A comparative study of growth: different body weight trajectories in three species of the genus *Eublepharis* and their hybrids

Daniel Frynta¹, Jitka Jančúchová-Lásková³, Petra Frýdlová¹ & Eva Landová¹,²

An extensive research effort is devoted to the evolution of life-histories and processes underlying the variation in adult body weight; however, in this regard, some animal taxa remain neglected. Here we report rates and timing of growth recorded in two wild-derived populations of a model lizard species, *Eublepharis macularius* (M, W), other two related species, i.e., *E. angramainyu* (A) and *E. sp.* (D), and their between-species hybrids. We detected clear differences among the examined species/populations, which can be interpreted in the terms of “fast – slow” continuum of life-history strategies. The mean asymptotic body size was the highest in A and further decreased in the following order: M, W, and D. In contrast, the growth rate showed an opposite pattern. Counter-intuitively, the largest species exhibited the slowest growth rates. The final body size was determined mainly by the inflexion point. This parameter reflecting the duration of exponential growth increased with mean asymptotic body size and easily overcompensated the effect of decreasing growth rates in larger species. Compared to the parental species, the F1 and backcross hybrids exhibited intermediate values of growth parameters. Thus, except for the case of the F2 hybrid of MxA, we failed to detect deleterious effects of hybridization in these animals with temperature sex determination.

Body size is a crucial parameter determining the ecological and evolutionary attributes of animals¹,². Its phenotypic variation may be caused by both genetic and environmental components³. As a result, body size contributes to the fitness and varies substantially among individuals, populations, and species⁴–⁶. The final body size is not just a static trait, but is a product of an ontogenetic trajectory typically involving the growth process.

Growth trajectories are perfectly understood in fast-growing avian species⁷. A collection of datasets covering the entire period of growth is sometimes extremely laborious and time-consuming, especially in case of species with slow ontogenetic trajectories and/or indeterminate growers (but see in squamates reptiles⁸–¹⁴ and in fishes¹⁵–¹⁹). This subsequently simplifies the description of body growth as a function of growth increments (typically used in agri- and aqua-culture).

The growth trajectories typically consist of two major components contributing to the final body size. In a typical case, these are an intrinsic growth rate and a duration of exponential growth period. The latter one is not estimated as a separate parameter by some widely-used theoretical growth models (e.g. von Bertalanffy, West production model), which are applicable even when the data points do not cover the whole course of ontogeny²⁰,²¹. The logistic growth model fits the empirical data concerning a detailed description of growth trajectories and produces the required information about the duration of exponential growth period further referred to as an inflexion point. The estimates from this model are the growth rate, inflexion point, and asymptotic body size²². Both the growth rate and the growth duration may contribute to the final body size and are inherently inter-correlated.

Besides the growth trajectories and their components (parameters), life-history variables comprise of the body size, maturation, longevity, mortality rates, reproductive investments, etc. In many animal taxa, these variables are tightly inter-correlated and arranged along a common gradient, typically forming an axis from slow to fast life-histories²³,²⁴. Thus, the composite measure of life-histories from a multivariate data set is used to classify the position across the current concept of the “fast-slow” continuum (e.g.,²⁴–²⁷). Even in the absence of complex data,
it is possible to estimate an approximate position of individual species/populations on this axis according to a limited number of reliable life-history variables. In this respect, growth rates and/or duration of exponential growth may be, under some circumstances, helpful.

In our study, we monitored three closely related species of eyelid geckos of the genus *Eublepharis*. During the last century, leopard gecko (*Eublepharis macularius*, Blyth, 1854) became a laboratory animal as well as a captive bred pet. It is routinely used as a model species for studies of incubation temperature and its hormonal consequences influencing brain development, antipredatory strategies, etc. *Eublepharid* geckos (Eublepharidae) vary considerably in body size – the largest species *E. angramainyu* (Anderson and Leviton, 1966) is more than 20 times heavier than the smallest *Coleonyx brevis* (Stejneger, 1893). Thus, the family was repeatedly used as a model for studies dealing with the evolution of body size, parental investment, growth, allometries of cell size, DNA content, and metabolism.

Growth rates and trajectories may properly reflect the animal’s life-history strategy only if these parameters were solely determined by the underlying trade-offs and the corresponding strategic decisions concerning an investment. Growth may be constrained by fitness (performance, health status) of the animal. In this respect, the efficiency of growth can be useful during the monitoring of the processes that are suspected to cause deleterious effects.

We compared the growth parameters to explore the effect of experimental crossing of the species/populations of the eublepharid geckos. The view on the real size of the effect of hybridization on fitness is still controversial. Both negative and positive outcomes were associated with hybridization in natural and experimental conditions; for reviews, see. Historically, natural hybridization was considered as exceptional and erroneous events, but the current increase of literature concerning the importance of hybridization for both speciation and adaptation implies the opposite.

Genomic and epigenetic insights into the molecular bases of heterosis are indicating that the role of natural hybridization is important in the formation of new species. Because of exceptional time demands, experimental studies dealing with hybridization covering the observation of real parameters of fitness (fertility, viability, body growth) are still very scarce.

The aims of our study were 1) to compare the growth parameters of leopard geckos to demonstrate contrasting life-history strategies of selected parental species/populations; and 2) to compare the growth parameters of parental species with parameters of F1 and F2 hybrids and subsequent backcrosses to reveal the putative beneficial (heterosis in F1 generation of hybrids) and/or deleterious (incompatibilities leading to segregation load in F2 and backcrosses) effects of hybridization on fitness.

**Results**

The estimated growth parameters for distinct populations/species, their F1 and F2 hybrids, and backcrosses are presented in Table 1. The logistic regression model fits well our longitudinal growth data (Table 1 and Fig. 1).

**Comparisons among parental species/populations.** Growth parameter $a$ significantly differed (Table 1) among distinct species/populations (ANOVA: $F_{3,132} = 88.337, P < 0.001$). Moreover, *E. angramainyu* exhibited significantly lower growth rate $K$ (ANOVA: $F_{3,132} = 16.3791, P < 0.001$) and bigger inflexion point $T$ (ANOVA: $F_{3,132} = 37.057, P < 0.001$) than all of the other species/populations. The growth parameters revealed from the logistic regression model were inter-correlated. The asymptotic body weight ($a$) was closely correlated to parameter $T$ ($r = 0.64, 0.75$ and $0.65$ for yellow, white, and dark species/populations, respectively). No such correlation was found between $a$ and $K$ parameters.

The whole course of body growth of distinct species/populations is illustrated by Fig. 2.

