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Quantitative genetics of lifetime growth curves in a lizard

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Abstract

While body size is an iconic trait in quantitative genetics, it bears little meaning without age information for species with indefinite growth. Instead, lifetime growth curves capture the same central aspect of individuals life-history, while accounting for its dynamics through time. Growth curve is a complex, function-valued traits, which requires a specialised framework to study its quantitative genetics. Here, we study growth in a squamate, the common lizard (*Zootoca vivipara*). We use two large datasets with available pedigree information: one from a wild population in a colder, montane environment; the other from an experimental population in a warmer, lowland environment. We found slower growth and larger asymptotic sizes in the colder population. We also found faster growth to lower asymptotic sizes for males. Inferences using a non-linear animal model show very low to moderate heritabilities in the parameters of individual growth curves, varying across populations and sexes. The decomposition of the additive genetic variance show a small to moderate heritability of the overall growth curves, with a stronger importance of the heritability in the *shape* of growth curves (variation in the dynamics of growth) than on their offset (variation between smaller and larger individuals). Genetic variation in growth curves differed between the two populations, with higher heritabilities in the experimental population. It also differed between sexes: there was more genetic variation in the growth rate at earlier ages for males, while genetic variation was larger for asymptotic size and at later ages for females. Our results tend to show that there is more adaptive potential in the earlier ages for males and in the later ages for females, which seems to be linked to their different life-history strategies. They also suggest that climate might have a positive impact on the adaptive potential of growth, which remains to be confirmed.

Key words: adaptation, evolutionary ecology, body size, Zootoca vivipara, function-valued trait, non-linear animal model

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Introduction

The body size of individuals impacts a large variety of their biology, from their ecology to their physiology (LaBarbera, 1989). While this is true for all species, species with indefinite growth (i.e. continued growth after initial development stages) have an even more intricate relationship between the dynamics of their size with time and their life-history. Body size at a given age indeed has a strong impact on the rest of their life-history, such as survival, age at first reproduction, competitive ability or reproductive investment (Barbault, 1988; Brown et al., 2004, 2022). One particular aspect of body size, for most species, is that it is generally among the most heritable traits, including in wild populations (Charmantier et al., 2014). For this reason, and also because it is generally easily measured, body size is possibly the most iconic quantitative traits (Roff, 2007). Due to this generally large heritable variation in body size, this trait is also expected to harbour a large adaptive potential and respond efficiently to selection, an expectation largely validated by a number of experimental evolution studies (e.g. Falconer, 1973; Partridge et al., 1999; Amaral and Johnston, 2012; Mallard et al., 2023, noting that most of these studies also confirm the tight evolutionary link between body size and life-history). However, especially for species with indefinite growth, body size is not generally considered as an actual life-history trait, growth is. This begs the following question: if body size (at any given age) tends to be heritable, what does it mean for body size integrated throughout the life-history of individuals. In other words, the question becomes: is growth itself a heritable trait? To study such question, one should stop considering "body size" as the phenotypic trait of interest, and rather consider the entirety of individual growth curves as the trait under study.

Here, we propose to study growth as a function-valued trait (Stinchcombe et al., 2012; Gomulkiewicz et al., 2018), using individual growth curves instead of instantaneous size data. Studying the quantitative genetics of such non-linear functions is not straightforward, but de Villemereuil and Chevin (2025) has recently provided a statistical and quantitative genetic framework for the study of such non-linear functions in the context of phenotypic plasticity. This framework can be applied to growth curves as well, by substituting the environment for age, and estimate the full heritable genetic variation in growth strategies across individuals. Further, the method allow to disentangle heritable genetic variation stemming from *intrinsic size* (i.e. the propensity of some individuals to be larger than others, regardless of the dynamics of growth) from heritable genetic variation stemming from the *shape of growth* (i.e. variations in the shape of the growth curve itself). Such decomposition helps distinguishing static and purely morphological aspects of body size from the dynamic life-history aspects of growth throughout the lifetime of individuals. More precisely, the first component of variance (about intrinsic size) will measure heritable genetic variation between individuals in their overall tendency to be larger or smaller. By contrast, the second component (focusing on the shape of growth curves) will measure heritable genetic variation in the dynamics of individuals' growth throughout their lifetime. Ultimately, these tools allow for a finer description of the genetic variations in growth strategies among individuals and distinguish between adaptive potential in morphology from adaptive potential in life-history through the impact of growth.

Among species with indefinite growth, terrestrial ectotherm vertebrates such as reptiles, are of particular interest. First because growth plays a central role in their ecology (e.g., competition for territory, access to competition, Losos, 1990; Meiri, 2008). Second, because in such species growth affects size, thermoregulation and metabolism (Brown et al., 2004; Huey and Kingsolver, 2019), and therefore is a crucial part of the energetic budget that may influence the overall life-history strategies of individuals. Third, because ectothermic species are expected to experience an acceleration in their pace-of-life as a consequence of global warming (Bestion et al., 2015; Dupoué et al., 2022). In that regard, reptiles which specialise in cold environments may be among the most responsive, as they have evolved growth strategies that are constrained by a limited active season where individuals must trade-off energy budgets between optimizing growth, immediate survival, long-term survival (i.e., hibernation) and reproductive effort (Brown et al., 2004, 2022). However, little is known regarding the quantitative genetics of growth in reptiles and its variation between individuals (but see Le Galliard et al., 2006; Martins et al., 2019; Kar et al., 2023), especially based on wild populations.

Here, we studied the quantitative genetics of the individual growth curves in the common lizard (*Zootoca vivipara*, Lichenstein 1823). We compared two large datasets (thousands of individuals records) of pedigreed populations: one from a cold-conditions wild population atop Mt Lozère (at 1400 m a.s.l.), and the other of a warm-conditions semi-natural experimental population located at the Metatron experimental facility in the South of France (400 m a.s.l.). To infer individual and genetic variation in growth curves, we used pedigree information and repeated size measurement at each age to fit a non-linear hierarchical animal model, while using the quantitative genetic framework in de Villemereuil and Chevin (2025) to relate genetic variation in the parameters of growth curves to genetic variation in size and growth.

