

Relative role of population density and climatic factors in shaping the body growth rate of Lilford's Wall Lizard (*Podarcis lilfordi*)

A. Rotger, J.M. Igual, J.J. Smith, and G. Tavecchia

Abstract: The body growth rate in small reptiles is modulated by per-capita food resources and recent evidences suggested that this constraint is the mechanism underlying differences between cohorts. Per-capita food resources depend on population size and climatic factors, but their relative role in explaining the variations in growth rate is unclear. We used morphological data collected over 6 years to model the body growth of an insular lizard (Lilford's Wall Lizard, *Podarcis lilfordi* (Günther, 1874)). We used nonlinear equations to describe the appropriate length-at-age relationship. For each sex, seasonal growth was observed and the oscillatory von Bertalanffy curve was fitted to the data. Three age classes were recognized, and we investigated the relative role of density, spring rainfall, and temperature in explaining the variation of the growth rate in each sex-by-age class. Results showed that the relative role of density and climatic factors varied according to the age considered. While population size and temperature had a negative effect on the growth rate of juveniles, rainfall had a positive influence on the growth of subadults. Adult growth was near zero and constant over time. The different role of density-dependent and climatic factors in explaining age-dependent growth rate provides an important insight in understanding lizard population dynamics and life-history tactics.

Key words: density-dependent growth, climate, capture–recapture, oscillatory growth, age classes, Balearic Islands, Lilford's Wall Lizard, *Podarcis lilfordi*.

Résumé : Le taux de croissance du corps chez les petits reptiles est modulé par les ressources alimentaires par individu, et des observations récentes donnent à penser que cette contrainte est le mécanisme qui sous-tend des différences entre cohortes. Les ressources alimentaires par individu dépendent de la taille de la population et de facteurs climatiques, mais l'incidence relative de ces différents facteurs sur les variations des taux de croissance n'est pas bien établie. Nous avons utilisé des données morphologiques recueillies sur une période de six ans pour modéliser la croissance corporelle d'un lézard insulaire (le lézard de Lilford, *Podarcis lilfordi* (Günther, 1874)). Nous avons utilisé des équations non linéaires pour décrire la relation de la longueur selon l'âge pertinente. Pour chacun des sexes, la croissance saisonnière a été observée et la distribution oscillatoire de von Bertalanffy a été calée sur les données. Trois classes d'âge ont été détectées, et nous avons examiné les rôles relatifs de la densité, des pluies printanières et de la température pour expliquer les variations du taux de croissance dans chaque classe de sexe selon l'âge. Les résultats montrent que les incidences relatives de la densité et des facteurs climatiques varient selon l'âge. Si la taille de la population et la température ont un effet négatif sur le taux de croissance des juvéniles, la pluie a une influence positive sur la croissance des sous-adultes. La croissance des adultes est presque nulle et constante dans le temps. Ces différents rôles de facteurs dépendant de la densité et de facteurs climatiques pour expliquer le taux de croissance selon l'âge jettent un nouvel éclairage important sur la dynamique des populations de lézards et les tactiques associées à leurs cycles biologiques. [Traduit par la Rédaction]

Mots-clés : croissance dépendant de la densité, climat, capture–recapture, croissance oscillatoire, classes d'âge, îles Baléares, lézard de Lilford, *Podarcis lilfordi*.

Introduction

In species with continuous growth, the rate at which individuals attain the size of sexual maturity represents an important life-history trait and is involved in multiple evolutionary trade-offs (Stearns 1992; Caley and Schwarzkopf 2004; Laver et al. 2012). Large variation in growth rate across individuals and populations may result from differences in genetic components (Niewiarowski and Roosenburg 1993), food availability (Dunham 1978), environmental factors, and their interactions (Sinervo and Adolph 1989; Angilletta et al. 2004). However, inter- and intra-population variations in growth suggest a high degree of phenotypic plasticity

(Stamps et al. 1998; Badyaev 2002; Sears and Angilletta 2004), and the realized body size-at-age relationship is not only the result of evolutionary links, but also of this complex interplay between local resource abundance (Van Valen 1965; Hentschel 1999) and environmental conditions (Schoener and Schoener 1978; Stamps 1993). Despite these two factors being expected to concurrently influence individual growth rate, their role has been usually assessed separately (Le Gaillard et al. 2010; Mugabo et al. 2013). Consequently, the relative importance of population size and climatic factors on body growth rate is often unclear (but see Henle et al. 2004; Zabel et al. 2006). Moreover, the effects of density-dependent and independent factors can vary according to

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Table 1. Growth models for individuals of unknown age.

