



The limits of the energetical perspective: life-history decisions in lizard growth

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Abstract

The study of energy allocation is essential in understanding the regulation of major life history traits. It is often assumed automatically that the limitation of an energy budget or higher allocation to a single trait affect all life history traits. This assumption was inherently included in influential models of ontogenetic growth. We aim to challenge this perspective by focusing on growth in lizards. Summarizing the results of a series of long-term manipulative experiments in the Madagascar ground gecko (*Paroedura picta*), we show that although growth is generally assumed to be highly plastic in reptiles and other ectothermic vertebrates, it is at least in this species largely canalized and does not seem to be affected by energy limitations under several experimental conditions. Diet restriction, resulting in lower allocation to fat storage and reproduction, and the allocation to energetically demanding traits such as reproduction in both sexes and tail regeneration had little if any effect on structural growth. We document that sexual size dimorphism does not emerge in the ontogeny of the studied species directly due to differential allocation to structural growth in males and females. Instead, sex-specific growth trajectories are driven by a signaling of ovarian hormones as the key proximate mechanism shaping sex-specific allocation decisions during ontogeny. We suggest that the large degree of canalization of the structural growth can reflect hierarchy in energy allocation with the structural growth being prioritized to investment in other traits. The prioritized allocation to structural growth can reflect selective advantage of reaching a final, optimal size for a given sex as fast as possible.

Keywords Growth · Energy · Trade-offs · Gonadal hormones · Sexual size dimorphism · Reptiles

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Direct split of energy: an untested assumption of growth models

The study of energy in living organisms is essential for understanding the regulation of major life history traits such as growth and reproduction. All living organisms have a limited amount of allocable energy, which force them to optimize allocation to energetically demanding life-history traits such as growth, maintenance and reproduction (Stearns 2000; West et al. 2001; Taborsky 2017). The concept of such energy allocation trade-offs is widespread in evolutionary ecology (Angilletta et al. 2003) and we can hardly imagine an alternative to it. Nevertheless, it is often assumed automatically that the limitation of an energy budget or higher allocation to a single trait affects all other life history traits. Several models that tried to describe the ontogenetic growth trajectories from the energetical perspective are based on this rarely tested assumption (von Bertalanffy 1957; West et al. 2001; Martin et al. 2019; Sibly and Brown 2020). In other words, these growth models assumed that ontogenetic growth is very phenotypically plastic and that changes in growth are directly affected by allocation to other traits, mainly to reproduction. For example, the general model by West et al. (2001) suggests that acquired energy related to metabolic rate is split into three components: to the maintenance of existing tissue, the replacement of cells and the formation of new tissue. According to this model, a substantial portion of energy is later in ontogeny allocated to reproduction, which is accompanied directly due to energy limitations with a reduction in growth (West et al. 2001). Similar logic was also applied to explain the ontogeny of sexual size dimorphism (SSD), i.e. differences in size between the sexes. The so called “reproductive cost” hypothesis states that allocation to growth should be smaller in the sex with higher reproductive cost (Cox 2006), i.e. that the amount of energy allocated to reproduction is directly traded-off with the allocation to growth.

The idea that ontogenetic growth is plastic with respect to the total energy budget or to the amount of energy allocated to reproduction and other energetically demanding traits is so appealing that it is in fact rarely tested. It has straightforward predictions: growth and hence final body size should correlate with the total amount of available energy and with the allocation to other energetically demanding processes such as reproduction and tissue regeneration. Nevertheless, we realized in the series of growth experiments in the model lizard species Madagascar ground gecko, *Paroedura picta* (Peters, 1854), that these intuitive predictions are not followed. Here, we summarized the observed effect of manipulations with diet, allocation to reproduction and tissue regeneration on structural growth, i.e. increase in snout-vent length (SVL) reflecting skeleton dimensions, in this species. As typical reptile with “indeterminate growth”, *P. picta* mature at a size representing a small fraction of its final body size (males can mature at the body mass of c. 3 g and continue to final body mass of 35–40 g, females mature at about 4 g and their final mass is around 15–19 g; own data). An enormous fraction of postembryonic growth in this species thus proceeds after the start of reproduction, which is convenient for the manipulative growth experiments focused on energy allocation. We provide insights into the proximate control of sex-specific growth trajectories and suggests an explanation at the ultimate level, why the predictions based on direct differential allocation were not followed.

Sexual dimorphism in growth is not directly related to allocation to reproduction

One field where an energetical perspective on the control of growth became prevalent is the ontogeny of SSD. SSD in body size is widespread in animals including reptiles and male- or female-biased SSD can be found across taxa, sometimes even closely related species being at the opposite side of the spectrum (Cox et al. 2007). For instance, our model species *P. picta* experiences male-biased SSD while the closely related species *P. vazimba* and *P. androyensis* are female larger (Starostová et al. 2010). The “reproductive cost” hypothesis based on an energetical perspective states that a trade-off between reproduction and growth due to the high energetical cost of reproduction is at the core of SSD development. This hypothesis was tested mostly in reptiles with male-biased SSD (Cox 2006), but it can also be relevant for species with female-biased dimorphism since the cost of reproduction has been found for both sexes across taxa (Hayward and Gillooly 2011).