Changes in mean absolute and relative body weight increments (computed from real body weighting) during the post-hatching ontogeny are shown in Fig. 3.

**Comparison among parental species (*E. angramainyu* and *E. macularius*), their F1 and F2 hybrids, and backcrosses.** Growth parameters significantly differed among parental species of *A* and *M* and their F1 hybrids (ANOVA: $a: F_{(2,60)} = 57.725, P < 0.0001$; $K: F_{(2,60)} = 10.0467, P = 0.000127$; $T: F_{(2,60)} = 24.9932, P < 0.0001$). F1 hybridization was not successful (except for one individuum, which had poor body growth with the lowest prediction of parameter $a = 36.546$ g) in comparison with the parental population and F1 hybrids. The course of body growth of the parental species and F1 and F2 hybrids is depicted in Fig. 4. The asymptotic body weight significantly differed in both backcrosses (MAXM and MxMA) from the parental species of *E. angramainyu* and F1 hybrids (ANOVA: $F_{(2,10)} = 29.771, P < 0.0001$). The estimations of asymptotic body mass were similar for both backcrosses (see Table 1).

**Comparison among parental species (yellow and white *E. macularius* and dark *E. sp.*) and their F1 and F2 hybrids.** The growth parameters significantly differed among the parental species of M and D and their F1 hybrids (ANOVA: $a: F_{(3,16)} = 31.980, P < 0.0001$; $K: F_{(3,16)} = 9.8493, P = 0.000008$; $T: F_{(3,16)} = 5.4302, P = 0.001571$). The parental species differed in all growth parameters (all $p < 0.01$). This difference is in accordance with our prediction of the parental species’ genetic distinction. F1 hybrids differed in parameter $a$ ($P = 0.019977$ and $0.005097$ in comparison with M and D, respectively). Moreover, F1 hybrids also differed in parameter $K$ in comparison with D ($p = 0.006029$). The inflexion point $T$ was similar in F1 and F2 hybrids in comparison with the parental species. The course of body growth of the parental species and F1 and F2 hybrids is shown in Fig. 5.

Hybridization of W with D also revealed distinctiveness of the parental species. Growth parameters of F1 and F2 hybrids were intermediate compared with values among the parental species (see Table 1).

**Discussion**

Leopard geckos of the genus *Eublepharis* are long-living animals (maximum lifespan > 25 years, personal observation) laying multiple clutches per season. The clutches are of an invariant size, each consisting of two eggs, which are
and a father is an F1 hybrid of the yellow population of *E. macularius*. *E. macularius* belongs to the yellow population of *E.*, (MxMA) the first-generation backcross with the yellow population of *E. macularius*, (MAxM) the first-generation backcross with the yellow population of *E. macularius*, (MxD) the reciprocal first-generation hybrid, a mother/father of the yellow population of *E. macularius* and a mother/father of the dark population of *E. sp.*, (WxD) – the first-generation hybrid, a mother of the white population of *E. macularius* and a father of the dark population of *E. sp.*, (MxA) the first-generation hybrid, a mother of the yellow population of *E. macularius* and a father of the white population of *E. macularius*, (MxM) the parental generation of the white population of *E. macularius*, (W) the parental generation of the white population of *E. macularius*, (A) the parental generation of *E. angramainyu*, (D) the parental generation of the dark population of the genus *Eublepharis*, (MDxMD) the second-generation hybrid, both parents are F1 hybrids of the yellow population of *E. macularius* and *E. angramainyu* and a father belongs to the yellow population of *E. macularius*, (MxM) the first-generation backcross with the yellow population of *E. macularius*, a mother is an F1 hybrid of the yellow population of *E. macularius* and *E. angramainyu* and a father is an F1 hybrid of the yellow population of *E. macularius* and *E. angramainyu*. First, there is always an abbreviation for a female, followed by the one for a male with a cross (x) between.

Table 1. The estimated values (mean ± SE) of the asymptotic body mass a (g), growth rate K and inflexion point T (days), and variance explained by the model (R²) with a number of individuals (N) for the examined species, hybrids, and backcrosses of eublepharid geckos. Abbreviations: (P) parental generation, (F₁) the first and the second (F₂) filial generation hybrids, (B) the first-generation backcross, (M) the parental generation of the yellow population of *E. macularius*, (W) the parental generation of the white population of *E. macularius*, (A) the parental generation of *E. angramainyu*, (D) the parental generation of the dark population of the genus *Eublepharis*, (MxA) the first-generation hybrid, a mother of the yellow population of *E. macularius* and a father of the *E. angramainyu*, (MxM) the reciprocal filial-backcross hybrid, a mother/father of the yellow population of *E. macularius* and a mother/father of the dark population of population *E. sp.*, (WxD) – the first-generation hybrid, a mother of the white population of *E. macularius* and a father of the dark population of *E. sp.*, (MxA) the first-generation hybrid, a mother of the yellow population of *E. macularius* and a father of the white population of *E. macularius*. 

| Generation | Species/population | a ± SE   | K ± SE   | T ± SE   | R² ± SE  | N  |
|------------|--------------------|---------|---------|---------|---------|----|
| P          | A                  | 101.135 ± 4.782 | 0.0055 ± 0.0021 | 381.17 ± 22.21 | 0.989 ± 0.003 | 6  |
| P          | W                  | 39.461 ± 1.852 | 0.0153 ± 0.0008 | 167.68 ± 8.67 | 0.985 ± 0.001 | 40 |
| P          | D                  | 30.44 ± 1.876  | 0.0194 ± 0.0008 | 140.79 ± 8.71 | 0.991 ± 0.001 | 39 |
| P          | M                  | 49.188 ± 1.64  | 0.0144 ± 0.0007 | 182.96 ± 7.62 | 0.987 ± 0.001 | 51 |
| F₁         | WxD                | 35.851 ± 4.782 | 0.0149 ± 0.0021 | 145.14 ± 22.21 | 0.98 ± 0.003 | 6  |
| F₁         | MxW                | 43.764 ± 2.928 | 0.0151 ± 0.0013 | 160.95 ± 13.66 | 0.988 ± 0.002 | 16 |
| F₁         | MxA                | 78.501 ± 2.254 | 0.0108 ± 0.0001 | 264.14 ± 10.47 | 0.981 ± 0.002 | 27 |
| F₁         | MxD                | 40.484 ± 2.687 | 0.0137 ± 0.0012 | 168.37 ± 12.48 | 0.986 ± 0.002 | 19 |
| F₁         | WDxWD              | 34.243 ± 4.427 | 0.019 ± 0.002  | 136.59 ± 20.57 | 0.991 ± 0.003 | 7  |
| F₁         | MWxWM              | 38.483 ± 2.841 | 0.0187 ± 0.0013 | 137.92 ± 13.2  | 0.989 ± 0.002 | 17 |
| F₁         | MAxMA              | 36.546 ± 1.713 | 0.0102 ± 0.0052 | 178.52 ± 54.41 | 0.984 ± 0.008 | 1  |
| F₁         | MDxMD              | 36.87 ± 3.532  | 0.0195 ± 0.0016 | 135.19 ± 16.41 | 0.992 ± 0.002 | 11 |
| B          | MAxM               | 45.199 ± 3.704 | 0.0131 ± 0.0016 | 155.54 ± 17.21 | 0.98 ± 0.003 | 10 |
| B          | MxMA               | 57.347 ± 3.024 | 0.0115 ± 0.0013 | 202.94 ± 14.05 | 0.984 ± 0.002 | 15 |
| B          | MxMD               | 40.595 ± 8.282 | 0.0206 ± 0.0037 | 128.34 ± 38.47 | 0.991 ± 0.006 | 2  |