Methods

Data collection

Studied species and populations

The common lizard (*Zootoca vivipara*) is a small ectotherm squamate specialised in cool and damp environments distributed throughout Northern Eurasia. Most populations are viviparous (Surget-Groba et al., 2006). The species is characterized by three age-classes: juveniles (zero year old), generally non-reproductive yearling (one year old) and reproductive adults (two years old or more). In viviparous populations, gestation time is of roughly two months and females lay an average of five soft-shelled eggs (one to ten), which hatch quickly after parturition.

The studied wild population is located at the top of *Mont-Lozère* (Cévennes, France), at 1400 m a.s.l., in the South-Western margin of the viviparous population distribution. Each year since 1989, yearlings and adults were captured in June, soon after mating season (in May Bleu et al., 2011). Immediately after capture, individuals were measured, identified or marked using toe-clipping. Then, they were released at the location of capture, except for gestating females which were hosted in captivity until they gave birth ($\simeq$1 month). Within two days after birth, their juveniles were measured and marked using toe-clipping. Females and juveniles were then both released at the exact location of the female's capture. In captivity, females were kept in individual terrariums (18 $\times$ 11 $\times$ 12 cm), filled with 3 cm of peat. A shelter was provided for thermoregulation. Terrariums were placed with one corner below a 25 W heating bulb (active 6 hours a day: 9 am – 12 pm / 2 pm – 5 pm) to create a thermal gradient. The room followed an artificial 10 h–14 h day-night cycle starting from 2003 and natural day-night cycle before that (roughly 15 h–9 h). Terrariums were humidified three times a day and females were fed with two medium-size house crickets (*Acheta domesticus*) every two days.

The semi-natural experimental lizard population was made of lizards inhabiting 16 mesocoms in the Metatron facility, at the Station of Theoretical and Experimental Ecology (Ariège, France, 43°01' N, 1°05' E). The population was established in 2010 for the purpose of warming experiments (Bestion et al., 2015; Pellerin et al., 2022). The Metatron is an enclosure system composed of 48 mesocosms of 100 m^2 each hosting a diverse community of plant and invertebrate species similar to natural wetland habitats (Bestion et al., 2015; Legrand et al., 2016). Each mesocosm is fully enclosed by underground tarpaulins and fine-meshed nets to prevent species to enter and exit. The lizards used in the experiments were descendants of lizards captured in the Cévennes in 2010, 2012 and 2014. The monitoring and hosting procedures were similar to the ones used in the natural population.

Given the location difference between the populations, the environment, especially the thermal environment, was very different: the mesocosm at Metatron was a warmer environment, with an average summer temperature of 19.0 °C, while the wild population had an average summer temperature of 13.7 °C.

Phenotypic data

Snout-vent length (SVL), i.e. the length from the extremity of the snout to the cloaca, was measured for all individuals (juveniles and individuals caught in the field) using a transparent ruler and gently stretching individual alongside it. The reproductive stage (juvenile, non-reproductive yearling, reproductive adult of age $\geq$ 2), as well as the sex of all individuals, were recorded. For the juveniles, the sex was inferred from counting ventral scales, as individuals with more ventral scales are more likely to be females (Lecomte et al., 1992). Individuals were subsequently sexed as yearlings and/or adults, and if necessary sex was corrected, as errors became unlikely as individuals grew older due to sexual dimorphism.

Pedigree reconstruction

For each new individual (caught in the field or born in the lab), a tail tip tissue ($<$ 1 cm for yearlings or adults, $<$ 3 mm for juveniles) was collected (tail grows back in this species). DNA was extracted from tail tissue using DNeasy Blood & Tissue (Qiagen) purification kits. We then genotyped all individuals at 8 microsatellite loci (2 different sets for the wild or experimental population). The CERVUS software (Marshall et al., 1998) was used to reconstruct paternities of juveniles born in the lab (20% failure to reconstruct parternities for both populations). Maternities were known from observation. They could also be reconstructed for juveniles born in the field for the experimental population. The maximum pedigree depth was 8 in both populations, with mean depth of 2.24 and 2.79 for the wild and experimental populations respectively.

Ethics statement

Captures were allowed by the French DREAL (Licence no. 2010-189-16, 2013-274-0002 & 2021-s-22) and measurements were performed under the approval of the Cuvier Ethics Committee (authorisation number APAFIS#15897-2018070615164391, APAFIS#19523-201902281559649 v3 & APAFIS #34093-2021112211094302

v4) in animal breeding facilities accredited with permit DDETSPP-SPAE-2022-262-001 for the wild population and B09583 for the experimental population.

Statistical analysis

From size series to growth curve

Thanks to repeated measurements on individuals caught in successive years, we obtained series of measures of size (SVL) for 1,592 individuals with an average of 2.85 measurements per individuals in the wild population, and 972 individuals with an average of 2.81 measurements per individuals in the experimental population. For size at birth, data were available on 5,404 and 4,043 juveniles, respectively on the wild and experimental populations. To analyse these series as growth curves, i.e. function $f(t)$ yielding length L_t at age t, we first investigated the fit between our data and three different choices of growth curves classically used in the literature (Schoener and Schoener, 1978; Johnston, 2011; Hernández-Salinas et al., 2019; Yang et al., 2019; Rotger et al., 2023): *(i)* a von Bertalanffy growth curve:

$$f(t) = L_\infty - (L_\infty - L_0)e^{-kt}; \tag{1}$$

(ii) a logistic-by-length growth curve:

$$f(t) = \frac{L_\infty}{1 + \frac{L_\infty - L_0}{L_0} e^{-kt}}; \tag{2}$$

and *(iii)* a Gompertz curve:

$$f(t) = L_\infty e^{\log\left(\frac{L_0}{L_\infty}\right)e^{-kt}}. \tag{3}$$

In each of these models, L_0 is the SVL at birth ($t = 0$), L_∞ is the asymptotic SVL at old ages and k is a growth parameter determining the speed of growth at early ages (differently for each model). The fitting and model selection are described below. For the experimental data, given the considerable spread in birth dates, we used a measure of age precise to the day. This was not possible for the wild population because many date of birth are missing for animals captured as yearlings or adults for the first time. Yet the spread of birth dates is less important there which minimizes this problem (s.d. of 3.9 v. 11.1 for the experimental population).