In male-larger species, the “reproductive cost” hypothesis was traditionally tested by removing female allocation to reproduction by ovariectomy, which should remove the energetical cost of reproduction and therefore lead to higher allocation to growth. Higher growth rate and/or larger structural body in females comparable to male-typical pattern was indeed observed in ovariectomized females in the Yarrow’s spiny lizard, *Sceloporus jarrovi* (Cox 2006), brown anole, *Anolis sagrei* (Cox and Calsbeek 2010; Cox et al. 2014) and the Madagascar ground gecko *P. picta* (Starostová et al. 2013; Kubička et al. 2017; schematically depicted in Fig. 1), which could be taken (and often was) as support for the “reproductive cost” hypothesis (Cox 2006; Cox and Calsbeek 2010). As characteristic for geckos, *P. picta* lay maximally two eggs per clutch, but the clutches are very frequent in this species leading to enormous reproductive effort (Kubička and Kratochvíl 2009; Kubička et al. 2012; Starostová et al. 2012). The idea that non-reproducing females allocate saved energy to growth is thus seemingly supported.

However, Starostová et al. (2013) also used social isolation as another way of blocking energy allocation to egg production next to ovariectomy in *P. picta* as females of this species do not produce eggs if they do not have access to sperm. Surprisingly, females in reproductive isolation did not differ in growth trajectory in SVL and in final SVL from regularly reproducing females (Fig. 1), which suggests that the female reproductive cost is not responsible for the ontogeny of SSD in this species.

These authors suggested that ovariectomy removed not only reproductive cost but also production of ovarian hormones, which can drive females to female-typical growth trajectory leading to decreased final SVL directly, not via allocation to reproduction. A follow up study by Kubička et al. (2017) extended the test of the “reproductive cost” and “ovarian hormone” hypotheses. They found that contrary to the predictions of the “reproductive cost” hypothesis, unilaterally ovariectomized females that produced around half of eggs in comparison to sham operated females while maintaining normal hormonal cycling, reached a comparable final size in terms of SVL via the same growth trajectory as control sham operated females (Fig. 1). Moreover, ovariectomized females of *P. picta* receiving exogenous estradiol reached a smaller size, which suggests that female growth can be suppressed by gonadal estrogens (Kubička et al. 2017).

Manipulations in males also found little support for the “reproductive cost” hypothesis. Sperm production is energetically demanding and can be restricted by metabolic rate and total available energy (Hayward and Gillooly 2011). Removal of allocation to gonads in growing males should thus lead to higher allocation to structural growth.

However, growth rate and final SVL in males of *P. picta* was not affected by castration both under constant temperature (Starostová et al. 2013) and in a thermal gradient (Kubička et al. 2015) (Fig. 1). These results also suggest that male gonadal androgens are not responsible for the increased growth in males in comparison to females and by extension for the ontogeny of SSD in *P. picta*. Control of male growth by male gonadal androgens was suggested as a major mechanism of evolutionary changes in SSD in squamate reptiles (Cox et al. 2005, 2009). The evidence for masculinized growth by the application of exogenous androgens in females was initially taken as a support for the control of SSD ontogeny by male gonadal androgens (Cox et al. 2009). However, this assumption has been challenged as it is not consistent with the lack of the effect of castration on growth in males *P. picta* (Kubička et al. 2015) and other lizard species (Kubička et al. 2013; Bauerová et al. 2020). Equally as ovariectomy, application of exogenous androgens likely causes defeminization, i.e. the suppression of the development of female-typical morphology via interference with normal ovarian hormonal production, not masculinization of female growth trajectory (Starostová et al. 2013). The agreement of various, mutually complementary experimental data (schematically presented in Figs. 1 and 2) implies that SSD in *P. picta* is caused by suppressed growth in females, which cannot be attributed to their high allocation to reproduction but is likely driven by ovarian hormones as the key proximate mechanism switching between sex-specific growth trajectories.

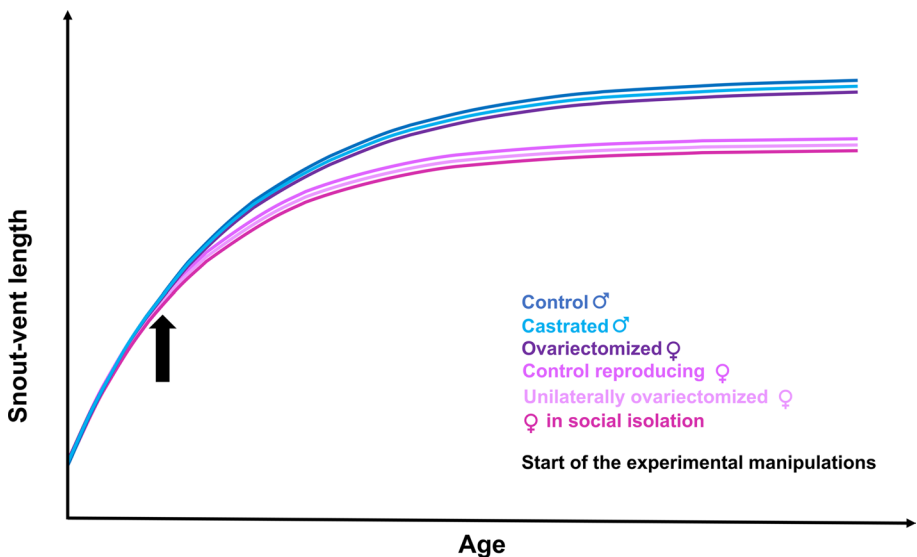


Fig. 1 Schematic depiction of postembryonic structural growth trajectories in accordance to sex and treatment in *Paroedura picta*. Only ovariectomy affects female growth and final snout-vent length likely causing defeminization in absence of hormones produced by ovaries. All other experimental treatments depicted fail to affect the growth of experimental animals. Arrow indicates the start of experimental manipulations. Schematic growth depiction for experimental groups (from above): control males, castrated males, ovariectomized females, control reproducing females, unilaterally ovariectomized reproducing females, females in social isolation