Model	Equation	AIC		References
		Males	Females	
Logistic	$L_2 = A \cdot L_1 / [L_1 + (A - L_1)e^{-K \cdot D}]$	3983.23	2529.34	Schoener and Schoener 1978
von Bertalanffy	$L_2 = A - (A - L_1)e^{-K \cdot D}$	3964.31	2508.54	Fabens 1965
Schnute†	$L_2 = L_1 \cdot e^{-K \cdot D} + (y_2 - y_1 \cdot e^{-K(T_1 - T_2)}) \cdot 1 - e^{-K \cdot D} / 1 - e^{-K(T_1 - T_2)}$	3937.17	2478.52	Schnute 1981; Baker et al. 1991
Seasonal	$L_2 = L_1 + (A - L_1) \cdot (1 - e^{-K \cdot D + S(t_1) - S(t_2)})$	3609.63	2352.95	Somers 1988

Note: AIC, Akaike's information criterion; A, asymptotic body size (mean \pm SE); K, characteristic growth constant (day⁻¹; mean \pm SE); L₁, snout-vent length (SVL) at time i; L₂, SVL at time i + 1; D, days between i and i + 1; y₁, minimum size observed at a given age (T₁); y₂, maximum sizes observed in the sample at a given age (T₂). S(t_i) = (C · K/2π) · sin[2π/365 · (t_i - t_s)], where i = 1 or 2, t₁ is the time at first capture, t₂ is the time at recapture (t₂ = t₁ + D), C is the proportion of decrease in growth (days; mean \pm SE), and t_s is the time shift for the annual cycle (days; mean \pm SE). The retained model is in boldface type.

individual sex or age (e.g., Massot et al. 1992; Grant and Benton 2000; Coulson et al. 2001). In lizards, for example, the sexes play different roles in reproduction and typically have divergent growth that results in different adult sizes, i.e., sexual size dimorphism (Badyaev 2002). In general terms, female body size and growth rate is shaped by selective pressures on fecundity, whereas male size and growth rate is thought to be driven largely by male-male competition (Taylor and DeNardo 2005). Stage-specific and sex-specific life-history data are therefore often needed to produce realistic dynamics of structured populations regulated by density and climatic fluctuations (Coulson et al. 2001; Zabel et al. 2006). Here, we used individual-based data to fit the length-at-age curve of the endemic Balearic wall lizard (Lilford's Wall Lizard, *Podarcis lilfordi* (Günther, 1874)) from capture-recapture data of uniquely identified individuals. Once the length-at-age relationship was described, we quantified the relative role of population size and climatic factors affecting the body growth rate of juvenile, subadults, and adult lizards. Overall, insular populations of lizards attain a density that is 10 times higher than the mainland counterparts (Buckley and Jetz 2007). This high density, promoted by the lack of predators (Buckley and Jetz 2007; Pérez-Mellado et al. 2008), is expected to limit individual growth rate because per-capita resources are low (Adler and Levins 1994; Grant 1998). Consequently, a first expectation is that individual growth is negatively related to population size (Le Gaillard et al. 2010). Besides the common features of insular populations, the Mediterranean environment (characterized by dry summers and relatively mild winters) imposes different constraints from those found in oceanic climate (Pérez-Mellado and Corti 1993). The high summer temperatures limit resource availability in islands, promoting herbivory, despotic competition, and in the extreme cases, cannibalism (Pérez-Mellado and Traveset 1999; Cooper et al. 2015; Pérez-Cembranos and Pérez-Mellado 2015; Pérez-Mellado et al. 2015). Thus, climatic conditions such as rainfall and temperature are expected to be positively associated with individual growth rate through their influence on habitat quality and lizard physiological processes, respectively (Lorenzon et al. 1999; Jordan and Snell 2002; Marquis et al. 2008). We thus predicted a difference in the growth rate of males and females due to sexual differences in physiology, morphology, and behavior (Le Gaillard et al. 2005, 2010). We assessed these predictions using individual data collected over 6 years on individually recognized lizards of known sex.

Materials and methods

Study area and species

Podarcis lilfordi is a medium-sized lizard endemic to the Balearic archipelago. Formerly found on the islands of Mallorca and Menorca, human-introduced predators have relegated the species to sur-

rounding islets of the archipelago, prompting its listing as Endangered by the International Union for Conservation of Nature and Natural Resources (IUCN) (Pérez-Mellado and Martínez-Solano 2009). Males are typically 10% larger than females, but morphological traits, including mean body size, can vary greatly from one population to another (Salvador 1980, 1986). Even though *P. lilfordi* is active all year round, lizards seem to reduce their daily activity during the coldest months of the year. The mating period is not well defined, but it is thought to go from the beginning of the spring to the end of the summer, with the peak of births occurring around June (Pérez-Mellado and Salvador 1988; Castilla and Bauwens 2000). We used capture-recapture data collected on a 5 ha islet of the southern coast of Mallorca (Moltona; 39°18'17.3"N, 03°00'43.2"E) between June 2009 and April 2015 over 16 sessions separated by a minimum of 60 days. In each session, animals were captured for three consecutive days on a grid of 47 pit-fall traps positioned along paths and vegetation edges, encompassing an area of 0.23 ha (more details in Ruiz de Infante Anton et al. 2014). Each captured lizard was measured from snout to vent (SVL) to the nearest millimetre and photographed for individual identification based on the unique pattern of pectoral scales (Perera and Perez-Mellado 2004; Sacchi et al. 2010) using the software APHIS (Moya et al. 2015). Adult lizards were sexed by visual inspection of sexually dimorphic characters (Dellinger and von Hegel 1990). Juveniles and subadults, whose secondary sexual characters are not clearly differentiated, have been sexed by counting the number of ventral-row scales (Salvador 1980; Lecomte et al. 1992; Le Gaillard et al. 2005). To do this, we used photographs of the ventral region of a subset of adult lizards (185 males and 76 females) unequivocally sexed by secondary sexual characters to assess the number of scale rows of each sex. Females have a mean of 1–2 scale rows more than males (for more information see Supplementary material and Figs. S1 and S2¹). By this method, we were able to sex almost 75% of the 303 previously unsexed lizards. The remaining unsexed individuals were excluded from the analyses.