extraordinarily large compared to the maternal body ³⁵,⁵⁵. This place their life-history strategy close to the “slow” end of the “fast-slow” continuum reported in lizards. Our analyses uncovered strong differences in growth trajectories among the examined species which were clearly associated with the asymptotic body weight. This suggests that the examined species/populations still significantly differ in their position along the fast-slow axis.

A three-parameter logistic regression model fits our long-term data covering the course of ontogeny from hatching to adulthood very well. Parental species/populations (A, M, W and D) differed significantly in the estimated asymptotic body weights and growth rates (except the growth rate and inflexion point, which were similar for two closely related populations of the yellow and white form of *E. macularius*).

We found that the growth parameters estimated by the logistic regression model were inter-correlated. Asymptotic body weight is tightly predicted by parameter K. Given the mutual relationship of growth parameters, we decided to compute separately the growth rate expressed as absolute and relative body weight increments. This approach allowed us to compare real increments of studied species/populations across the ontogeny (Fig. 3) and revealed similar results as those deduced from the estimates of parameter K. The growth rate was counterintuitively the lowest in large *E. angramainyu* (A) and highest in small *E. sp.* (D). The final body size was determined by the inflexion point parameter (T). The inflexion point reflects that the duration of the exponential growth period increases with mean asymptotic body size and thus easily overcompensates the effect of decreasing growth rates in the larger-bodied species.

A general life-history relationship described as the Rosa Lee phenomenon ³⁶,³⁷ may provide an explanation for the decrease in the growth rate parameter (K) with asymptotic body size (a) found in our data set. Lee's studies concerning age and growth determination in fishes demonstrated that individuals in a population with slower growth rates suffer less from mortality when they are young, which points to the existence of a trade-off between the growth rate and survival. This phenomenon was traditionally examined in fishes ³⁸–⁴¹ and only exceptionally applied to other vertebrates ³²–³⁶. If further proved in geckos, large-bodied species might be selected to avoid mortality risk by reducing the growth rates. A preliminary inspection of our unpublished data sets suggests that within each species/population, the fast-growing individuals of the leopard gecko tend to suffer equal or even lower rates of juvenile mortality. However, the mortality pattern under laboratory conditions substantially differs from that under natural conditions. Thus, we have to search for alternative explanations for the reported reduced...
growth rates in larger geckos. Metabolic rates may be slightly constrained, e.g., by a positive allometric relationship between erythrocyte size and body size, which has been demonstrated in lizards including the eublepharid geckos\(^2\). Body growth of the whole organism, as well as the growth of particular organs and body segments, is orchestrated by hormones, growth factors and cell-cycle regulations\(^3\). These represent fundamental proximate mechanisms controlling growth rate and final body size. Beside growth hormones, there are sexual steroids, which are reported either to stimulate or to inhibit body growth. This was demonstrated especially in sexually dimorphic species\(^4\). Recent studies revealed that the deceleration of body growth is caused by the suppression of cell proliferation and is driven primarily by local rather than systemic mechanisms\(^5\).

Clear differences detected among the examined species/populations can be interpreted in terms of the “fast – slow” continuum of life-history strategies. *E. angramainyu* is a large-bodied species with a slow growth rate. This species attained the body weight close to asymptotic values at the age of about three years, but the first copulation was recorded at the age of five years. On the contrary, *E. macularius* is smaller, grows more slowly, and matures earlier (1–2 years). The sexual maturation is not known from the nature, but it is reasonable to suppose that it takes more time due to seasonality. However, the clutch size is invariant in eublepharid geckos and the relationship between body size and egg size is isometric\(^6\).

A similar analysis of the growth parameters is ideal for the comparison of parental and descendant individuals in the experimental crossing of the species/populations. It may also contribute to our knowledge of the influence the hybridization has on fitness, viability and competitiveness of F\(_1\) and F\(_2\) hybrids and backcrosses. Both positive and negative effects of hybridization are discussed in current literature\(^2\). A heterosis effect accompanying hybridization is traditionally used in agriculture and aquaculture because of an increased vigour (e.g., larger body size, faster growth rate, higher reproductive output, enhanced tolerance to environmental conditions). Similar experiments dealing with the effect of hybridization on body growth in squamate reptiles are completely missing. A pioneering study of hybridization among species of the genus *Lacerta*\(^4\) provided the first insight into the issue concerning hybridization in reptiles. Rykena reported intriguing data concerning hatchability, survival, fertility, and physical deformities of F\(_1\) and F\(_2\) hybrids and backcrosses\(^5\). The lacertids have genetic sex determination (GSD)\(^7\) and conclusions concerning the hybridization of GSD species may differ from those with temperature sex determination (TSD). Species with TSD are more abundant and are considered to be ancestral within the squamate reptiles\(^8\).

Our study is a continuation of a long-term project dedicated to experimental hybridization of eyelid geckos. *E. macularius* belongs among the species with TSD\(^9\). Although sex determination of the *E. angramainyu* has never been experimentally tested, we expect it to be TSD as well, similarly like the closely related *Hemithoeconyx caudicinctus*\(^9\). Moreover, the analysis of the karyotype in eyelid geckos revealed the absence of sex chromosomes\(^10\), which implies that the genome is the same in both sexes.