Imputation of missing birth size

For the wild population, when individuals were caught as juvenile or yearling for the first time, their age was known and we only missed their size at birth, which corresponds to the parameter (L_0) of our model. Given the low variability of size at birth (coefficient of variation of 0.057), and the relatively high number of individuals caught as yearlings, we imputed their size at birth, to be able to analyse the rest of their SVL series. We verified that removing individuals with imputed size at birth did not impact model selection. To do so, we used multiple imputation (Rubin, 1987) and the `mice` R package (van Buuren and Groothuis-Oudshoorn, 2011) to produce 20 imputed datasets. Individuals caught as adults for the first time were excluded do to missing age. For the experimental dataset, the yearly effort of capture being much more important (10 sessions a year) and the probability of capturing all individuals in each mesocosm being higher in the experimental population, such imputation was not necessary.

Model fitting and growth curve selection

Using a Bayesian framework and `brms` R package (Bürkner, 2018), we fitted the models in Equation 1, Equation 2 and Equation 3 as non-linear models of size against age. Models were compared using their widely applicable information criterion (WAIC) (Vehtari et al., 2017). We selected individuals for which at least two records were available (we also checked with three records, with no improvement on the credible intervals of the estimates), resulting in 6714 measures on 2809 individuals for the wild population and 2734 measures on 972 individuals for the experimental population. Because WAIC is not defined for multiple imputed models, we provided the average imputed values for the model selection phase for the wild population, then the best model was re-fitted using multiple imputation. We defined informative, but wide, priors based on previous studies providing information on the size-age relationship of the common lizard (Heulin, 1985; Le Galliard et al., 2006; Horváthová et al., 2013a; Clobert et al., 2014). For each model, 10 chains were run for 3000 iterations, with a warm-up of 1000 iterations. The final, best model was run with a unique chain of 2000 iterations with a warm-up of 1000 iterations and thinning of 5. Effective sample size (ESS > 800) and $\hat{R} < 1.05$ (Vehtari et al., 2021), as well as graphical inspection of the traces of parameters, were used to diagnose issues with the algorithm, except for the final model using multiple imputed datasets, which impacts the validity of these statistics.

Table 1. Table providing the Widely Applicable Information Criterion (WAIC) for the two datasets (wild and experimental populations) and the three shapes of growth curve tested: a von Bertalanffy curve, a logistic-by-length curve and a Gompertz curve. The best fitting curve has the lowest WAIC.

	Wild			Experimental		
Model	**WAIC**	**ΔWAIC**	**Std. Error**	**WAIC**	**ΔWAIC**	**Std. Error**
Logistic	32542.3	0.0	0.0	8968.2	0.0	0.0
Gompertz	33933.7	-695.7	28.2	9325.6	-178.7	25.8
Von Bertanlanffy	35273.4	-1365.6	50.3	10074.6	-553.2	51.0

Quantitative genetics models and variance decomposition

We used the best-fitting curve $f(t)$ for growth to fit a non-linear hierarchical animal model, i.e. a model where the parameters k and L_∞ were allowed to vary across individuals, according to an additive genetic effect, based on the measure of relatedness between individuals obtained from the pedigree (Henderson, 1950; Kruuk, 2004). Since the size at birth is both a parameter of the model (L_0) and an observed value (even part of the response variable), it was impossible to include effects on its in the hierarchical part of the model, due to limitations in the syntax of `brms`. Instead, size at birth was considered as a directly observed parameter L_0 in the non-linear model, and we analysed its variation in a separate linear animal model. As we did not fit the covariance between the different parameters, this two-step approach did not impact our ability to combine all estimations in a common **G**-matrix for the three parameters. Separated inference between sexes for the additive genetic variance in the model for L_0 did not yield different additive genetic variances between sexes and thus a unique additive genetic variance was inferred for this parameter. On the contrary, separated additive genetic variances between sexes were inferred for k and L_∞.

Apart from the additive genetic effect, we also included a maternal environmental and a cohort effects for all three parameters, as well as a permanent environment effect for k and L_∞, as random effects (Wilson et al., 2010). Only the permanent environment effects were inferred separately between sexes.

Sex was included as a fixed effect for all three parameters, as well as the date of birth (number of days since the first of June) for L_0. Models were run using the brms package (Bürkner, 2018). The non-linear animal model, for k and L_∞, was run for 2000 iterations, with a warm-up of 1000 iterations, one chain for each of 20 imputed datasets. The linear model for L_0 was run with 10 chains of 3000 iterations, with a warm-up of 1000 iterations. To compute and decompose the additive genetic variance contained in the growth curve, we applied the framework described by de Villemereuil and Chevin (2025) and the `Reacnorm` package. This package allowed us *(i)* to compute the additive genetic variance V_{Add} of "growth" (i.e. contained in the growth curve); *(ii)* to separate V_{Add} into

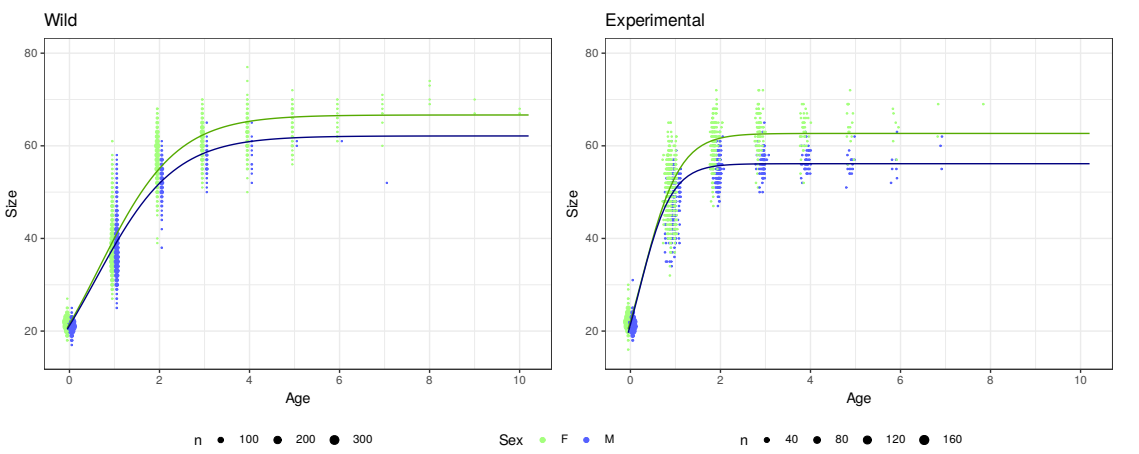

Fig. 1. Growth curves (size against age) for males (blue) and females (green) for the logistic model, for the wild and experimental populations. Actual data are shown in the background for males (pale blue) and females (pale green), with dot size reflecting the number of individuals sharing the same couple of size and age.

the additive genetic variance in "intrinsic size" (i.e. due to genetic differences between individuals in their average size along their life, V_{A}) and the additive genetic variance in the shape of growth curve (i.e. due to additive-by-age interaction, V_{AxAge}); and *(iii)* to decompose V_{Add} (γ-decomposition) and V_{AxAge} (ι-decomposition) into the relative contribution of each of the three parameters of the model (L_0, k, L_∞).