Growth patterns and length-at-age curve

We assessed which model adequately described the length-at-age curve using individual data of SVL over time. To do this, we included positive and negative growth data because measurement errors might occur in both directions; furthermore, individuals can shrink in size due to senescence or in response to extreme resource limitation (Wikelski and Thom 2000; Smith et al. 2010). We considered four asymptotic growth equations to describe the size changes of individuals of unknown age (Table 1). The first two equations, the logistic-by-length model (Schoener and Schoener 1978) and von Bertalanffy's growth function (Fabens 1965; Schoener and Schoener 1978), are the classical models used to describe growth in vertebrates (Lorenzen 1996; Katsanevakis and Maravelias

¹Supplementary material and figures are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2015-0188>.

2008; Tsai et al. 2014). We also considered two additional models, Schnute's equation (Schnute 1981) and the oscillatory model (Somers 1988) (Table 1), which are different formulations of von Bertalanffy's growth function. In Schnute's equation, the main parameters of von Bertalanffy's model are expressed using the observed range of sizes to reduce their correlation. The oscillatory model incorporates a seasonal oscillation into von Bertalanffy's equation (Somers 1988), with a parameter C to modulate the amplitude of the growth so that if $C = 0$, then the equation reverts to the standard von Bertalanffy's growth function, and a parameter t_s to set the time at which oscillations begin. This latter parameter also defines the winter point, which expresses the period of time when individuals grow more slowly (Pauly et al. 1992). The four models were implemented using a nonlinear mixed-effects model ("nlme" package; Pinheiro et al. 2008) in the R statistical package (R Core Team 2013). We considered the individual to be a random effect and included sex as a covariate in each parameter. We used Akaike's information criterion (AIC) to select the most parsimonious of the four growth models (Burnham and Anderson 2004). Following Pinheiro and Bates (2000), we performed diagnostic tests to assess heteroscedasticity of residuals and over-parameterization of random effects in the retained model.

Predictors of growth rate variation

The continuous growth curves described above were used to estimate the correct length-at-age curve, but these models cannot be used to assess the temporal variation in the growth rate because (i) the correlation among model parameters is high (Pilling 2002) and (ii) individuals might respond differently according to their age. Consequently, we sorted male and female lizards into three age classes according to the retained length-at-age curve: juveniles (0–1 year), subadults (1–2 years), and adults (>2 years) (see a similar approach in Galán 1999; Le Galliard et al. 2010). In each age class, we calculated the individual growth rate and assessed whether it varied according to sex, year, and their statistical interaction using GLM with normal error structure (Nelder 1972). When yearly variation proved to be significant, we assessed the effect of two covariates as predictors of temporal variability: the spring population size (see below) and the cumulative spring rainfall (May and June) (Figs. 1A, 1B). In addition, because Mediterranean climate is characterized by hot and dry summers, we took the log-transformed number of days in summer (from June to August) with a maximum temperature equal or more than 32 °C as an indication of harsh condition (Van Damme et al. 1991). Total lizard density, i.e., including all sizes, was estimated in April, except in 2009 when it was estimated during the first week of June, using Spatially Explicit Capture Recapture models (Efford 2004). This model uses capture–recapture data collected with an array of detectors (traps) to estimate population density and is based on a distance-dependent detection function of recapture, with mean g_0 and variance σ (Efford 2004). We used a common detection function across all sessions and modelled the parameters as a function of sex, time, and their interaction as in Ruiz de Infante et al. (2014). We included sex as a predictor of detection probability to ensure that males and females had different capture probability. During the 3 day session, the population was assumed to be closed, i.e., no births, deaths, immigration, or emigration occurred. Monte Carlo goodness-of-fit test was performed from the best model; this approach calculated a statistic from the model and related this statistic to the distribution of the statistic under the fitted model estimating the distribution with 99 simulation data from the model. Model selection followed the AIC criterion (see above; Burnham and Anderson 2004). Climatic variables during 2009 to 2014 were taken by a meteorological station at 5 km from the study area and provided by the Spanish State Meteorological Agency (available from <http://www.aemet.es/es/portada>) (Fig. 1B). The amount of variation accounted for by the covariates was calculated as $[\text{DEV}(c) - \text{DEV}(\cdot)] / [\text{DEV}(t) - \text{DEV}(\cdot)]$, where $\text{DEV}(t)$ is the

deviance of the full-time dependent model, $\text{DEV}(\cdot)$ is the deviance of a model with no effects, and $\text{DEV}(c)$ was the model assuming an effect of a given covariate (Harris et al. 2005). This measure (hereafter D^2) corresponds to the proportion of explained variation and was comparable with a squared correlation coefficient (Schemper 1990).