Preliminary results concerning the fitness indicators of F\(_1\) and F\(_2\) hybrids and backcrosses were published by J. Š. Š. Stein. It was demonstrated that M is able to hybridize with congeneric A and produces viable and fertile hybrids without apparent malformations. Moreover, the introgression of the *E. angramainyu* genes into the *E. macularius* genome is possible via backcrossing. To examine the real competitiveness of hybrids and backcrosses with parental species and consequent advantages of hybridization, the observation of growth parameters is crucial. Hybridization produces novel genotypes that may be able to outperform their parental species and persist in unoccupied niches if necessary. The individual fitness and the extent to which hybrids interact with their parents (e.g., assortative mating or differential habitat use) is essential for evolutionary consequences of hybridization.

Our results of growth parameters revealed that F\(_1\) hybrids are an intermediate form between the parental species (Fig. 4). The body growth of only one F\(_2\) hybrid was very poor with asymptotic body size smaller than the parental yellow population of *E. macularius* (M). Poor fitness of this F\(_2\) hybrid is in congruence with the whole poor hatchability (6%) and viability (25%) of F\(_2\) hybrids demonstrated previously\(^6\). The growth parameters unequivocally corroborated that the putative fitness losses affect more hybrids of F\(_2\) generation, which is
in accordance with the general Dobzhansky-Muller incompatibilities and empirical evidence. MAxM and MxMA backcrosses had better hatchability and survival rate than F₂ hybrids. The egg hatchability also dramatically differed between MAxA backcross and MAxM and MxMA backcrosses. While the latter one was possible to incubate (for details, see 43), the hatchability of the opposite backcrosses (MAxA) was zero, even though the females laid eggs regularly. This fact again points to some genetic incompatibilities.

Concerning the growth parameters, backcross MAxM did not differ in the asymptotic body size and growth rate from the MxMA backcross. The only difference was in the timing of the deceleration of the body growth. These backcrosses attained larger body size than the parental yellow population of *E. macularius*. In this case, the effect of hybridization on body growth was positive. It is expected that the advantages of hybridization for backcrosses exert in an increased heterozygosity, avoidance of the inbreeding depression and more successful occupation of new habitats.

Parental species of the yellow population of *E. macularius* and dark *E. sp.* differed in all of the growth parameters (all p < 0.01). Such a difference is in accordance with our prediction of genetic distinctiveness of these parental species. Hybridization of these two species reveals a similar effect on F₁ hybrids. The growth parameters a and T were intermediate, but the growth rate was close to the smaller *E. sp.* in F₁ hybrids. The success rate of gaining F₂ hybrids was better than in the hybridization of M with A. The growth parameters of F₂ hybrids were close to the F₁ hybrids. The distribution of *E. macularius* and *E. sp.* is most probably allopatric, but the sequence divergence is not as striking as in M vs. A. The growth parameters of backcrosses (MxMD) were not monitored; nevertheless, the egg hatchability was high (92%, Landová et al., in prep.)

The crossing of the white population of *E. macularius* (W) with dark *E. sp.* revealed intermediate values of growth parameters in F₁ and F₂ hybrids in comparison with the parental species. It was not possible to test exactly the differences among the F₁ and F₂ hybrids due to the low number of hybrids, but the mean values of estimated

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**Figure 2.** Mean body weight as a function of age predicted by the logistic growth model in studied species of eyelid geckos. Growth parameters were estimated from pooled records of either species/populations. Dotted curves are ±95 confidence intervals for means of studied species/populations. Abbreviations: (M) yellow population of *E. macularius*, (W) white population of *E. macularius*, (A) *E. angramainyu*, (D) dark population of *E. sp.*

**Figure 3.** Absolute body weight increments (aBWI) as a function of age (A) and relative body weight increments (rBWI) as a function of actual body weight for distinct species/populations (B). Abbreviations: (M) yellow population of *E. macularius*, (W) white population of *E. macularius*, (A) *E. angramainyu*, (D) dark population of *E. sp.*
growth parameters were comparable. Substantial differences in the results of hybridization of M/W with D were probably caused by the body size of the parental species (i.e., the body size of W is very similar to D).

In conclusion, we demonstrated that the growth parameters revealed by the three-parameter logistic regression model described the pattern of body growth of the studied species/populations of leopard geckos well. The pattern of body growth supports the "fast-slow" life-history continuum with species growing slowly but attaining large asymptotic body size and vice versa. Based on estimated growth parameters, it is possible to distinguish among these species/populations. We used this approach to study the effect of hybridization on fitness. We enriched our knowledge concerning the ability to hybridize in distinct species of the genus *Eublepharis*, which was previously observed in long-term geographic and evolutionary separated species of *E. macularius* and *E. angramainyu* by the additional experimental crossing of *E. macularius* with *E. sp*. The current approach tested competitiveness of *F*₁ and *F*₂ hybrids and backcrosses by comparison of their body growth parameters. Our results revealed that growth parameters are intermediate in both *F*₁ hybrids. The poor fitness of *F*₂ hybrid (*MAxMA*) is corroborating the outbreeding depression usually observed in *F*₂ and other segregating generations of between-species hybrids. However, the introgression of *A* genes into *M* genome is enabled via backcrossing. This fact employs natural hybridization into the concept of species adaptation and speciation. A similar pattern concerning the occurrence of fertile hybrids of distinct species may be also expected in other taxa of Squamata.

**Figure 4.** Mean body weight as a function of age predicted by the logistic growth model in parental species of the yellow population of *E. macularius* (M), the dark population of *E. sp.* (D), *F*₁ (MxD) and *F*₂ (MDxMD) hybrids. Growth parameters were estimated from pooled records of either species and the hybrids. Dotted curves are ±95 confidence intervals for means of studied groups. Note the growth curve of *F*₁ hybrids (*N* = 27), which is between the parental species’ curves and the poor growth of *F*₂ hybrid.

**Figure 5.** Mean body weight as a function of age predicted by the logistic growth model for parental species of the yellow population of *E. macularius* (M), the dark population of *E. sp.* (D), *F*₁ (MxD) and *F*₂ (MDxMD) hybrids. Growth parameters were estimated from pooled records of either species and the hybrids. Dotted curves are ±95 confidence intervals for means of studied groups. Note the growth curve of *F*₁ hybrids (*N* = 11) which are between the parental species’ curves.
Methods

Experimental animals and their maintenance. In the breeding stock of parental species, there were 51 E. macularius individuals of the yellow population (M), 40 E. macularius individuals of the white population (W), 6 individuals of large-bodied E. angramainyu (A), and 39 individuals of E. sp., which we further refer to as a dark population (D). Authors of the previous studies examining D geckos of the same stock considered the description of E. fuscus (Börner, 1981), and referred to this taxon, which is closely related to E. macularius sensu stricto, as E. cf. fuscus43,50,88.