From the additive genetic variances and the total variance (V_{Tot}, excluding the variance arising from the average shape of the growth curve, i.e. conditional to the average impact of age), we computed the heritability of the growth curve $h^2_{\mathrm{Growth}} = \frac{V_{\mathrm{Add}}}{V_{\mathrm{Tot}}}$, the heritability of intrisic size (i.e. of being on average larger or smaller than other individuals across ages) $h^2_{\mathrm{Size}} = \frac{V_{\mathrm{A}}}{V_{\mathrm{Tot}}}$ and the heritability in the shape of the growth curve $h^2_{\mathrm{Shape}} = \frac{V_{\mathrm{AxAge}}}{V_{\mathrm{Tot}}}$. Since posterior medians are the best point estimates for variances (Pick et al., 2023) and generally not very different from the mean for fixed effects, we report it for all estimates, along with the 95% credible intervals (CI) computed from the posterior quantiles. All point estimates and their CI are reported with 3 significant digits, with omitted trailing zeros.

Data Availability

The data and code necessary to replicate this study are available at `https://github.com/devillemereuil/CodeLizardGrowth`.

Results

Growth curve selection

For both the wild and experimental populations, the model with the best fit was the logistic growth model, with a large difference in WAIC compared to the second best model (695.7 & 178.7 for the wild and experimental populations respectively, Table 1). The logistic growth curve for males and females, in the wild and experimental populations, are shown in Figure 1. For all ages, males were on average smaller than females. In the wild population, the asymptote was reached near the third year, with an asymptotic size near 65mm for the females and close to 60mm for the males. By comparison, individuals from the experimental population reached their asymptotic size sooner, near their second year. Their asymptotic size was also slightly smaller, with slighlty stronger sexual dimorphism (near 63mm for females v. 56mm for males).

Size at birth

The average size at birth (L_0) was comparable between the wild and experimental populations, between 21 and 22 mm (Table 2). It differed between sexes, with males being shorter than females on average (wild: $\Delta = -0.637$ mm $[-0.681$ mm, -0.592 mm$]$, $p < 5\text{E-}5$; experimental: $\Delta = -0.684\,[-0.741, -0.626]$, $p < 5\text{E} - 5$). It also depended on the birth date (wild:$b = -0.0171\,[-0.0264, -0.00799]$, $p = 1\text{E-}4$; experimental: $b = -0.0267\,[-0.0305, -0.0228]$, $p < 5\text{E-}5$), with earlier juveniles showing larger size. For both populations, the most important explanatory factor of size at birth was the cohort effect (V_{Y}, Table 2), reflecting the strong impact of the current environmental conditions on the ability of females to invest in their offspring size. This effect was followed by maternal, then additive genetic, effects (V_{M} and V_{A}, Table 2). However, both V_{M} and V_{A} contributed more to explain the total variance in the experimental population, compared to the wild population. Consequently, heritability of size at birth was small, but with support away from zero, in the wild population ($h^2_{L_0} = 0.112[0.0654, 0.171]$, Table 2), and substantially larger in the experimental population ($h^2_{L_0} = 0.222[0.138, 0.296]$, Table 2).

Parameters of growth curve

The average intrinsic growth rate k was twice as small in the wild population compared to the experimental population (Table 2). In both case, there was considerable variation among individuals depending mainly on their identity and year of birth ($V_{\mathrm{PE}} + V_{\mathrm{A}}$ and V_{Y}, Table 2). Maternal effects were still a substantial factor (V_{M}, Table 2), especially in the experimental population. There was no difference in average intrinsic growth rate between males and females in the wild population ($\Delta = 0.0389\,[-0.0843, 0.00067]$, $p = 0.0935$), but the intrinsic growth rate was larger for males in the experimental population ($\Delta = 0.328\,[0.221, 0.436]$, $p < 5\text{E-}5$). By contrast, the additive genetic variance was ten times larger for males than for females in the wild population (log10-ratio $= 1.03\,[6.15\text{E-}4, 3.62]$, $p = 0.0498$), but not in the experimental population (log10-ratio $= 0.2\,[-0.354, 0.865]$, $p = 0.408$). The resulting heritabilities followed the same pattern, with heritability being ten times larger for males than for females in the wild population (log10-ratio $= 1.06\,[0.0484, 3.65]$, $p = 0.0396$). Male heritability was also

Table 2. Estimates of the phenotypic mean (μ), additive genetic variance V_A, maternal effect variance (V_M), cohort effect variance (V_Y), fixed-effects variance (V_F, without the effect of sex), permanent environment effect (V_{PE}) and residual variance (V_R) for each of the three parameters of the model, from both the wild and experimental populations. For L_0, estimates come from the linear animal model with size at birth as a response variable. For k and L_∞, estimates come from the non-linear animal model with size at different ages as a response variable. The total "phenotypic" variance (V_P) is the sum of all the variance components. For non-linear model parameters, the (intra-individual) residual variance is replaced by a permanent environment effect which plays virtually the same role. All estimates are provided here conditional to the effect of sex.