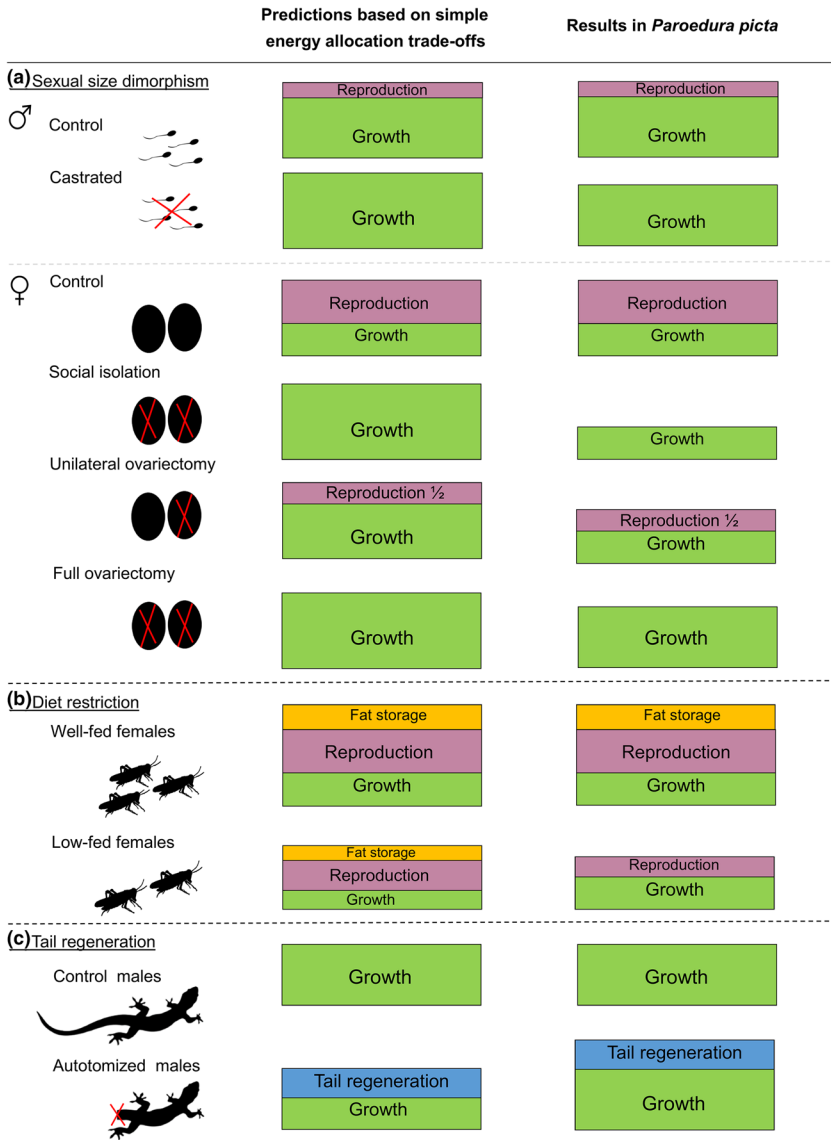


Fig. 2 Summary of the results from case studies in *Paroedura picta* that show that growth does not seem to be influenced by variations in allocable energy. **a** The “reproductive cost” hypothesis predicts that removal of the costs of reproduction should lead to higher allocation to growth in both sexes. However, castrated males attained the same size as non-castrated control males (Starostová et al. 2013). Socially isolated non-reproducing females and females with highly decreased allocation to reproduction due to unilateral ovariectomy maintained similar body size (SVL) and growth rate as control regularly egg-laying females (Kubička et al. 2017). Only full ovariectomy led to higher allocation to structural growth in females, which indicates that ovarian hormones, not directly allocable energy, controls ontogeny of sexual size dimorphism via negative effect on growth in females (Kubička et al. 2017). **b** In the case of food restriction, we expected that restricted diet would lead to reduced allocation to reproduction, growth and fat storage. However, structural growth was not affected by food limitations, which reduced only allocation to reproduction and fat storage (Kubička and Kratochvíl 2009). **c** The simple energy allocation trade-off predicts that growth should be decreased in the lizards during tail regeneration. Nevertheless, geckos with and without growth regeneration had similar growth rates and reached similar structural body size (Starostová et al. 2017). Silhouette images were taken and modified from: <https://pixabay.com/>

Food restriction: limited reproduction and fat storage, but not structural growth

Energy allocation to growth and reproduction was studied in females of *P. picta* also through restriction of allocable energy via manipulation with food quantity (Kubička and Kratochvíl 2009). Two balanced groups of young, still growing females kept at different food levels were followed for six months until cessation of growth. The expectation based on direct differential allocation was that the limited energy intake would impair growth rate and possibly final structural body size represented by final SVL (Fig. 2). Nevertheless, females on a restricted diet maintained growth rate and attained the same final SVL as females with higher food intake (Kubička and Kratochvíl 2009). They did however compromise on their reproduction. Females on the restricted diet laid smaller eggs in longer intervals. Diet restriction also led to the lower body mass and thus fat reserves when compared to females with higher food intake. A trade-off between growth and reproduction does not seem to occur in its simplest form here with an expected allocation compromise between these processes. In this case study, the allocation to structural growth was clearly more canalized than allocation to reproduction.