The distribution of E. macularius covers large territories of Afghanistan, Pakistan, and India89, although a detailed distribution of the white and yellow form is not available. The B, W, and D populations were imported directly from unknown localities in Pakistan. E. angramainyu is native to Mesopotamia and SW Iran89, M and A are allopatric, their territories are separated by the Iranian Plateau and Zagros Mountains that are at least several million years old89. Thus, there was a long-lasting geographical isolation between E. macularius complex and E. angramainyu (cf. great sequence divergences between mitochondrial genes; uncorrected p-distances for 303 bp fragment of cyt b gene exceed 19%; Palupčíková, unpublished data).

All experimental parental species (M, W, D, and A) were the first generation of descendants of wild-caught animals. Parental A individuals were wild-caught as well, a putative locality of origin is Choqa Zanbil, Khuzestan province, Iran, 32°00'N 48°31'E, for more details about the locality see89.

The adult animals were housed individually in glass terrariums (60 × 30 × 20 cm or 30 × 30 × 20 cm, according to their body size). The floor of each cage was covered with bark substrate. Feeding and drinking dishes, as well as paper shelters, were provided. During the laying season, containers with adequately humid coconut substrate for egg deposition were added. The geckos were fed crickets and mealworms dusted with vitamins and minerals (Nutri Mix) weekly; AD3 and E vitamins were provided once per 14 days. The ambient temperature in the breeding room was about 28 °C with the permanent presence of basking sites in every terrarium to maintain a temperature gradient. During the egg-laying season (February to September), we checked the egg-deposition containers three times per week. The eggs were placed in the incubator and temperature was set to 28 ± 0.5 °C, which is the optimal and preferred temperature of E. macularius12,28,93. The incubation temperature of E. angramainyu was set lower (26 ± 0.5 °C) according to our previous experience with this species’ incubation. The hatchlings were housed individually in plastic boxes (20 × 20 × 15 cm) and were fed exclusively with crickets dusted with vitamins up to the three months of age.

To acquire F1 hybrids, females of the selected parental species/population were allowed to copulate with one breeding male of the second parental species/population. The resulting F1 hybrids were reared to sexual maturity and further bred to obtain F2 hybrids and/or backcrosses with either of the parental species. As the geckos of the studied genus Eublepharis can store sperm for several months, each experimental female was allowed to copulate exclusively with a single male during a given mating season (lasting from January/February to July/August). In contrast, males could copulate with multiple females within a single breeding season. From this hybridization, we got 68 viable F1 hybrids, 36 F2 hybrids, and 27 backcrosses.

All the individuals were weighed regularly by a digital balance to the nearest 0.01 g initially once per week (up to the age of 5 months), subsequently twice a month and later only once a month.

We studied the following thirteen categories of parental species/populations, their hybrids, and backcrosses that are further referred to as follows (the abbreviations are given in parentheses; there is always an abbreviation for a female followed by the one for a male with a cross (x) between:

1. M - a parental generation of the yellow population of E. macularius, both parents belong to the yellow population of E. macularius (M);
2. W - a parental generation of the white population of E. macularius, both parents belong to the white population of E. macularius (W);
3. A - a parental generation of E. angramainyu, both parents belong to E. angramainyu (A);
4. D - a parental generation of the dark population of the genus Eublepharis, both parents belong to this dark population (D);
5. MxA - the first-generation hybrid (F1), the mother of the yellow population of E. macularius (M) and the father of E. angramainyu (A);
6. MxD – the first-generation hybrid (F1), a mother of the yellow population of E. macularius (M) and a father of the dark population of E. sp. (D) grouped together with the mother of the dark population of E. sp. (D) and the father of the yellow population of E. macularius (M), we did not examine the mother’s identity effect;
7. WxD – the first-generation hybrid (F1), a mother of the white population of E. macularius (W) and a father of the dark population of E. sp. (D);
8. MxW – the first-generation hybrid (F1), a mother of the yellow population of E. macularius (M) and a father of the white population of E. macularius (W) grouped together with a mother of the white population of E. macularius (W) and a father of the yellow population of E. macularius (M), we did not examine the mother’s identity effect;
9. MxMA - the second-generation hybrid (F2), both parents are F1 hybrids of the yellow population of E. macularius and E. angramainyu (MxA);
10. MDxMD – the second-generation hybrid (F2), both parents are F1 hybrids of the white population of E. macularius and the dark population of E. sp. (MxD);
11. WxDxW – the second-generation hybrid (F2), both parents are F1 hybrids of the white population of E. macularius and the dark population of E. sp. (WxD);
12. MxM – the first-generation backcross with the yellow population of E. macularius, a mother is an F1 hybrid (MA) and a father belongs to the yellow population of E. macularius (M);
13. MxMA – the first-generation backcross with the yellow population of E. macularius (reciprocal to 12), a mother belongs to the yellow population of E. macularius (M) and a father is an F1 hybrid (MA).
Experiments were performed in accordance with the Czech law implementing all corresponding European Union regulations and were allowed by institutional Animal Care and Use Committee of the Charles University in Prague, and approved by Ethical Committee of Ministry of Education, Youth and Sports of the Czech Republic license no. 18147/203 and 24773/2008–10001.

Statistical methods. We applied a three-parameter logistic regression model (Equation 1) to analyse the growth trajectories of the overall sample of a given species, hybrids, backcrosses. We have previously found that this model fits very well the data covering the body growth of reptiles from hatching to adulthood. We used the Levenberg-Marquardt algorithm (with 1000 maximum number of iterations), which minimized the sum of squares between the predicted and observed growth values.

\[
\text{Body weight [grams]} = a/(1 + e^{-(K(age - T))})
\]

(1)

Growth parameter \(a\) predicts the asymptotic body size, parameter \(K\) estimates the growth rate, and the last one, parameter \(T\), expresses the age at the inflexion point (i.e., a place of the maximal growth rate where the growth curve changes from convex to concave and the individual growth rate starts decreasing). We set these parameters’ starting values as follows: \(a = 30\), \(K = 0.005\) and \(T = 150\). Growth equations were computed separately for each individual. As the number of females (290) highly exceeded the number of males (35) and the intersexual differences were much smaller than the interspecific ones, we pooled the data of both sexes in distinct groups for each species, hybrids, and backcrosses.

Interspecific differences in growth curve parameters were tested by a general linear model (ANOVA, post-hoc Tukey’s test for unequal N). The effect of growth rate and inflexion point on asymptotic body weight was tested by multiple regression separately for each group. All calculations were performed using STATISTICA, version 6.0.