	Wild					**Experimental**				
	L_0	k		L_∞		L_0	k		L_∞	
Estim.		Female	Male	Female	Male		Female	Male	Female	Male
μ	21.4	1.2	1.16	65.5	62	21.8	2.32	2.65	62.7	56
	[21, 21.8]	[1.11, 1.3]	[1.07, 1.26]	[64, 67]	[60.3, 63.9]	[21.2, 22.5]	[2.03, 2.62]	[2.35, 2.95]	[61.2, 64]	[54.6, 57.3]
V_A	0.227	2.28E-3	0.0259	8.13	3.57	0.716	0.0918	0.145	7.35	1.06
	[0.16, 0.299]	[5.32E-6, 0.0153]	[4.92E-3, 0.0476]	[0.0609, 18.2]	[9.13E-3, 15.3]	[0.587, 0.849]	[0.019, 0.178]	[0.0426, 0.272]	[2.74, 12.4]	[6.23E-3, 3.45]
V_M	0.285	3.05E-3	3.05E-3	2.05	2.05	0.951	0.0665	0.0665	1.39	1.39
	[0.238, 0.338]	[1.68E-5, 9.16E-	[1.68E-5, 9.16E-	[9.39E-3, 7.28]	[9.39E-3, 7.28]	[0.803, 1.12]	[0.0309, 0.11]	[0.0309, 0.11]	[0.293, 2.67]	[0.293, 2.67]
V_Y	1.04	0.0462	0.0462	9.44	9.44	1.04	0.177	0.177	3.28	3.28
	[0.548, 2.15]	[0.0249, 0.0936]	[0.0249, 0.0936]	[4.37, 21]	[4.37, 21]	[0.471, 2.92]	[0.0749, 0.552]	[0.0749, 0.552]	[1.19, 11.5]	[1.19, 11.5]
V_F	4.25E-3	—	—	—	—	0.127	—	—	—	—
	[6.6E-4, 0.0106]					[0.0924, 0.166]				
V_{PE}	—	0.0458	0.0159	6.22	5.21	—	0.14	0.104	3.43	2.09
		[0.033, 0.058]	[3E-4, 0.0371]	[0.0249, 17.1]	[0.0172, 17.5]		[0.075, 0.209]	[0.0138, 0.198]	[0.134, 7.61]	[0.372, 3.53]
V_R	0.435	—	—	—	—	0.322	—	—	—	—
	[0.388, 0.483]					[0.247, 0.398]				
V_P	1.99	0.0993	0.0924	26.9	22.7	3.16	0.48	0.501	15.8	8.02
	[1.5, 3.1]	[0.0752, 0.148]	[0.0681, 0.14]	[19.2, 39.8]	[13.2, 37.9]	[2.56, 5.05]	[0.362, 0.857]	[0.376, 0.879]	[12.3, 24.2]	[5.58, 16.2]
h^2	0.112	0.0224	0.276	0.3	0.161	0.224	0.185	0.282	0.458	0.125
	[0.0654, 0.171]	[5.3E-5, 0.154]	[0.0511, 0.533]	[2.15E-3, 0.662]	[4.03E-4, 0.588]	[0.138, 0.296]	[0.0365, 0.377]	[0.078, 0.544]	[0.168, 0.746]	[7.68E-4, 0.426]

Table 3. Estimates obtained from the additive genetic variance decomposition of the growth curves using the Reacnorm package, depending on the sex (Females v. Males) and ages to average over (all ages, or adults of age ≥ 2 only). The total additive genetic variance of growth V_{Add} is decomposed into the additive genetic variance of intrisic size V_{A} (genetic variation in being smaller or larger than other individuals on average across ages) and the additive-by-age variance V_{AxAge} (genetic variance in the shape of growth curve). Dividing by V_{Tot} (total variance, without the variation due to the average shape of the growth curve) provides the heritabilities of growth, intrisic size and shape of growth curve (h^2_{Growth}, h^2_{Size} and h^2_{Shape}). The γ- and ι-decomposition detail the relative contributions of genetic variation in each parameter to V_{Add} (total additive genetic variance in growth) and V_{AxAge} (additive genetic variance the shape of growth) respectively.

	Wild		**Experimental**	
Estim.	Females	Males	Females	Males
Variances				
V_{Add}	1.39 [0.307, 2.63]	2.62 [0.911, 4.53]	3.11 [1.81, 4.63]	2.48 [1.24, 4.48]
V_{A}	0.524 [0.218, 0.876]	0.946 [0.396, 1.55]	1.12 [0.766, 1.53]	0.898 [0.599, 1.43]
V_{AxAge}	0.864 [0.0928, 1.77]	1.68 [0.504, 3.02]	1.99 [1.02, 3.07]	1.57 [0.644, 3.06]
V_{Tot}	14.7 [12.1, 19.3]	13.7 [11, 18]	13.7 [10.5, 23.7]	12.6 [9.14, 23.5]
Heritabilities				
h^2_{Growth}	0.0941 [0.0202, 0.187]	0.191 [0.0669, 0.334]	0.225 [0.109, 0.336]	0.192 [0.0905, 0.324]
h^2_{Size}	0.0353 [0.0138, 0.0639]	0.0686 [0.029, 0.114]	0.0819 [0.0453, 0.117]	0.071 [0.038, 0.106]
h^2_{Shape}	0.0586 [0.00583, 0.123]	0.122 [0.0378, 0.222]	0.143 [0.0626, 0.222]	0.121 [0.05, 0.22]
γ-decomposition				
γ_{L_0}	0.151 [0.0676, 0.652]	0.0792 [0.0398, 0.211]	0.175 [0.113, 0.292]	0.222 [0.123, 0.433]
γ_k	0.146 [3.75E-4, 0.737]	0.767 [0.28, 0.934]	0.343 [0.0884, 0.618]	0.695 [0.329, 0.85]
γ_{L_∞}	0.672 [0.0213, 0.888]	0.15 [7.65E-4, 0.6]	0.478 [0.195, 0.712]	0.084 [5.48E-4, 0.316]
ι-decomposition				
ι_{L_0}	0.0157 [0.00665, 0.149]	0.0078 [0.0036, 0.0243]	0.0413 [0.0233, 0.0806]	0.052 [0.023, 0.134]
ι_k	0.167 [4.18E-4, 0.922]	0.821 [0.3, 0.99]	0.424 [0.118, 0.73]	0.857 [0.491, 0.964]
ι_{L_∞}	0.81 [0.0349, 0.985]	0.17 [8.75E-4, 0.686]	0.532 [0.227, 0.829]	0.0923 [5.73E-4, 0.41]

higher in the experimental population, but not significantly so (log10-ratio $= 0.184\,[-0.347, 0.829]$, $p = 0.416$). For males, heritability estimates were comparable across the wild and experimental populations (Table 2).