Little effect of energy limitation through tail autotomy on structural growth

Another factor that should affect the allocable energy to life history traits is tail autotomy, a widespread defence strategy of a vast number of lizard species, which is commonly followed by tail regeneration (Arnold 1988; Bateman and Fleming 2009). By shedding a tail lizards can lose a substantial proportion of body mass (Jagnandan and Higham 2018) and possibly also an energy reserve since tails are an important organ for fat storage (Pond 1978; Paz et al. 2019). Tails also need to be regenerated since they are important for locomotion and balance (Gillis et al. 2009; Gillis and Higham 2016; Jagnandan and Higham 2018) as well as social interaction (Fox et al. 1990; Martín and Salvador 1993). The energetical cost of tail regeneration can come to the expense of growth (Ballinger and Tinkle 1979; Niewiarowski et al. 1997; Lynn et al. 2013) or reproduction (Dial and Fitzpatrick 1981; Wilson and Booth 1998; Chapple et al. 2002), but the support is ambiguous (e.g., Fox and McCoy 2000; Goodman 2006; Webb 2006). In a study on *P. picta*, the cost of tail regeneration in growing juvenile males was evaluated (Starostová et al. 2017). Tail autotomy was induced in juvenile, approximately four months old males still in the phase of rapid growth and their growth was followed and compared to intact control group for more than five months. The prediction based on a simple direct differential energy allocation was that the growth rate and final SVL of the juveniles that suffered tail autotomy would be hindered compared to intact juveniles (Fig. 2). However, tail autotomy and its subsequent regeneration did not affect structural growth and resulted in a similar SVL. Furthermore, mass-corrected metabolic rate was not significantly affected by tail loss and allocation to regeneration. It seems that fast growing juveniles can compensate tail autotomy at least under unrestricted food conditions without a notable change in mass-specific metabolic rate. Future studies should test whether the same pattern would be observed also under food limitation.

Structural growth is still plastic with respect to temperature

The above discussed findings suggested that structural growth represented by change in SVL during the postembryonic ontogeny in *P. picta* is less phenotypically plastic than generally assumed under manipulation with energetically demanding processes. But, is it plastic with respect to other factors than energy allocation? Considering ectotherms, i.e. animals that rely on external sources for body heat, a clearly essential factor influencing structural growth is environmental temperature. The Temperature size rule states that ectotherms develop faster but mature at smaller body sizes at higher temperatures whereas ectotherms maintained at low temperatures grow more slowly, but attain a larger final body size (Atkinson 1994; Zuo et al. 2012). Temperature has indeed a strong influence on growth in *P. picta* (Starostová et al. 2010). Animals incubated and reared until cessation of growth under three different environmental temperatures did not follow the Temperature size rule, but body size in terms of SVL was higher especially in males at the intermediate temperature (Starostová et al. 2010). The effect of temperature at least in *P. picta* does not operate via changes in number of trunk vertebrae (Kratochvíl et al. 2018), but partially via influence on cell size at least in some tissues (Czarnoleski et al. 2017). The influence of temperature on growth and final body size in animals was considered as an energy allocation problem (Zuo et al. 2012); however, this hypothesis deserves further attention and seems less likely taking into account that growth responses of *P. picta* to manipulation with energetically demanding processes are rather limited.

Why is growth highly canalized when facing energy limitations?

Being indoctrinated by the simple energy allocation perspective before we conducted these growth studies introducing both decreased and increased demands of other energetically demanding processes, we did not expect that growth would be so canalized with respect to manipulations affecting energy and were ever surprised by the results. The growth experiments challenged the idea of simple direct allocation of growth versus other energetically demanding processes (summarized in Fig. 2). Growth was affected neither by reduced energy uptake through food restriction (Kubička and Kratochvíl 2009) nor by hindering the energy balance during growth through tail autotomy and regeneration (Starostová et al. 2017). By extension, simple trade-offs in energy allocation between growth and reproduction was not supported by studies in *P. picta* (Kubička and Kratochvíl 2009; Starostová et al. 2013; Kubička et al. 2017).

The inherent insignificant role of simple energy allocation in the case of growth in *P. picta* is even more evident when comparing the role of energy in another life history trait, reproduction. Reproduction was found to be more sensitive to allocable energy in the study on food restriction (Kubička and Kratochvíl 2009). This difference in variation between growth and reproduction is also highlighted through a substantial difference in environmental plasticity. Reproduction in *P. picta* is also heavily influenced by temperature (Starostová et al. 2012). Overall, females at higher temperatures produced smaller eggs which is consistent with the pattern found in ectotherms (e.g., Blanckenhorn 2000; Oufiero et al. 2007), and rate of reproduction (amount of energy allocated to reproduction per unit of time) was smaller for females at the lowest of the tested

temperatures (Starostová et al. 2012). The plasticity of growth regarding temperature is clearly less significant than in reproduction indicating the more plastic nature of reproduction compared to growth.