In addition to the comparison of growth parameters revealed by the logistic regression model, we compared body weight increments from real measurements calculated as an absolute body weight increment (abWI = actual body weight - previous body weight) and a relative body weight increment (rbWI = abWI/actual body weight).

Data availability. All data generated or analysed during this study are included in this published article (and its Supplementary Information files).

References

1. Clark, T. D., Wang, T., Butler, P. J. & Frappell, P. B. Factorial scopes of cardio-metabolic variables remain constant with changes in body temperature in the varanid lizard Varanus rosenbergii. *American Journal of Physiology-Regulatory and Comparative Physiology* **288**, R992–R997, https://doi.org/10.1152/ajpregu.00593.2004 (2005).
2. Schmidt-Nielsen, K. Scaling: why is animal size so important? (Cambridge University Press, 1984).
3. West-Eberhard, M. J. Developmental plasticity and evolution. (Oxford Univ. Press, 2003).
4. Darwin, C. The descent of man and selection in relation to sex. J. 1st edn, (Murray, 1871).
5. Boback, S. M. Body size evolution in snakes: Evidence from island populations. *Copeia*, 81–94, https://doi.org/10.1643/0045-8511(2003)003[0808:beisie]2.0.co;2 (2003).
6. Fairbairn, D. J. Allometry for sexual size dimorphism: Pattern and process in the evolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**, 659–687, https://doi.org/10.1146/annurev.ecolsys.28.1.659 (1997).
7. Srinivasan, M. V. & Chisholm, W. R. Avian growth and development: evolution within the allometric-precoital spectrum. (Oxford University Press, 1998).
8. Guarino, F. M., Di Gaspero, A. & Zani, C. Age and growth of the sand lizards (Lacerta agilis) from a high Alpine population of northeastern Italy. *Acta. Herpetologica* **5**, 23–29 (2010).
9. Frynta, D. et al. Ontogeny of sexual size dimorphism in monitor lizards: Males grow for a longer period, but not at a faster rate. *Zoological Science* **27**, 917–923, https://doi.org/10.10110/ajps.27.917 (2010).
10. Roitberg, E. S. & Smirina, E. M. Age, body size and growth of Lacerta agilis boemica and L. striata: A comparative study of two closely related lizard species based on skeletalchronology. *Herpetological Journal* **16**, 133–148 (2006).
11. Hanelt, P. & John-Alder, H. B. Experimental and demographic analysis of growth rate and sexual size dimorphism in a lizard, Sceloporus undulatus. Oikos **96**, 70–81, https://doi.org/10.1034/j.1600-0706.2002.10915.x (2002).
12. Shine, R. & Charnov, E. L. Patterns of survival, growth, and maturation in snakes and lizards. *American Naturalist* **139**, 1257–1269, https://doi.org/10.1086/285385 (1992).
13. Dunham, A. E. Food availability as a proximate factor influencing individual growth rates in iguanid lizard Sceloporus merriami. *Ecology** 59**, 770–778, https://doi.org/10.2307/1938781 (1978).
14. Schoener, T. W. & Schoener, A. Estimating and interpreting body-size growth in some Anolis lizards. *Copeia*, 390–405, https://doi.org/10.2307/1443602 (1978).
15. Lester, N. P., Shuter, B. J. & Abrams, P. A. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society B: Biological Sciences* **271**, 1625–1631, https://doi.org/10.1098/rspb.2004.2778 (2004).
16. Ali, M., Niczey, A. & Wootton, R. J. Compensatory growth in fishes: a response to growth depression. *Fish and Fisheries* **4**, 147–190, https://doi.org/10.1046/j.1467-2979.2003.00120.x (2003).
17. Dutta, H. Growth in fishes. *Gerontology* **40**, 97–112 (1994).
18. Palohelmo, J. E. & Dickie, L. M. Food and growth of fishes I. A growth curve derived from experimental data. *Journal of the Fisheries Research Board of Canada* **22**, 521–525 (1965).
19. Parker, R. R. & Larkin, P. A. A concept of growth in fishes. *Journal of the Fisheries Research Board of Canada* **16**, 721–745 (1959).
20. Bertalanffy, L. von. Untersuchungen über die Gesetze des Wachstums. I. Allgemeine Grunlagen der Theorie; mathematische und physiologische Gesetzshheiten des Wachstums bei Wassertieren. *Arch. Entwicklungsmech.* **131**, 613–652 (1934).
21. West, G. B., Brown, J. H. & Enquist, B. J. A general model for ontogenetic growth. *Nature* **413**, 628–631 (2001).
22. Winsor, C. P. The Gompertz curve as a growth curve. *Proceedings of the national academy of sciences* **18**, 1–8 (1932).
23. Bennett, P. M. & Owens, I. P. F. Evolutionary ecology of birds: life histories, mating systems, and extinction. 1st edn, (Oxford University Press, 2002).
24. Stearns, S. C. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* **41**, 173–187, https://doi.org/10.2307/3544261 (1983).
25. Gaillard, J. M. et al. An analysis of demographic tactics in birds and mammals. *Oikos* **56**, 59–76, https://doi.org/10.2307/3566088 (1989).
26. Biely, J. et al. The fast-slow continuum in mammalian life history: An empirical reevaluation. American Naturalist 169, 748–757, https://doi.org/10.1086/516847 (2007).
27. Jones, O. R. et al. Senescence rates are determined by ranking on the fast-slow life-history continuum. Ecology Letters 11, 664–673, https://doi.org/10.1111/j.1461-0248.2008.01187.x (2008).
28. Coomber, P., Cresw, D. & Gonzalez Lima, F. Independent effects of incubation temperature and gonadal sex on the volume and metabolic capacity of brain nuclei in the leopard gecko (Eublepharis macularius), a lizard with temperature-dependent sex determination. Journal of Comparative Neurology 380, 409–421, https://doi.org/10.1002/cne.20380.3–0.aid-cncn8-3.0.co;2-6 (1997).
29. Cresw, D., Coomber, P., Baldwin, R., Azad, N. & Gonzalez Lima, F. Brain organization in a reptile lacking sex chromosomes: Effects of gonadectomy and exogenous testosterone. Hormones and Behavior 30, 474–486, https://doi.org/10.1016/S0018-506X(96)80051-6 (1996).