The average asymptotic size L_∞ was larger for the wild population compared to the experimental population (Table 2). Males had significantly smaller asymptotic size than females for both population (wild: $\Delta = -3.50$ mm $[-4.88$ mm, -2.01 mm$]$, $p < 5\text{E-}5$; experimental: $\Delta = -6.67$ mm $[-7.35$ mm, -5.99 mm$]$, $p < 5\text{E-}5$). There was substantial variation among individuals, again depending mainly on their identity and year of birth ($V_{\text{PE}} + V_{\text{A}}$ and V_{Y}, Table 2). Maternal effects were small compared to other effects acting on the asymptotic size variation (V_{M}, Table 2). In both populations, the additive genetic variance was smaller in males compared to females, although the discrepancy is significant only in the experimental population (wild: log10-ratio $= -0.3\,[-2.88, 1.75]$, $p = 0.612$; experimental: log10-ratio $= -0.843\,[-3.01, -0.222]$, $p = 0.0094$). This resulted in lower heritability for males than for females in both populations.

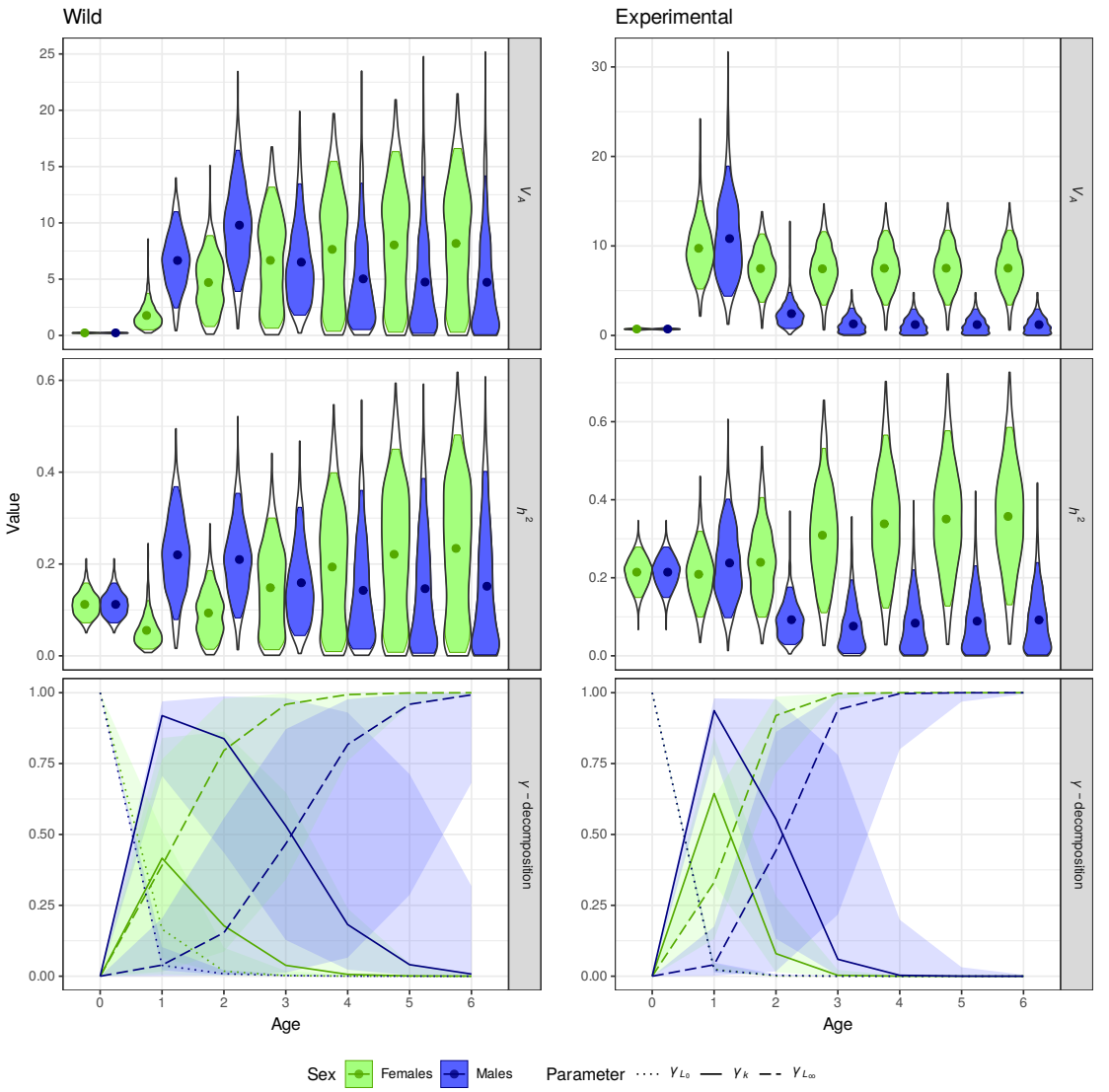

Fig. 2. Additive genetic variance, heritability and γ-decomposition of the growth curve conditional to age and sex. The γ-decomposition shows, for each age, the contribution of the three parameters of the model (size at birth L_0, intrinsic growth rate k and asymptotic size L_∞) to the additive genetic variance. Filling areas of the violin plots and transparent areas beyond the curves show the 95% credible intervals of the estimates.

Additive genetic variation in growth

The decomposition of the additive genetic variance of growth curve showed that the heritability of growth curve conditional to its average shape (see Methods, h^2_{Growth}) was small to moderate for both populations, (Table 3). Such heritability was larger for males in the wild population, but not in the experimental population (Table 3). The dynamics of heritability along age depended strongly on sex and population (Figure 2). In the wild population, a maximum of heritability was reached at age 1 for the males. Instead, it was a minimum for the females at age 1 and larger at latter stages of life (although the uncertainty became considerable). In the experimental population, heritabilities were comparable between sexes until age 1, but the heritability were again smaller for males in latter stages of life.