Results

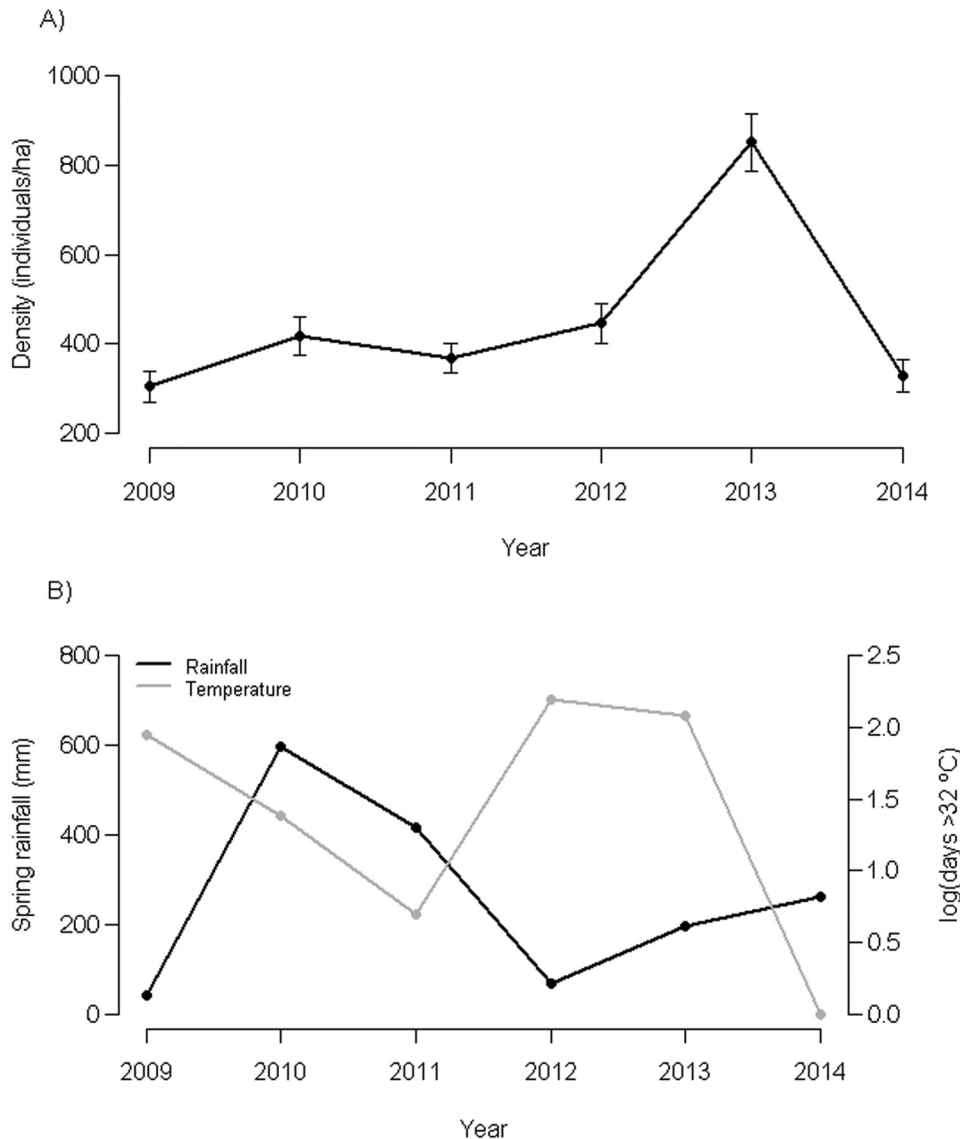
Growth patterns and length-at-age curve

Body size growth was modelled using 1496 observations from 586 lizards (345 males and 241 females) captured at least twice. The AIC values indicated that the oscillatory model (fourth equation) was the best model to describe the growth of both males and females (Table 1). Given this result, we combined data into a single analysis and assessed whether growth parameters were sex-specific using model information theory. The modelling of the joint data indicated that males have a significantly larger asymptotic size than females ($A_{\text{males}} = 76.32 \pm 0.26$, $A_{\text{females}} = 68.33 \pm 0.20$; $t = 29.68$, $p < 0.001$), but both sexes had similar values of the characteristic growth parameter K ($K_{\text{males}} = 0.002 \pm 0.00007$, $K_{\text{females}} = 0.0019 \pm 0.00008$; $t = 1.15$, $p = 0.2513$). Although they presented a statistically significant difference, both sexes shared similar values that reflect the intensity of the seasonal growth oscillation (C) ($C_{\text{males}} = 1.2 \pm 0.12$, $C_{\text{females}} = 1.01 \pm 0.10$; $t = 2.13$, $p = 0.033$), whereas the time when sinusoid growth begins (t_s) ($t_{s\text{-males}} = -0.46 \pm 0.03$, $t_{s\text{-females}} = -0.54 \pm 0.03$; $t = -0.30$, $p = 0.76$) was the same for both sexes. Therefore, we reduced this general model by assuming a shared growth constant and the starting point of oscillation in both sexes, but no further simplifications of the model structure were possible. According to our final model, parameter estimates (mean \pm SE) were as follows: $A_{\text{males}} = 76.76 \pm 0.33$, $A_{\text{females}} = 68.69 \pm 0.26$; $K = 0.0019 \pm 0.00014$; $C_{\text{males}} = 1.2 \pm 0.13$, $C_{\text{females}} = 1 \pm 0.11$; $t_s = -0.48 \pm 0.03$. Estimates of A in this final model were still statistically different between the sexes ($t = 24.03$, $p < 0.001$), with only K as a random effect. Expected growth trajectories from a 31.9 mm SVL hatchling (Castilla and Bauwens 2000) to a hypothetical maximum age of 10 years showed no overlap between males and females (Fig. 2A). The estimated size-at-age growth curves indicated that males and females differed in size from hatchling as growth trajectories diverge at the first moment (Fig. 2A). The amplitude of growth oscillation (C) is virtually 1 in both sexes, suggesting that growth increased by 100% during spring–autumn and becomes 0 during the winter. This result is supported by the observed growth data recorded in the two seasons ($n_{\text{winter}} = 335$ observations, $n_{\text{summer}} = 417$ observations; Fig. 2B). Following the retained growth curve, we estimated that juveniles (0–1 year) ranged from 31.9 to 58 mm for males and from 31.9 to 53 mm for females, yearlings (1–2 years) ranged from 59 to 67 mm for males and from 54 to 62 for females, and larger lizards were considered adults (2+ years; SLV >68 mm for males and SVL >63 mm for females).