Why do the predictions from differential energy allocations fail so much (Fig. 2)? The structural growth rate and final SVL has some capability for phenotypic plasticity as exemplified by manipulations with rearing temperature described above. Also, structural growth trajectories can be shaped in *P. picta* by hormonal manipulations bringing further evidence that growth trajectories are not totally fixed. So, why is structural growth to a high extent canalized with respect to changes in an energy budget, even more so when compared to reproductive traits? One possible explanation is that selection in geckos and possibly other lizards is preferring the allocation rules prioritizing structural growth to other traits such as reproduction, fat storage and regeneration. It is possible that the allocation to particular traits is not totally mutually plastic as commonly assumed under the intuitive logic of “higher allocation to reproduction means less allocation to growth”, but that the allocation of energy followed a hierarchical rule with the priority given to structural growth. This hypothesis was suggested by Kubička and Kratochvíl (2009) interpreting the results of their food limitation experiment. They concluded that energy is allocated to reproduction only after demands of structural growth are fulfilled, and to fat storage only when the maximal possible allocation to reproduction was achieved.

The degree of phenotypic plasticity, more specifically canalization (e.g., Walzer and Schausberger 2014), should reflect selective pressures. Canalization—no matter whether against environmental or genetic perturbations—should evolve when there is a stabilizing selection on a trait value (Stearns and Kawecki 1994). At the current stage of knowledge, we can only speculate why structural growth should be prioritized in *P. picta* over other traits. Body size is a crucial fitness-related trait and as such it should be optimized. Body size is connected with food intake—in a gape limited predators like geckos body size determines maximal and minimal prey size (Daza et al. 2009), antipredator strategies (Roth and Johnson 2004), dealing with competitors (Pafilis et al. 2009) and optimal reproductive performance, e.g. due to positive egg size-body size relationship demonstrated in geckos (Kratochvíl and Frynta 2006) and other reptiles (e.g. Escalona et al. 2018). Reaching an optimal size as fast as possible for a given ecological niche and keeping it as long as possible throughout life span might be important. Of course, reptiles including *P. picta* start reproduction well before reaching the final/close to asymptotic structural body size. This hypothesis trying to explain the canalization of allocation to structural growth expects that the performance, including reproductive performance, should be suboptimal before the period of the cessation of growth. We welcome tests of this hypothesis in the future.

The optimal size could be sex-specific, e.g. due to sexual selection or other sex-specific roles (Darwin 1871; Cox et al. 2003; Fairbairn et al. 2007). Males of *P. picta* are highly combative (Golinski et al. 2014; Schořálková et al. 2018) and intrasexual selection can thus be a selective force responsible for male-larger SSD in this species. At the proximate level, it seems that males in this species are not larger because females do not have enough energy for growth as they allocate more to reproduction, but because each sex has their own optimal trajectory of ontogenetic structural growth. Gonadal hormones, particularly ovarian hormones seem to be the signal to cells in the body which of these trajectories should be followed during the ontogeny (Starostová et al. 2013; Kubička et al. 2017).

Limits of our approach

We acknowledge the limits for generalizations brought by focusing on one species. However, in this review we chose to focus on a well-studied—and hopefully not too special and exceptional—gecko since we considered it would help to tell a complex story as best as possible and at the same time to control several potentially confounding issues. While we have attempted to add arguments from other species, we found such parallels between species to be harder to establish, as we doubt that there is another species where similar manipulative long-term growth experiments were performed under so many treatments under so similar conditions, and partial studies (e.g. only a test of the effect of tail autotomy on growth in one species, but of the removal of the allocation to female reproduction in the other) might be confounded by differences in life-history decisions and other aspects of species biology. Although we tried to analyze as many parameters as possible in our growth experiments, we are aware that these studies are not complete. For example, activity has been found to influence distribution of energy and the expression of life history traits such as reproduction or immunity (Lailvaux and Husak 2014; Husak and Lailvaux 2017; Husak et al. 2017), but it was mostly not considered in our experiments. We only found that castrated and control males did not differ in the activity in the open field test performed in the neutral arena (Kubička et al. 2015), but we lack data for other experiments. As all treatment groups in each of our former experiments were held in the same environment (the same thermal environment, social isolation, the same size and equipment of cages) and hence likely possessed similar activity patterns, it is not very likely that the difference in the activity pattern would explain the notable lack in the response in the structural growth. In the case of different activity pattern among treatment group, groups would have to precisely counterbalance the allocation to growth with differences in activity, which seems unlikely. However, the energetical cost of activity and its influence on other life history traits such as growth and reproduction should be more explored in the future. As natural conditions certainly are more demanding for energy intake than conditions in the laboratory, it will be important to do more energetically focused research on growth also in the field, which will be especially important to elucidate the evolutionary context of growth canalization observed by us in the laboratory experiments.