The influence of the parameters in the additive genetic variation in growth (γ-decomposition of h^2_{Growth}, Table 3) strongly depends on sex and population: k was the most impacting parameter for males, while it was L_∞ for the females. L_0 played a minor to negligible role in the total genetic variation, although it was the second most important factor for males in the experimental population. The dynamics of the γ-decomposition against age reflected the biological interpretation of the parameters: while only L_0 mattered at birth, k was the most important parameter in the earlier stages of life, then L_∞ in the latter stages. The sex modulation of this dynamics reflected the sexual differences in the genetics of growth curves discussed above. Interestingly, the influence of the genetic variation in L_0 was not entirely null at age 1 (Figure 2). Similarly, the influence of the genetic variation in k prolonged even after the asymptotic size was reached (age of 4 in the wild population and age of 2 in the experimental population). Comparing populations, the dynamics of the influence of k sharply reflected the observed difference in growth rates in Figure 1: its influence lasted for longer in the wild population than for the experimental population.

The heritability of intrinsic size h^2_{Size} was very small (Table 3), though with statistical support away from 0, for all sexes and populations (but especially so for females in the wild population). The heritability of the shape of growth curve, h^2_{Shape} was larger than h^2_{Size} in all cases (Table 3). It was larger for males in the wild population, but not in the experimental population. Looking at the influence of each parameter to such genetic variation in the shape of growth (ι-decomposition, Table 3), the most important parameter was k for the males and L_∞ for the females in both populations, following the pattern observed for the γ-decomposition. The importance of L_0 for the additive genetic variance in the shape of growth was expectedly negligible.

Discussion

To study the genetic bases of growth dynamics in a continuous growth species, we considered growth curve as a function-valued trait and analysed it with a non-linear animal model. We then applied a framework design to perform quantitative genetics on non-linear models (de Villemereuil and Chevin, 2025) to decompose the additive genetic variance in growth curves into an additive genetic variance of intrinsic size (i.e. of being larger or smaller than other individuals on average) and an additive genetic variance of the shape of the growth curve. We are also able to disentangle the influence of the genetic variance in the parameters of the growth curve (i.e. initial size, asymptotic size and speed of growth) on such variances.

Environmental comparison of the populations

By comparing a wild population in a colder, montane environment with a warmer, experimental population in the lowlands, we were able to glimpse at the impact of the environment on lifetime growth dynamics. We found, as expected from previous studies Chamaillé-Jammes et al. (2006); Bestion et al. (2015); Dupoué et al. (2017), that growth was faster in the warmer environment, with a roughly doubled intrinsic growth rate parameter. As a result, in the cold environment, individuals reach the asymptotic size only near the age of 4, meaning that very few individuals can reach such size. By contrast, in the warmer population, asymptotic size is reached sooner, at the age of 2. Another difference between the populations was the shorter asymptotic size in the experimental population. When comparing different populations of the common lizard across a large-scale climatic gradient, Roitberg et al. (2013, 2020) found an overall decrease of female adult size with increasing winter temperatures. However, they found a positive slope between female adult size and winter temperature, when focusing on the Western viviparous populations, the clade to which our populations belong. Similarly, using an experimental approach, Pellerin et al. (2022) found both an increase in juvenile growth rate in warmer environment, as we do here, and no impact of temperature on adult growth and adult size. Overall, the direct comparison between the results of these studies is made difficult by the heterogeneity of comparative/experimental approaches, and different characterisations of size, growth, climatic window studied and even definition of "adult" stage. Given the importance of size in the life-history of the common lizard (Sorci et al., 1996; Le Galliard et al., 2006, 2010; Bestion et al., 2015; Dupoué et al., 2017; Rutschmann et al., 2021), this environmental variation in growth curve is likely to impact most aspects of age-structured competition and selection in the population. In any case, these results are in agreement with both the metabolic theory of ecology (Brown et al., 2004; Huey and Kingsolver, 2019), predicting higher growth rate at higher ambient temperatures; and with the temperature-size rule (Atkinson, 1994; Atkinson and Sibly, 1997; Forster and Hirst, 2012), predicting that shorter asymptotic sizes are expected in warmer environments, with longer reproductive seasons (Adolph and Porter, 1996). In our case, the overall differences in growth curves between populations could be a direct effect of faster growth in the experimental population (k was twice as large than in the wild population), meaning that individuals have less time (i.e. less years) to accumulate resources to grow to bigger final sizes. This notably reflects the historical growth and development rates mismatch hypothesis

to explain the temperature-size rule (van der Have and de Jong, 1996; Forster and Hirst, 2012). Alternatively, the observed differences between populations could be explained by other life-history traits such as access to early reproduction (sometimes at age 1 in the experimental population, Bestion et al., 2015) or impact of temperature on breeding phenology (Massot et al., 2017; Le Galliard et al., 2010); or any environmental differences between the populations other than temperature, such as humidity (Lorenzon et al., 2001), the quality of preys, or even genetic differences (Le Galliard et al., 2006).

Quantitative genetics of growth

We found heritable variation in all parameters of the growth curves, with the exception of intrinsic growth rate k for females in the wild population, for which the estimate was very low. Interestingly the influence of each parameter tends to spread beyond its direct influence on the growth curve: genetic variation in size at birth still has a small impact on individuals of age 1 and genetic variation in intrinsic growth rate still impacts genetic variation in size after the asymptotic size is reached. Without a quantitative analysis like our γ-decomposition, it could thus be hard to circumscribe the ages affected by each parameters of the model.

Such heritable variation resulted in a moderate heritability of growth around 0.2, again with the exception of females in the wild population. Our framework allow us to decompose such heritability into the heritability of intrinsic size ("do individuals genetically vary in their tendency to be consistently larger or smaller than others across ages?") and heritability of the shape of growth curve ("do individuals genetically vary in their growth rate, for a given general size?"). We found that, generally, two-third of the heritability of growth curve came from variation in their shape and only one-third in variation from their intrinsic size across ages. This means that genetic variation comes mostly from genetic variation in the growth strategy across individuals, rather than some individuals being taller or smaller across their lifetime.

Environmental and genetic sources of sexual dimorphism

Size is an important ecological trait for both males and females in the common lizard, but partly for different reasons (Le Galliard et al., 2006; Horváthová et al., 2013a; Roitberg et al., 2013, 2020): while the advantage lays in competition for a territory or early access to reproduction in males (Gvozdík and Damme, 2003), it is more directly linked to fecundity in females (Horváthová et al., 2013b; Roitberg et al., 2013, 2020; Jurczyk and Borczyk, 2022). This results in a sexual dimorphism in size and growth in this species, with males tending to be smaller than females (Le Galliard et al., 2006; Roitberg et al., 2020).