Predictors of growth rate variation

The oscillatory model indicated that lizards did not growth during the winter; consequently, we only considered the growth rate from April to October and modelled its variation within each age-by-sex class as a function of population size and climatic variables (see below). As expected, the growth rate abated with age (juveniles = 0.066 ± 0.024 mm/day, yearlings = 0.027 ± 0.015 mm/day, adults = 0.006 ± 0.010 mm/day; ANOVA: $F_{[2,414]} = 312.6$, $p < 0.0001$). Yearly variation was retained in juveniles and yearlings only with an additive difference between males and females (Table 2). In these two age classes, we assessed how much of this variation was explained by intrinsic and extrinsic factors (Table 3). In juveniles, we found a significant effect of density ($F_{[1,43]} = 14.92$, $p = 0.0004$), rainfall ($F_{[1,43]} = 4.12$, $p = 0.05$), and temperature ($F_{[1,43]} = 10.37$, $p = 0.002$). For juveniles, while density and temperature had a

Fig. 1. Predictors for body growth of Lilford's Wall Lizard (*Podarcis lilfordi*). (A) Estimated lizard population size in April (except in 2009 when it was June) with associated SE based on the results from the Spatially Explicit Capture Recapture model (see text for details). (B) Rainfall (cumulative rainfall in May and June) and temperature (number of days with maximum temperature equal or greater than 32 °C).



statistically significant negative influence on growth rate, the cumulative rainfall had a positive one (Figs. 3A–3C). Note that the negative relationship holds even when the extreme value of 2013 was not considered (results not shown). In yearlings, the only variable that influenced the growth rate was the cumulative rainfall in spring (density: $F_{[1,116]} = 0.001$, $p = 0.98$; rainfall: $F_{[1,116]} = 10.49$, $p = 0.002$; temperature: $F_{[1,116]} = 0.014$, $p = 0.9$; Figs. 3D–3F).

Discussion

In vertebrates, the length-at-age curve is thought to be shaped by the optimal allocation of energy between fertility and somatic growth or somatic maintenance (Charnov 1993). Consequently, a description of growth patterns and the factors influencing them can provide an important insight into an individual's life-history tactics and demography (Caley and Schwarzkopf 2004; Laver et al. 2012; Tsai et al. 2014). Here we contrasted different growth models to select the most appropriate length-at-age curve for *P. lilfordi*. As expected, we found a different growth pattern for males and females, likely because of different energy allocations (Shine 1990; Heino and Kaitala 1999; Wikelski and Thom 2000). Males had the

same growth parameter (K) as females, but differed in the asymptotic maximum size, which suggest a faster growth (Figs. 2A, 2B). Consequently, males reached sexual maturity at a similar age and matured at a larger size than females. Although this pattern is observed in many other *Podarcis* species (Bocage's Wall Lizard, *Podarcis bocagei* (Seoane, 1884); Galán 1999; Milos Wall Lizard, *Podarcis milensis* (Bedriaga, 1882); Adamopoulou and Valakos 2000; Carbonell's Wall Lizard, *Podarcis carbonelli* Pérez-Mellado, 1981; Almeida et al. 2001; Common Wall Lizard, *Podarcis muralis* (Laurenti, 1768); Bauwens and Díaz-Uriarte 1997), the common pattern observed in many reptiles is a positive correlation in sex differences between sexual size maturity and asymptotic maximum size (Trivers 1976; Schoener and Schoener 1978; Gibbons and Lovich 1990; Stamps 1993). A common K value for males and females indicates that environmental factors affecting the growth of males have similar effects on females (Stamps 1993). Moreover, the selected model included an oscillatory term, suggesting periods of no or very slow growth (Fig. 2B). The growth of most plant species and ectothermic animals is strongly seasonal (Pauly 1990; Alcoverro et al. 1995; Coma et al. 2000), but there are very few

Fig. 2. (A) Estimated seasonal growth in males and females of Lilford’s Wall Lizard (*Podarcis lilfordi*). (B) Growth rate versus initial snout–vent length (SVL) from winter (October to April) and summer (April to October).

