SYMPOSIUM

Do Adult Phenotypes Reflect Selection on Juvenile Performance? A Comparative Study on Performance and Morphology in Lizards

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Synopsis When competing for food or other resources, or when confronted with predators, young animals may be at a disadvantage relative to adults because of their smaller size. Additionally, the ongoing differentiation and growth of tissues may constrain performance during early ontogenetic stages. However, juveniles must feed before they can become reproductively active adults and as such the adult phenotype may be the result of an ontogenetic filter imposing selection on juvenile phenotype and performance. Here we present ontogenetic data on head morphology and bite force for different lizard species. We test whether adults reflect selection on juveniles by comparing slopes of growth trajectories before and after sexual maturity in males and females and by examining the variance in head morphology and bite force in juveniles versus adults. Finally, we also present the first results of a selection study where animals were measured, marked and released, and recaptured the subsequent year to test whether head morphology and bite force impact survival.

Introduction

That size has a major impact on organismal function has long been appreciated (Schmidt-Nielsen 1984; Brown and West 2000). Indeed, the scaling of performance to body size is often non-linear (Hill 1950; Carrier 1996) and as such young animals may be at a disadvantage relative to adults because of their smaller size. This is likely to be most important when competing for food or other resources, or when confronted with predators and may lead to lower survival (Herrel and Gibb 2006). Additionally, the ongoing differentiation and growth of tissues may constrain performance during early ontogenetic stages (Carrier 1996). However, juveniles must move, feed, and survive before they become reproductively active

adults. In a seminal paper, Carrier (1996) suggested that "as a possible result of ontogenetic canalization, the adult phenotype may be determined as much or more by selection on the locomotor performance of juveniles as by direct selection on the locomotor abilities of adults." As such, the adult phenotype may, at least, partly be the result of an ontogenetic filter imposing selection on juvenile phenotype and performance. Although this was postulated to be the case for locomotor performance specifically, one can imagine this being applicable to other types of performance such as biting if resources are scarce and competition strong. Alternatively, this may only hold for certain performance traits and not others. Despite the important ramifications for our understanding of

the evolution of form and function, this idea has rarely been tested.

However, this idea was proposed following studies on birds and mammals (Carrier 1983, 1995; Carrier and De Leon 1990) where growth is essentially arrested once animals reach adulthood. Ecothermic vertebrates, in contrast, continue growing throughout their life and as such selection may mold performance at the adult stage through growth-related changes in morphology. In the present paper, we explore whether this is indeed the case by examining data on morphology and performance in lizards, focusing specifically on bite force and locomotor performance. However, both performance types may not be equally impacted by selection. As juveniles likely need to escape from a broader range of predators compared to adults, selection on locomotion should induce high levels of performance. In contrast, juveniles may shift their resource utilization to smaller or different types of prey suggesting that for bite forces they may not show disproportionate levels of performance (Herrel and Gibb 2006).

We posited the following hypotheses based on the idea that adult phenotypes may be shaped by selection on juvenile performance:

(1) trait variance should be lower in adults compared to juveniles.

If the adult phenotype is the result of the selective filter acting on juvenile performance, then the overall variance in traits related to the performance trait of interest in adults should be lower. Indeed, natural selection should eliminate phenotypes characterized by lower performance from the population, resulting in adults that are less variable in morphology and performance than juveniles (Fox 1975). Alternatively, reduced trait variance may be the result of the process of ontogosenescence (Levitis 2011) which suggests that these patterns are driven by intrinsic developmental constraints rather than external selective pressures.

(2) the relationships between performance and morphology and body size should be identical in juveniles and adults.

If selection is indeed acting on juvenile performance then this will impact growth trajectories, allowing juveniles to reach high levels of performance rapidly. If adult performance is not under selection and the cost of maintaining performance not too great, then one may predict that growth trajectories should be identical in adults and juveniles. However, rapidly growing tissues may also compromise performance if they lead to weaker bones, for example. Alternatively, resource allocation trade-offs may

drive growth trajectories independent of selection on performance.

(3) adults should typically be over performers compared to juveniles.

If prediction two is indeed true, then selection driving rapid increases in performance in juveniles may produce adults that perform at levels that are largely above what they need in their ecological context. Alternatively, selection may be relaxed in adults and as such modify growth trajectories avoiding costly investment in muscles and bones. A third possibility is that selection acts on the performance of adults and enhance performance even more rapidly. This could be possible in the case that the performance trait of interest is submitted to sexual selection through, for example, male–male interactions or female choice. Adults showing higher levels of performance, would, however, go against the observation that in some animals juveniles perform at levels equivalent to those of adults (Carrier 1996).

(4) survival should be non-random depending on trait values in juveniles but not in adults.