Our models confirmed a well-known pattern of sexual dimorphism in this species (Le Galliard et al., 2006; Roitberg et al., 2020). With our approach, we were able to examine this dimorphism over the lifetime of individuals and across two contrasted environments. Expectedly, the dimorphism rather lies in adult ages, and is thus more profoundly observed in the asymptotic size (L_∞). The difference in the average asymptotic size was also found to be more intense in the warmer population, but there was a difference in the variance of asymptotic size between sexes, with males being less variable (Table 2). This result is consistent with the findings of Roitberg et al. (2020) that adult sizes of males are less variable across different populations. Note, however, that our results of increased dimorphism in asymptotic size contradicts Roitberg et al. (2020) observation that sexual dimorphism is generally lessen with increased temperature.

Further, the addition of sex-dependent additive genetic variances in the model allowed us to find a considerable difference between males and females in their genetic variation of growth. On the one hand, the genetic variation among males was mostly driven by their genetic variation in the intrinsic growth rate (k) and was maximised early in life around the age of 1. On the other hand, the genetic variation among females was mainly driven by the genetic variation in their asymptotic size (L_∞) and was maximised at late ages. When comparing estimates across populations, the general levels of heritabilities, at all levels, were very comparable between populations for males (with a small exception for size at birth). By contrast, estimates for the females were different between the two populations: the heritability of growth was smaller than males in the wild population, and larger than males in the experimental population. The most important difference between both populations for females was the very low estimated heritability for the intrinsic growth rate found in the wild population, which strongly affected the dynamics of heritability across ages: it becomes very low at the age of 1 and start increasing again at the age of 2. Yet, most (56%) of the females reaching recruitment at the age of 2 breed only once. This means that the vast majority of the females never reach ages with the highest heritabilities, explaining the low overall heritability observed in the wild population.

Ecological and evolutionary consequences

Size and growth strategies are key ecological traits for squamates, as it influences many parts of their life-history, their metabolism or their thermoregulation (Barbault, 1988; Brown et al., 2004, 2022). Here, growth (or "size across ages") was moderately heritable. On the one hand, this confirms the strong importance of the environment, and probably phenotypic plasticity, in the growth strategy of individuals. A confirmation that is further supported by our comparison between two environmentally different populations. On the other hand, this result also highlights the adaptive potential in size and growth. Further, since roughly two-third of such heritability stems from genetic variation in the shape of growth curve, it highlights adaptive potential in growth strategies, i.e. the possibility for evolution to select strategies with e.g. different growth rates. In a context where global warming seems to mainly impact a species like the common lizard by accelerating their pace-of-life (Bestion et al., 2015; Dupoué et al., 2017, 2022), this means that a counter-gradient adaptive response (De Jong, 1988) is possible: i.e. an evolution toward decreasing the genetic value for the intrinsic growth rate, while the phenotypic value of the intrinsic growth rate remain constant, to counteract the effect of a warmer environment. This could result in evolutionary rescue in some populations. Although given the observed and predicted pace of phenotypic response to warming (Bestion et al., 2015; Dupoué et al., 2017), the impact on population dynamics (Dupoué et al., 2022; Pellerin et al., 2022) and the moderate heritabilities inferred in this study, it seems that the likelihood of such scenario for most populations of common lizards at the Southern margin is thin. This is especially true as the most important sex for population dynamics, the females, were inferred to have a more limited adaptive potential for the evolution of growth in our wild population.

Methodology

In this study, we applied a non-linear animal model framework, combined with a framework to decompose the additive genetic variance of non-linear function-values trait designed to study reaction norms. Applying such framework allowed us to fit a parametric growth curve, combining information from all ages together, and yet, be able to relate additive genetic variation in the parameters back to the phenotypic traits of size and growth. This approach is close to the approach used by Kar et al. (2023) to study the quantitative genetics of growth on the delicate skink (*Lampropholis delicata*), with the notable difference that they relied on a quadratic curve, which is a linear approach from the parameter perspective (see de Villemereuil and Chevin, 2025). Such quadratic approach is possible in the early stages of development studied by Kar et al. (2023), but high order polynomials (with a large number of parameters) would be required to fit the lifetime growth curve of most squamates, which is not practical. By contrast, our non-linear approach only required three parameters to fit the growth curves. Another strong difference of our study is that we used a full pedigree of a wild population of common lizards to estimate the heritability of growth. Animal model based estimates of wild population heritabilities are scarce on squamates, and to our knowledge, this study is the first to provide such estimates for age-specific size and growth in a wild population of lizards. This is important as, for example, our estimates of heritability of size at birth is substantially smaller than previous estimates based on sib analysis (Le Galliard et al., 2006) and even on animal model with smaller sample size in the experimental population (Bestion et al., 2023).

Conclusion

We provided a comprehensive quantitative genetic analysis of growth curves in the common lizard, demonstrating significant genetic variation in growth parameters across two populations in different environments, especially regarding their climate. By applying a novel framework of additive genetic variance decomposition, we have gained valuable insights into the genetic basis of growth strategies in this species. These findings highlight, at least in this species: *(i)* the existence of adaptive potential for the evolution of the shape of growth curves; *(ii)* a very different ecological and evolutionary context for males and females; and *(iii)* a strong influence of the environmental context on both growth dynamics and its genetic determinants. Further studies regarding selection and the eco-evo dynamics of growth are needed to better understand the putative role of the evolution of growth to respond to selection, e.g. in the context of climate change.

Competing interests

No competing interest is declared.

Author contributions statement

P.d.V. designed the study. A.A. and P.d.V. performed the statistical analysis. A.A., P.d.V., A.R., M.R. and J.Co. interpreted the results. A.R., M.R., M.M., J.Cl. and P.d.V. collected data for the wild population. E.B., F.P., L.W., L.-M.S.J. L.D.G., E.D., J.C. and J.Co. collected data for the experimental population. M.R. produced the pedigree for both populations. A.A. and P.d.V. wrote the manuscript, with contribution from all co-authors.

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