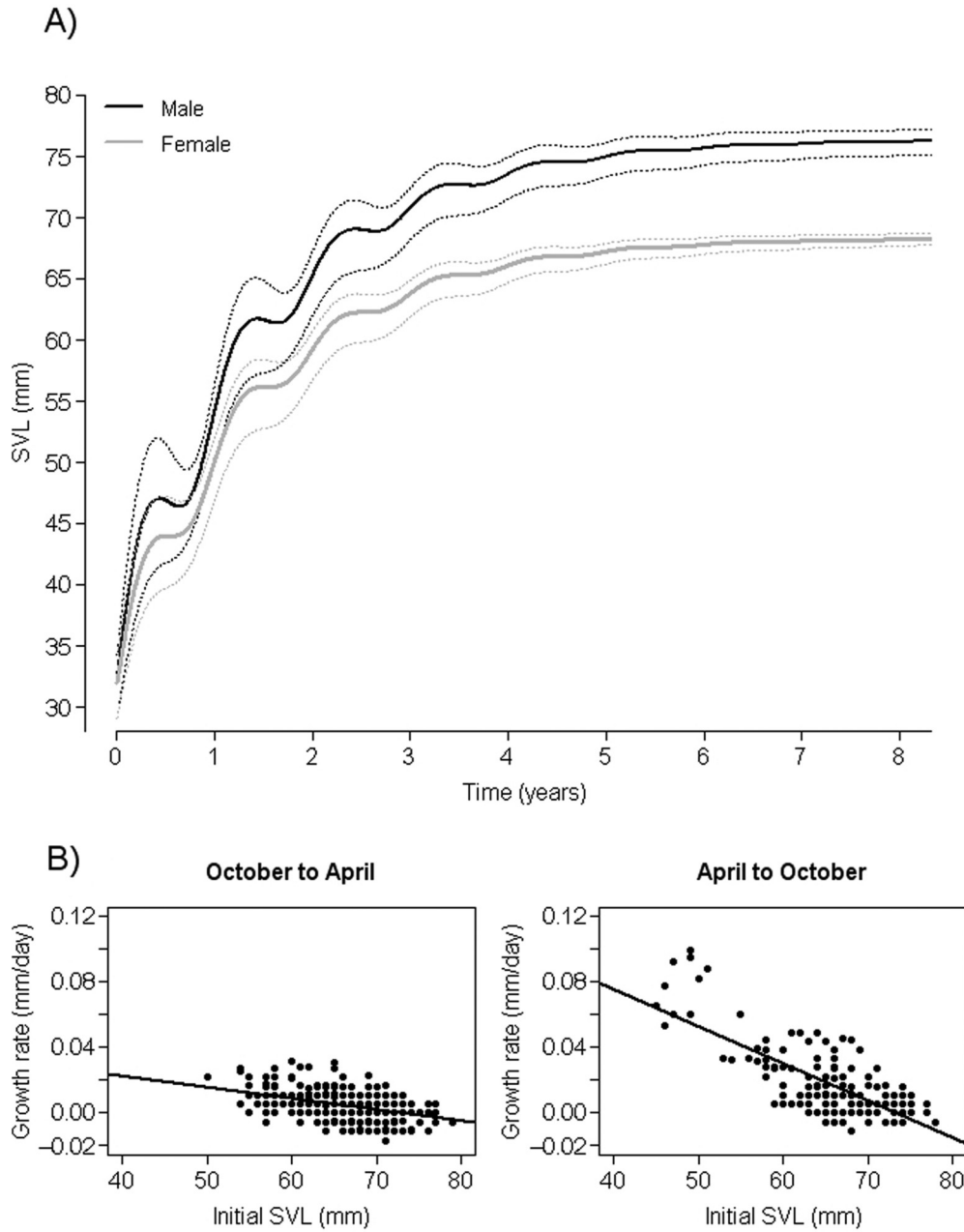


Table 2. Akaike’s information criterion (AIC) values of models assuming the effect of year and sex on the growth rate of juvenile, yearling, and adult Lilford’s Wall Lizards (*Podarcis lilfordi*).

Model	No. of parameters	Juvenile	Yearling	Adult
Year × sex	10	327.03	773.73	1344.51
Year + sex	6	322.95	768.42	1340.45
Year	5	327.92	776.36	1345.27
Sex	2	335.52	785.72	1337.71
Null	1	335.25	793.53	1342.81

Note: × denotes the presence of a statistical interaction between main effects, whereas + denotes its absence, i.e., additive relationship. Best models are in boldface type. Because in adult lizards the effect of year was not retained, a possible effect of covariates was not evaluated.