Conclusions and future perspectives

Overall, we documented that although structural growth has some potential to be plastic and it is sexually dimorphic in *P. picta*, it is at the same time to a large degree canalized with respect to an energy budget. This pattern is consistent with the idea that structural growth is carefully regulated and that allocation to it is prioritized to other life history traits, most importantly to reproduction. Importantly, this observation challenges the general growth models based on dynamic energy budgets as they assume that the limitation of an energy budget or higher allocation to a single trait—mostly to reproduction—affects all other life history traits (von Bertalanffy 1957; West et al. 2001) and neglect that there might exist a strict hierarchical rules shaped by selection for priority allocation of metabolized energy to structural growth (or other traits). The simplified energetical perspective became also influential in macroecology being claimed responsible for major ecological rules in the so called “metabolic theory of ecology” aiming to quantify the processes of acquisition

and use of resources, to explain different biological patterns of life history traits such as growth (Brown et al. 2004; Martin et al. 2019). However, the recent large-scale comparison across eukaryotes suggests that metabolism and thus energy income is not necessarily at the core control of biomass increase (Hatton et al. 2019). Hatton et al. (2019) propose that instead of a fundamental metabolic control and limitation of growth, metabolism adjusts to growth (understood there as a maximum population growth rate, i.e. intrinsic growth rate, multiplied by individual adult body mass) within major groups, which agrees with here advocated perspective that a simple and intuitive energy allocation rule is not operating at the individual level and that growth is carefully regulated endogenously. We argue that this endogenous control reflects past selective pressures shaping the structure of allocation rules. Future growth models should incorporate these findings and be based on carefully tested, not only intuitively appealing assumptions on energy allocations.

Next to growth, analogous situation challenging classical views based on simple trade-offs in energy allocation recently emerged in another key life-history trait, ageing (Lind et al. 2019). The classical disposable soma theory of ageing states that the limited amount of energy can be either used for maintenance and repair or growth and reproduction resulting in trade-offs, with energy limitations for repair leading to the accumulation of unrepaired cellular damage with age (Kirkwood et al. 1979; Lind et al. 2019; Maklakov and Chapman 2019). However, recent evidence suggests that simple energy allocation between life history traits is not at the heart of variability in ageing. Similar to structural growth, delayed ageing is highly endogenously controlled, in the case of aging by a conserved insulin/IGF-1 nutrient-sensing signaling pathway (Lind et al. 2019). In the case of ontogenetic growth, a prominent and well conserved pathway responsible for growth regulation and its variability and plasticity can be the insulin and insulin-like signalling network (Shingleton 2011; Stearns 2011). The ovarian hormones can be an important sex-specific modifier of the structural growth pathways. Evidence brought up for structural growth and aging demonstrates that trade-offs can be mediated at the proximate level by switches in signalling pathways independently from direct simple energy allocations (Flatt et al. 2011; Stearns 2011). As evolutionary ecologists, we should stop thinking in the framework of simple direct differential energy allocation unless based on solid empirical evidence and we should focus on the question how selective forces shape complex, likely hierarchical structure of allocation rules and how it is reflected in proximate mechanisms controlling life-history decisions.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

References

Angilletta MJ, Wilson RS, Navas CA, James RS (2003) Tradeoffs and the evolution of thermal reaction norms. *Trends Ecol Evol* 18:234–240