30. Cresw, D., Coomber, P. & Gonzalez Lima, F. Effects of age and socioeconomic sex on the morphology and metabolic capacity of brain nuclei in the leopard gecko (Eublepharis macularius), a lizard with temperature-dependent sex determination. Brain Research 758, 169–179, https://doi.org/10.1016/S0006-8993(97)00222-9 (1997).
31. Landová, E., Jančúchová-Lásková, J., Musilová, V., Kadochová, S. & Frynta, D. Ontogenetic switch between alternative antipredatory strategies in the leopard gecko (Eublepharis macularius): defensive threat versus escape. Behavioral Ecology and Sociobiology 67, 1113–1122, https://doi.org/10.1007/s00265-013-1536-3 (2013).
32. Landová, E., Musilová, V., Polák, J., Sedláčková, K. & Frynta, D. Antipredatory reaction of the leopard gecko Eublepharis macularius to snake predators. Current Zoology 62, 439–450, https://doi.org/10.1093/cz/ozw059 (2016).
33. Kratochvíl, L. & Frynta, D. Big brain, small body size: male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). Zoological Journal of the Linnean Society 76, 303–314, https://doi.org/10.1111/j.1095-8312.2002.tb02089.x (2002).
34. Kratochvíl, L. & Frynta, D. Body-size effect on egg size in eublepharid geckos (Squamata: Eublepharidae), lizards with invariant clutch size: negative allometry for egg size in ectotherms is not universal. Biological Journal of the Linnean Society 88, 527–532, https://doi.org/10.1095/1095-8312.2006.00627.x (2006).
35. Kratochvíl, L. & Frynta, D. Egg shape and size allometry in geckos (Squamata: Gekkota), lizards with contrasting eggshell structure: why lay spherical eggs? Journal of Zoological Systematics and Evolutionary Research 44, 217–222, https://doi.org/10.1111/j.1439-0489.2005.00339.x (2006).
36. Kratochvíl, L. & Frynta, D. Production-growth model applied in eublepharid lizards (Eublepharidae, Squamata): accordance between growth and metabolic rates. Folia Zoologica 52, 317–322 (2003).
37. Lee, R. M. Age and growth determination in fishes. Cambridge University Press, 1971.
38. Lee, R. M. An investigation into the methods of growth determination in fishes by means of scales. Transactions of the American Fisheries Society 89, 309–317, https://doi.org/10.1080/00028487.1960.10513392 (1960).
39. Lee, R. M. Production-growth model applied in eublepharid lizards (Eublepharidae, Squamata): accordance between growth and metabolic rates. Folia Zoologica 52, 317–322 (2003).
40. Life, F. M. & Arnold, M. L. Genetics and the fitness of hybrids. Annual Review of Genetics 35, 31–52, https://doi.org/10.1146/annurev.genet.35.100201.085719 (2001).
41. Scolithiuzen, G., Giebers, M. & Beukeboom, L. W. Haldane’s rule in the 21st century. Heredity 107, 95–102, https://doi.org/10.1038/hdy.2010.170 (2011).
42. Chen, Z. J. Genomic and epigenetic insights into the molecular bases of heterosis. Nature Reviews Genetics 14, 471–482, https://doi.org/10.1038/nrg3503 (2013).
43. Jančúchová-Lásková, J., Landová, E. & Frynta, D. Are genetically distinct lizard species able to hybridize? A review. Current Zoology 61, 155–180 (2015).
44. Maye, E. Animal species and evolution. 1st edn, (The Belknap Press, 1963).
45. Abbott, R. et al. Hybridization and speciation. Journal of Evolutionary Biology 26, 229–246, https://doi.org/10.1111/j.1420-9101.2012.02599.x (2013).
46. Dittrich-Reed, D. R. & Fitzpatrick, B. M. Transgressive hybrids as hopeful monsters. Evolutionary Biology 40, 310–319, https://doi.org/10.1007/s11692-012-9209-0 (2013).
47. Willis, P. M. Why do animals hybridize? Acta Ethologica 16, 127–134, https://doi.org/10.1007/s10432-013-0144-6 (2013).
48. de Verdial, H. et al. Response to selection for growth in an interspecific hybrid between Oresochromis mossambicus and O. niloticus in two distinct environments. Aquaculture 430, 159–165, https://doi.org/10.1016/j.aquaculture.2014.03.051 (2014).
49. Hatfield, T. & Schütz, D. Ecological speciation in sticklebacks: Environment-dependent hybrid fitness. Evolution 53, 866–873, https://doi.org/10.1111/j.2364-3621.1999.tb03376.x (1999).
50. Ryll, S. Experimental hybridization in green lizards (Lacerta s. str.), a tool to study species boundaries. Herpetologica 113, 78–88 (2002).
51. Kratochvíl, L. & Kubicka, L. Why reduce clutch size to one or two eggs? Reproductive allometries reveal different evolutionary causes of invariant clutch size in lizards. Functional Ecology 21, 171–177, https://doi.org/10.1111/j.1365-2435.2006.01202.x (2007).
52. Lee, R. M. An investigation into the methods of growth determination in fishes by means of scales. ICES Journal of Marine Science 1, 3–34, https://doi.org/10.1093/icesjms/sfj03.1 (1932).
53. Lee, R. M. Age and growth determination in fishes. Nature 106, 49–51 (1920).
54. Taylor, L. G. & Methot, R. D. Hiding or dead? A computationally efficient model of selective fisheries mortality. Fisheries Research 142, 75–85, https://doi.org/10.1016/j.fishres.2012.08.021 (2013).
55. Czernecki, M. & Rybczyk, A. Tanski, A., Kesza, S. & Antoszek, A. Growth rate and condition of Vimba, Vimba vimba (Actinopterygii: Cypriniformes: Cyprinidae), a species under restoration in the Odra river estuary. Acta Ichthyologica Et Piscatoria 31, 215–222, https://doi.org/10.3755/ap.2011.11.3.09 (2011).
56. Fossen, I., Albert, O. T. & Nilsen, E. M. Back-calculated individual growth of long rough dab (Hippoglossoides platessoides) in the Barents Sea. Ices Journal of Marine Science 56, 689–696, https://doi.org/10.1080/0165-7195.2019.1645380 (2019).
57. Walker, T., Taylor, B. L., Hudson, R. J. & Cottier, J. P. The phenomenon of apparent change of growth rate in gummy shark (Mustelus antarcticus) harvested off southern Australia. Fisheries Research 39, 139–163, https://doi.org/10.1016/S0165-7186/98/00380-5 (1998).
58. Bradshaw, S. D. Growth and mortality in a field population of Amphibolurus lizards exposed to seasonal cold and aridity. Journal of Zoology 165, 1–8 (1971).
63. Eklund, J. & Bradford, G. E. Longevity and lifetime body-weight in mice selected for rapid growth. *Nature* 265, 48–49, https://doi.org/10.1038/265048a0 (1977).