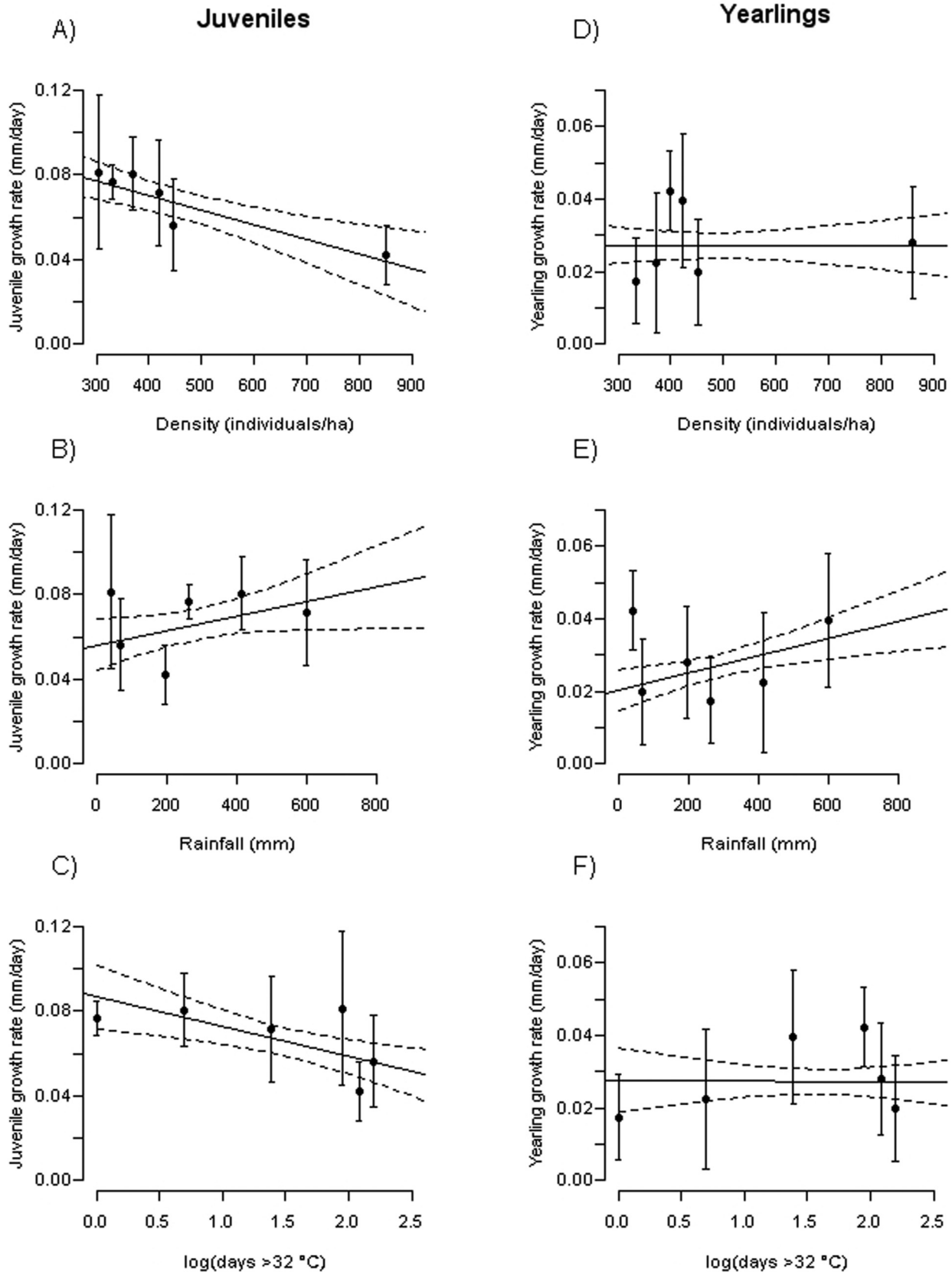
Table 3. Assessing the influence of population density (D), spring rainfall (R), and summer temperature (T) in explaining the yearly variation in the growth rate of juvenile and yearling Lilford’s Wall Lizards (*Podarcis lilfordi*).

Model	No. of parameters	Juvenile		Yearling	
		AIC	D ²	AIC	D ²
Year	7	322.95	1	768.42	1
D + T + R	6	319.64	0.98	775.12	0.74
D	3	320.74	0.81	787.72	0.30
R	3	331.51	0.39	775.60	0.62
T	3	326.33	0.60	787.23	0.31
Null	1	335.25	0	793.54	0

Note: All models assumed an additive effect of sex. Because in adult lizards the effect of year was not retained, a possible effect of covariates was not evaluated. AIC, Akaike’s information criterion; D², proportion of the temporal deviance explained by the covariate (see text). Significant effects are in boldface type ($p < 0.05$).

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Fig. 3. Variation in body growth rates of juvenile (A, B, C) and yearling (D, E, F) Lilford's Wall Lizards (*Podarcis lilfordi*) according to population density and climatic variables. In juveniles, relationships were all statistically significant, whereas only rainfall seemed to influence growth rate of yearlings (E; see text for details).