- Arnold EN (1988) Caudal autotomy as a defence. In: Gans C, Huey R (eds) *Biology of the Reptilia*. Volume 16. Ecology. B. Alan R. Liss, New York, pp 235–273
- Atkinson D (1994) Temperature and organism size—a biological law for ectotherms? *Adv Ecol Res* 25:1–58
- Ballinger R, Tinkle D (1979) On the cost of tail regeneration to body growth in lizards. *J Herpetol* 13:374–375
- Bateman PW, Fleming PA (2009) To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. *J Zool* 277:1–14
- Bauerová A, Kratochvíl L, Kubička L (2020) Little if any role of male gonadal androgens in ontogeny of sexual dimorphism in body size and cranial casque in chameleons. *Sci Rep* 10:26–73
- Blanckenhorn WU (2000) Temperature effects on egg size and their fitness consequences in the yellow dung fly *Scathophaga stercoraria*. *Evol Ecol* 14:627–643
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Chapple D, Mccoull C, Roy S (2002) Changes in reproductive investment following caudal autotomy in viviparous skinks (*Niveoscincus metallicus*): lipid depletion or energetic diversion? *J Herpetol* 36:480–486
- Cox R, Skelly S, John-Alder H (2003) A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* 57:1653–1669
- Cox RM, Skelly SL, John-Alder HB (2005) Testosterone inhibits growth in juvenile male eastern fence lizards (*Sceloporus undulatus*): implications for energy allocation and sexual size dimorphism. *Physiol Biochem Zool* 78:531–545
- Cox RM (2006) A test of the reproductive cost hypothesis for sexual size dimorphism in Yarrow's spiny lizard *Sceloporus jarrovi*. *J Anim Ecol* 75:1361–1369
- Cox RM, Butler M, John-Alder H (2007) The evolution of sexual size dimorphism in reptiles. In: Fairbairn DJ, Blanckenhorn WU, Székely T (eds) *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*. Oxford University Press, New York, pp 38–49
- Cox RM, Stenquist D, Calsbeek R (2009) Testosterone, growth and the evolution of sexual size dimorphism. *J Evol Biol* 22:1586–1598
- Cox RM, Calsbeek R (2010) Severe costs of reproduction persist in *Anolis* lizards despite the evolution of a single-egg clutch. *Evolution* 64:1321–1330
- Cox RM, Lovern MB, Calsbeek R (2014) Experimentally decoupling reproductive investment from energy storage to test the functional basis of a life-history trade-off. *J Anim Ecol* 83:888–898
- Czarnoleski M, Labecka AM, Starostová Z, Sikorska A, Bonda-Ostaszewska E, Woch K, Kubička L, Kratochvíl L, Kozłowski J (2017) Not all cells are equal: effects of temperature and sex on the size of different cell types in the Madagascar ground gecko *Paroedura picta*. *Biol Open* 6:1149–1154
- Darwin C (1871) The descent of man and selection in relation to sex. John Murray, London
- Daza J, Herrera A, Richard T, Hector C (2009) Are you what you eat? A geometric morphometric analysis of gekkotan skull shape. *Biol J Linn Soc* 97:677–707
- Dial BE, Fitzpatrick LC (1981) The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia* 51:310–317
- Escalona T, Dean A, Valenzuela N (2018) A lengthy solution to the optimal propagule size problem in the large-bodied South American freshwater turtle, *Podocnemis unifilis*. *Evol Ecol* 32:29–41
- Fairbairn D, Blanckenhorn W, Székely T (2007) *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*. Oxford University Press, New York
- Flatt T, Heyland A, Stearns SC (2011) What mechanistic insights can or cannot contribute to life history evolution: an exchange between Stearns, Heyland, and Flatt. In: Flatt T, Heyland A (eds) *Mechanisms of life history evolution*. Oxford University Press, New York, pp 375–379
- Fox SF, Heger NA, Delay LS (1990) Social cost of tail loss in *Uta stansburiana*: lizard tails as status-signaling badges. *Anim Behav* 39:549–554
- Fox SF, McCoy J (2000) The effects of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana* in the field. *Oecologia* 122:327–334
- Gillis G, Bonvini LA, Irschick DJ (2009) Losing stability: tail loss and jumping in the arboreal lizard *Anolis carolinensis*. *J Exp Biol* 212:604–609
- Gillis G, Higham TE (2016) Consequences of lost endings: caudal autotomy as a lens for focusing attention on tail function during locomotion. *J Exp Biol* 219:2416–2422
- Golinski A, Kubička L, John-Alder H, Kratochvíl L (2014) Elevated testosterone is required for male copulatory behavior and aggression in Madagascar ground gecko (*Paroedura picta*). *Gen Comp Endocrinol* 205:133–141
- Goodman RM (2006) Effects of tail loss on growth and sprint speed of juvenile *Eumeces fasciatus* (Scincidae). *J Herpetol* 40:99–102

- Hatton IA, Dobson AP, Storch D, Galbraith ED, Loreau M (2019) Linking scaling laws across eukaryotes. *Proc Natl Acad Sci USA* 116:21616–21622
- Hayward A, Gillooly JF (2011) The cost of sex: quantifying energetic investment in gamete production by males and females. *PLoS ONE* 6:e16557
- Husak J, Lailvaux S (2017) How do we measure the cost of whole-organism performance traits? *Integr Comp Biol* 57:333–343
- Husak J, Roy J, Lovern B (2017) Exercise training reveals trade-offs between endurance performance and immune function, but does not influence growth, in juvenile lizards. *J Exp Biol* 220:1497–1502
- Jagnandan K, Higham TE (2018) Neuromuscular control of locomotion is altered by tail autotomy in geckos. *J Exp Biol* 221:jeb179564
- Kirkwood TBL, Holliday R, Smith JM, Holliday R (1979) The evolution of ageing and longevity. *Proc R Soc Lond B* 205:531–546
- Kratochvíl L, Frynta D (2006) 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. *Biol J Linn Soc* 88:527–532
- Kratochvíl L, Kubička L, Vohralík M, Starostová Z (2018) Variability in vertebral numbers does not contribute to sexual size dimorphism, interspecific variability, or phenotypic plasticity in body size in geckos (Squamata: Gekkota: *Paroedura*). *J Exp Zool A* 329:185–190
- Kubička L, Kratochvíl L (2009) First grow, then breed and finally get fat: hierarchical allocation to life-history traits in a lizard with invariant clutch size. *Funct Ecol* 23:595–601
- Kubička L, Starostová Z, Kratochvíl L (2012) Temperature-dependent rate of clutch production in a tropical lizard (*Paroedura picta*: Gekkonidae): intraspecific test of the metabolic theory of ecology. *J Therm Biol* 37:179–184
- Kubička L, Golinski A, John-Alder H, Kratochvíl L (2013) Ontogeny of pronounced female-biased sexual size dimorphism in the Malaysian cat gecko (*Aeluroscalabotes felinus*: Squamata: Eublepharidae): a test of the role of testosterone in growth regulation. *Gen Comp Endocrinol* 188:183–188
- Kubička L, Starostová Z, Kratochvíl L (2015) Endogenous control of sexual size dimorphism: gonadal androgens have neither direct nor indirect effect on male growth in a Madagascar ground gecko (*Paroedura picta*). *Gen Comp Endocrinol* 224:273–277
- Kubička L, Schořálková T, Červenka J, Kratochvíl L (2017) Ovarian control of growth and sexual size dimorphism in a male-larger gecko. *J Exp Biol* 220:787–795
- Lailvaux S, Husak J (2014) The life history of whole-organism performance. *Q Rev Biol* 89:285–318
- Lind MI, Ravindran S, Sekajova Z, Carlsson H, Hinas A, Maklakov AA (2019) Experimentally reduced Insulin/IGF-1 signaling in adulthood extends lifespan of parents and improves darwinian fitness of their offspring. *Evol Lett* 3:207–216
- Lynn S, Borkovic B, Russell B (2013) Relative apportioning of resources to the body and regenerating tail in juvenile leopard geckos (*Eublepharis macularius*) maintained on different dietary rations. *Physiol Biochem Zool* 86:659–668
- Maklakov AA, Chapman T (2019) Evolution of ageing as a tangle of trade-offs: energy versus function. *Proc R Soc Lond B* 286:20191604
- Martin T, Thorbek P, Ashauer R (2019) Common ground between growth models of rival theories: a useful illustration for beginners. *Ecol Model* 407:108712
- Martín J, Salvador A (1993) Tail loss reduces mating success in the Iberian rock-lizard, *Lacerta monticola*. *Behav Ecol Sociobiol* 32:185–189
- Niewiarowski P, Congdon J, Dunham A, Vitt L, Tinkle DW (1997) Tales of lizard tails: effects of tail autotomy on subsequent survival and growth of free-ranging hatchling *Uta stansburiana*. *Can J Zool* 75:542–548
- Pafilis P, Meiri S, Foufopoulos J, Valakos E (2009) Intraspecific competition and high food availability are associated with insular gigantism in a lizard. *Sci Nat* 96:1107–1113
- Oufiero CE, Smith A, Angilletta MJ (2007) The importance of energetic versus pelvic constraints on reproductive allocation in the eastern fence lizard (*Sceloporus undulatus*). *Biol J Linn Soc* 91:513–521
- Paz MM, García NE, Semhan RV, Lobo FJ, Abdala CS (2019) Study of lipid reserves in *Liolaemus koslowskyi* (Squamata: Liolaemidae): reproductive and ecological implications. *J Comp Physiol B* 189:595–609
- Pond CM (1978) Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. *Annu Rev Ecol Syst* 9:519–570
- Roth ED, Johnson JA (2004) Size-based variation in antipredator behavior within a snake (*Agkistrodon piscivorus*) population. *Behav Ecol* 15:365–370
- Schořálková T, Kratochvíl L, Kubička L (2018) To fight or mate? Hormonal control of sex recognition, male sexual behavior and aggression in the gecko lizard. *Horm Behav* 97:18–24