64. Mangel, M. & Stamps, J. Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research* 3, 583–593 (2001).

65. Ölsner, M. & Shine, R. Growth to death in lizards. *Evolution* 56, 1867–1870 (2002).

66. Fejfarová, P. et al. Morphological characteristics of blood cells in monitor lizards: is erythrocyte size linked to actual body size? *Integrative Zoology* 8, 39–45, https://doi.org/10.1111/j.1749-4877.2012.00295.x (2013).

67. Lui, J. C. & Baron, J. Mechanisms limiting body growth in mammals. *Endocrine Reviews* 32, 422–440, https://doi.org/10.1210/er.2011-0001 (2011).

68. Cox, R. M. & John-Alder, H. B. Testosterone has opposite effects on male growth in lizards (*Sceloporus* spp.) with opposite patterns of sexual size dimorphism. *Journal of Evolutionary Biology* 208, 4679–4687, https://doi.org/10.1111/jeb.01948, 10.1111/j.1420-9101.2009.01772.x (2005).

69. Cox, R. M., Stenquist, D. S. & Calabrek, R. Testosterone, growth and the evolution of sexual size dimorphism. *Journal of Evolutionary Biology* 22, 1586–1598 (2009).

70. Starostova, Z., Kubíčka, L., Golinski, A. & Kratochvíl, L. Neither male gonadal androgen nor female reproductive costs drive development of sexual size dimorphism in lizards. *Journal of Experimental Biology* 216, 1872–1880, https://doi.org/10.1242/jeol.079442 (2013).

71. Kubíčka, L., Golinski, A., John-Alder, H. & Kratochvíl, L. Ontogeny of pronounced female-biased sexual size dimorphism in the Malaysian cat gecko (*Aechoroscalabates felinus*: Squamata: Eublepharidae): a test of the role of testosterone in growth regulation. *General and Comparative Endocrinology* 188, 183–188, https://doi.org/10.1016/j.ygcen.2013.03.016 (2013).

72. Kubíčka, L., Starostova, Z. & Kratochvíl, L. Endogenous control of sexual size dimorphism: Gonadal androgens have neither direct nor indirect effect on male growth in a Madagascan ground gecko (*Paroedura picta*). *General and Comparative Endocrinology* 224, 273–277, https://doi.org/10.1016/j.ygcen.2015.09.028 (2015).

73. Kubíčka, L., Schořálková, T., Cervenka, J. & Kratochvíl, L. Ovarian control of growth and sexual size dimorphism in a male-larger gecko. *Journal of Experimental Biology* 220(5), 787–795, https://doi.org/10.1242/jeb.146597 (2017).

74. Prüfer, C. & Frézal, J. Facultative mate choice drives adaptive hybridization. *Science* 318, 965–967, https://doi.org/10.1126/science.1146035 (2007).

75. Bosworth, S. B. & Waldhuis, G. General and specific combining ability of male and female blue catfish (*Ictalurus punctatus*) and fork-tailed catfish (*Ictalurus furcatus*) for growth and carcass yield of their F1 hybrid progeny. *Aquaculture* 420, 147–153, https://doi.org/10.1016/j.aquaculture.2013.10.026 (2014).

76. Yan, B. A. & Wang, Z. H. Growth, salinity tolerance and microsatellite analysis of the F2 reciprocal hybrids of *Oreochromis niloticus* and *Oreochromis aureus* at different salinities. *Aquaculture Research* 41, e336–e344, https://doi.org/10.1111/j.1365-2109.2010.02542.x (2010).

77. Johnson, J. B., Macedo, D. C., Passow, C. N. & Rosenthal, G. G. Sexual ornaments, body morphology, and swimming performance in naturally hybridizing swordtails (*Teleostei: Xiphophorus*). *Plos One* 9, https://doi.org/10.1371/journal.pone.0109025 (2014).

78. Odierna, G. et al. Evolutionary and biogeographical implications of the karyological variations in the oviparous and viviparous forms of the lizard (*Lacerta*: *Zootoca*) vivipara. *Ecography* 24, 322–340, https://doi.org/10.1111/j.1095-8312.2000.tb01208.x (2000).

79. Pokorná, M. & Kratochvíl, L. Phylogeny of sex-determining mechanisms in squamate reptiles: are sex chromosomes an evolutionary trap? *Zoo Journal of the Linnean Society* 156, 168–183, https://doi.org/10.1111/j.1096-3642.2008.00481.x (2009).

80. Wagner, E. Temperature-dependent sex determination in a ginkgo lizard. *Quarterly Review of Biology* 55, 21 (1980).

81. Pokorná, M. et al. Differentiation of sex chromosomes and karyotypic evolution in the eye-lid geckos (*Squamata*: *Gekkota*: *Eublepharidae*), a group with different modes of sex determination. *Chromosoma Research* 18, 809–820, https://doi.org/10.1007/s00432-010-09154-7 (2010).

82. Dobzhansky, T. H. Studies on hybrid sterility. II. Localization of sterility factors in *Drosophila pseudoobscura* hybrids. *Genetics* 21, 113 (1936).

83. Dobzhansky, T. & Dobzhansky, T. G. *Genetics and the Origin of Species* (Vol. 11). (Columbia University Press, 1937).

84. Muller, H. J. Isolating mechanisms, evolution and temperature. *Biol. Symp. 6*, 185–268 (1942).

85. Muller, H. J. Bearing of the *Drosophila* work on systematics. *The New systematics*, 185–268 (1940).

86. Turelli, M. & Orr, H. A. Dominance, epistasis and the genetics of postzygotic isolation. *Genetics* 154, 1663–1679 (2000).

87. Arnold, M. L. Natural hybridization and evolution. *Oxford University Press*, 1997.

88. Starostová, Z., Kratochvíl, L. & Fajšhans, M. Cell size does not always correspond to genome size: Phylogenetic analysis in geckos. 89. Fejfarová, P. et al. Morphological characteristics of blood cells in monitor lizards: is erythrocyte size linked to actual body size? *Integrative Zoology* 8, 39–45, https://doi.org/10.1111/j.1749-4877.2012.00295.x (2013).

89. Lui, J. C. & Baron, J. Mechanisms limiting body growth in mammals. *Endocrine Reviews* 32, 422–440, https://doi.org/10.1210/er.2011-0001 (2011).

Author Contributions
D.F. and E.L. conceptualized and designed the project. D.F. provided the material. J.J.L. was responsible for data collection and curation. D.F., P.F. and J.J.L. analysed the data. P.F. prepared the figures. D.F. and E.L. obtained funding acquisition. P.F. and D.F. wrote the original manuscript. All authors reviewed the draft.

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