive characteristics of *P. lilfordi* and with those found for other *lacerta* species (Bauwens and Verheyen 1987; Olsson and Shine 1997; Marco and Pérez-Mellado 1998; Galán and Rúa 2003). Even assuming a significant relationship between mother and offspring size, it should be noted that the inheritance function has a small impact on the *P. lilfordi* life cycle (see Supplementary Figure S1). In addition, the inheritance function in IPM is only an approximation of the role of genes in trait expression (Janeiro et al. 2017). Chevin (2015) concluded that it is generally safer to consider the trait of an adult parent and that of its newborn offspring as different traits in IPMs.

The IPM elasticity analysis (Easterling et al. 2000) indicated a contrasting role of body size in the 3 neighboring and sister populations, that is, belonging to the same subspecies and the same genetic clade. Large females in MO and ES showed the highest impact on population growth rate whereas we found that large individuals in NG do not contribute to population growth as they do in the other 2 islets due to the higher mortality found in the NG individuals. This fact resulted in a selective advantage of small (young) females turning out to be the most valuable part of the NG population unlike that found in MO and ES. This indicated that the average adult body size-observed in each population (larger adults in MO and ES than in NG) are adaptive. Moreover, the survival-growth function in ES had the highest elasticity even compared to the population in which adults are of similar size. With as few as 0.29 ha available, individuals in ES presented a slow growth, a high survival rate and a fecundity limited to individuals of large sizes, traits typically associated with the island syndrome (Adler and Levins 1994).



**Figure 5.** Life table response contribution of each demographic rate to the difference in population growth rate,  $\lambda$ , between the 3 islets (MO, NG, and ES, respectively). Surv., survival probability; F, fertility; Growth, average body size growth rate from 2 consecutive years.

Individuals from NG, which are ~10–14% smaller than those in the other 2 islets (MO and ES), exhibited size-independent fertility and have a higher mortality in large size classes compared to the other islands, but both lizard diet (Santamaría et al. 2019) and population density (Ruiz de Infante et al. 2013) were similar when compared to the largest island of MO, where individuals are ~10% larger. Therefore, food resources alone cannot explain why individuals in NG are smaller. Blanckenhorn (2000) listed 4 major possible costs associated with being large: 1) viability costs in juvenile development, 2) high predation/starvation probability of larger sizes, 3) decreased mating success of large males, and 4) decreased reproductive success of large females due to late reproduction. In our case, juvenile development, that is, growth, did not seem to generate a cost for larger sizes. Rotger et al. (2016) showed that juveniles' growth was under the influence of environmental conditions. A variable growth rate was not expected to generate a fixed cost in all cohorts. Bassar et al. (2013) showed that predation pressure caused morphological change in guppies *Poecilia reticulata*. Rats have been occasionally recorded in NG but their influence as predators or competitors of lizards is not clear. Several islets of the Balearic archipelago have been occupied by both species because historical time and lizard density in islets with and without rats are similar (Pérez-Mellado et al. 2008). In contrast to expectations, lizard density was lower in islets in which rats were eradicated (Pérez-Mellado et al. 2008). Avian predation has occasionally been recorded in MO and it is assumed to be similar among the 3 studied populations. Another possible explanation is that larger sizes in NG are too expensive to maintain. Wikelski (2005) reported that the body size differences in 2 insular populations of marine iguanas *Amblyrhynchus cristatus* was due to the energetic costs of maintaining larger sizes and the lower food availability. The absence of a SVL-related fecundity in NG suggested a high reproductive investment by small (young) females. This early investment may have a pleiotropic effect on mortality at older ages (Hillesheim and Stearns 1992; Blanckenhorn 2000).

Although we cannot pin down a single factor responsible for the different role of body size in NG, low reproductive value in large

animals seems to have constrained the evolution toward larger sizes on this islet. It is possible that multiple fitness peaks coexist in lizard strategy and drift processes, typically relevant in small and isolated populations, have shifted individuals on a different peak, as postulated by the Wright's shifting balance theory (Wright 1970). Further research, using single-nucleotide polymorphism analysis (Roesti et al. 2012; Fraser et al. 2015), can shed light on past selective/drift processes. At the moment, we do not have data to support any of these hypotheses.

Our results showed that individuals from neighboring and genetically similar populations exhibit contrasting size-dependent life-history tactics. To our knowledge, this is the first work that describes the different role of body size in 3 neighboring populations of reptiles using size-dependent demographic models. A limitation of our approach is that conclusions are drawn based on correlative relationships between SVL and demographic parameters. Correlative studies cannot fully explore the mechanisms underlying the contrasting role of body size (but see Coulson 2012) and more experiments are needed to elucidate the reasons behind the contrasting strategies found here.

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## Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

## Conflict of Interest Statement

The authors declare that they have no conflicts of interest to this work.

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