- Shingleton AW (2011) Evolution and the regulation of growth and body size. In: Flatt T, Heyland A (eds) Mechanisms of life history evolution. Oxford University Press, New York, pp 43–55
- Sibly RM, Brown JH (2020) Toward a physiological explanation of juvenile growth curves. *J Zool.* <https://doi.org/10.1111/jzo.12770>
- Starostová Z, Kubička L, Kratochvíl L (2010) Macroevolutionary pattern of sexual size dimorphism in geckos corresponds to intraspecific temperature-induced variation. *J Evol Biol* 23:670–677
- Starostová Z, Angilletta MJ, Kubička L, Kratochvíl L (2012) Thermal dependence of reproductive allocation in a tropical lizard. *J Therm Biol* 37:159–163
- Starostová Z, Kubička L, Golinski A, Kratochvíl A (2013) Neither male gonadal androgens nor female reproductive costs drive development of sexual size dimorphism in lizards. *J Evol Biol* 26:1872–1880
- Starostová Z, Gvoždík L, Kratochvíl L (2017) An energetic perspective on tissue regeneration: the costs of tail autotomy in growing geckos. *Comp Biochem Physiol A* 206:82–86
- Stearns SC, Kawecki TJ (1994) Fitness sensitivity and the canalization of life-history traits. *Evolution* 48:1438–1450
- Stearns SC (2000) Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* 87:476–486
- Stearns SC (2011) Does impressive progress on understanding mechanisms advance life history theory? In: Flatt T, Heyland A (eds) Mechanisms of life history evolution. Oxford University Press, New York, pp 364–374
- Taborsky B (2017) Developmental plasticity: preparing for life in a complex world. In: Naguib M, Podos J, Simmons LW, Barrett L, Healy SD, Zuk M (eds) Advances in the study of behavior. vol 49, Academic Press, pp 49–99
- von Bertalanffy L (1957) Quantitative laws in metabolism and growth. *Q Rev Biol* 32:217–231
- Walzer A, Schausberger P (2014) Canalization of body size matters for lifetime reproductive success of male predatory mites (Acari: Phytoseiidae). *Biol J Linn Soc* 111:889–899
- Webb JK (2006) Effects of tail autotomy on survival, growth and territory occupation in free-ranging juvenile geckos (*Oedura lesueurii*). *Austral Ecol* 31:432–440
- West GB, Brown JH, Enquist BJ (2001) A general model for ontogenetic growth. *Nature* 413:628–631
- Zuo W, Moses M, West GB, Hou C, Brown JH (2012) A general model for effects of temperature on ectotherm ontogenetic growth and development. *Proc R Soc Lond B* 279:1840–1846
- Wilson RS, Booth DT (1998) Effect of tail loss on reproductive output and its ecological significance in the skink *Eulamprus quoyii*. *J Herpetol* 32:128–131

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