studies on growth of reptiles that take into account a seasonality pattern (but see Adolph and Porter 1996; Smith et al. 2010). *Podarcis lilfordi*, like other lizard species that share similar climatic condition, seldom hibernates (Pérez-Mellado and Salvador 1981; Pérez-Mellado 1982; Galán 1997). Salvador (1986) reported that *P. lilfordi* reduces the daily activity period in the coldest months of the year and it is reasonable to think that food intake is too low to maintain a fast body growth. Moreover, the winter point near zero indicated the importance of per-capita resource availability during the spring–summer period, something we further investigated by sorting males and females into three age classes based on their respective length-at-age curve. In large vertebrates, density-dependent and independent factors have been shown to influence many life-history traits, but their relative role differed according to individual age or sex (Van Valen 1965; Andrews 1976; Ballinger and Congdon 1980; Massot et al. 1992; Coulson et al. 2001; Le Galliard et al. 2010; Mugabo et al. 2010, 2011, 2013). In small vertebrates, such a fine description of the role of density and climatic factors on multiple life-history traits is difficult to obtain in natural populations. Evidence for lizards come from artificial or seminatural populations, and the effect of density and climatic conditions has mainly been studied considering these factors separately (Andrews 1976; Le Galliard et al. 2010; Mugabo et al. 2010, 2011, 2013). Using long-term individual-based data, we were able to analyze these factors simultaneously and estimate their relative importance according to age and sex. We showed that the relative role of density and climatic factors in modulating the individual growth rate changed according to the age considered and in a similar way for males and females (Table 3). Furthermore, insular conditions are likely to intensify the effects of these factors because insular populations are typically very dense. Adults (2+ years) were not noticeably affected by either density or climatic factors. For adult males, this is probably the result of despotic competition for resources and their social dominance over smaller lizards (Massot et al. 1992; Lecomte et al. 1994; Mugabo et al. 2010). However, we found that growth rate was also constant in adult females, suggesting that intersexual competition does not affect somatic growth of females. Massot et al. (1992) suggested that body size in females is maintained to a detriment of their reproductive success. This seems like a plausible explanation, because it has been shown that growth was negatively linked to reproduction in reptiles (Laurie and Brown 1990) and more research should be done to further investigate this point. Contrary to adults, the growth of juvenile lizards was very variable over time. This temporal variability was negatively associated with population density and summer temperature, but positively associated with spring rainfall. This is in accordance with asymmetric trophic and social interactions because adult lizards are dominant over yearlings and juveniles (Pilorge 1988). The level of despotic competition can be high in particular periods of resource availability (Pérez-Mellado et al. 2015) and the reported cannibalism in insular population is its extreme degree (Castilla and van Damme 1996; Cooper et al. 2015). Otherwise, the level of competition is thus likely to be mediated by the interaction between density and food availability as experimentally demonstrated by the positive link between association between per-capita food intake and growth rate (Le Galliard et al. 2005). Dunham (1978) also found hatchlings that emerged in years with high rainfall had rapid growth rates. In juveniles, the effect of density was stronger than the one of the other covariates, explaining about 80% of the temporal variability in growth rate. Only 17% of the variability was explained by climatic variables. These results contrasted with those found in yearlings, as their growth rate was not influenced by population density and the only statistically significant predictor was the cumulative spring rainfall (positive effect). This agrees with Tinkle et al.'s (1993) study that reported body sizes attained by yearling Common Sagebrush Lizards (*Sceloporus graciosus* Baird and Girard, 1852) were positively correlated with annual rainfall

values. The effect of rainfall is likely to be indirect, as rainfall improves habitat humidity, plant growth, and insect productivity, thereby increasing the food intake of lizards (Stamps and Tanaka 1981; Madsen and Shine 2000). This is consistent with what we found for juveniles and yearlings, thus confirming the importance of water constraints in temperate lizards (Lorenzon et al. 1999; Le Galliard et al. 2010). We found a negative effect of temperature on body growth of juveniles. It is known that thermal requirements are crucial for the thermoregulation and energy balance of reptiles (see Lourdaïs et al. 2008). Although temperature variation among years was low, we expected a negative correlation between the number of hot days and the lizard's body growth. Van Damme et al. (1991) further showed the mass of Viviparous Lizards (*Zootoca vivipara* (Jacquin, 1787), formerly *Lacerta vivipara* Jacquin, 1787) were reduced when the temperature reached 35 °C. Therefore, the more days with high temperatures, the less growing lizards will have. This association was found in juveniles only, being the most sensitive to climate factors. Thermoregulation in juveniles is not good, yet it is possible that physiological functions experience a decline when temperature reaches the thermal maxima (Sunday et al. 2011; Hoffmann et al. 2013). The limited number of years hampered us from testing more complex relationships between growth rate and predictors. We cannot exclude nonlinear relationships or a possible role of the interaction between density and climatic variables. Despite these limitations, our results revealed the oscillatory pattern or growth and suggested a complex interplay between extrinsic and intrinsic factors on the variability of body growth rate. Their different roles according to individual stage (age or size) predict a complex pattern at the population level, considering that current climatic conditions will always have a delayed effect on future recruitments. Le Galliard et al. (2010) suggested that an environmental-dependent growth rate was the mechanism underlying the differences among cohorts. Our results support this view and suggest a more complex pattern because stochastic events, e.g., the alternation of wet and dry summers, can generate compensatory responses, e.g., a low growth during the juvenile stage can be partially compensated for by a faster growth at a yearling stage. Given a density-dependent body growth of juvenile and a climatic, but density-independent, driven growth of yearlings, it is not surprising to find a high heterogeneity of body sizes within the population (Figs. 2A, 2B). Further research is needed to assess the demographic consequence of this complexity.

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