If indeed selection on performance is acting principally at the juvenile life stage, then survival should be non-random and dependent on performance in juveniles. In contrast, the level of performance should not impact the survival in adults.

To test these hypotheses, we exploit previously published data on morphology and performance for a large sample of *Anolis carolinensis*. In addition, we test whether these patterns hold for three species of the lacertid lizard genus *Gallotia* for which good data on morphology and performance also exist. Finally, we provide previously unpublished data on a field study quantifying the survival of individuals of the species *T. itambere* and compare whether selection on bite force is non-random in juveniles compared to adults.

Materials and methods

Anolis carolinensis

Lizards ($N = 403$) were sampled in 2002 from vegetation along a 755-m transect that follows a straight dirt road which crosses Good Hope Field in St. Charles Parish, southeastern Louisiana (USA). Performance traits (cling force, jump acceleration, jump distance, bite force) and limb and head morphology were measured as detailed in Irschick et al. (2005a) and Vanhooydonck et al. (2005).

Gallotia lizards

During September 2011, we captured 280 specimens representing three species of *Gallotia* from the

Canary Islands (Spain): *G. atlantica*, *G. caesaris*, and *G. stehlini* (Lopez-Darias et al. 2015). Specimens were captured in the wild by noose or using traps baited with tomatoes. All permissions required for capturing and manipulating *Gallotia* species were provided by each island Council and the Government of the Canary Islands. All animals captured in the field were measured and released within 24 h of capture. Head dimensions and bite forces were measured as detailed in Lopez-Darias et al. (2015).

Tropidurus itambere survival study

Tropidurus itambere is a medium-sized (SVL: 55-99 mm) saxicolous lizard inhabiting open rocky habitats in central-southeastern Brazil (Rodrigues 1987; Rodrigues 1988). The species is sexually dimorphic and males are typically larger than females (Van Sluys 1997; Brandt and Navas 2013). The animals are diurnal and heliothermic and are found active throughout the year, but reproduce only during the wet season (Van Sluys 1993b). They are sedentary (Van Sluys 1997) sit-and-wait predators (Van Sluys 1993a). The study took place outside the city of Atibaia, São Paulo state, in southeastern Brazil. The field site consists of a hill occupied by granite boulders, isolated by cattle pasture (Fig. 1A). The population is effectively isolated due to the saxicolous habit of *T. itambere*. Vegetation is largely dominated by grass, but sparse trees and bushes are also found more closely associated to the boulders.

Animals were captured in the field and their position was recorded by GPS and the capture site was flagged with the number of the animal. Animals were returned to their exact site of capture within 48 h. After capture, animals were brought back to the lab and morphology and performance were measured. We measured snout-vent length, head length, depth, width, lower jaw length, the distance from the quadrate to the tip of the lower jaw, and the distance from the back of the jugal to the tip of the lower jaw using digital calipers (Mitutoyo). Body mass was measured using a Pesola spring balance. Based on these measurements, we further calculated the in-levers for jaw opening and jaw closing as the lower jaw length minus the distance from the quadrate to the tip of the jaw and the distance from the quadrate to the tip of the lower jaw minus the distance from the back of the jugal to the tip of the lower jaw, respectively. Next, we measured bite force using an isometric Kistler force transducer place in a custom-made set-up and attached to a Kistler charge

amplifier (see Herrel et al. 1999). Animals were made to bite five times and only the highest bite force was retained for further analyses.

In 2014, we captured 142 animals of which 51 were recaptured in 2015. Sampling effort was greater in 2015 when 303 animals were captured likely representing most animals in the population. Given the isolation of the population (the nearest boulders are more than 5 km away, separated by grassland and pasture) immigration and emigration can be considered negligible. As such we considered all animals not captured in 2015 as not having survived.

All experiments were approved by the respective institutional ethics committees.

Analyses

Individuals of all species were subdivided into juveniles and adults based on the published data on the size at sexual maturity (*A. carolinensis*: Irschick et al. 2005; *Gallotia*: Molina-Borja and Rodriguez-Dominguez 2004; Molina-Borja 2009; Molina-Borja et al. 2010; *T. itambere*: Van Sluys 1993b) and personal observations. Given that all the species included in our analysis are known to be sexually dimorphic, we separated adults into males and females for the analyses of trait variance. To calculate trait variance, we ran regressions of each Log_{10}-transformed trait on Log_{10} snout-vent length and extracted the unstandardized residuals for juveniles, adult males, and adult females separately. We used residuals as the two sexes span different ranges in body size which may artificially inflate calculations of trait variance since these co-vary with size. Next we calculated the variance of each residual trait for each group (see Tables 1–3). To explore whether growth patterns were different for juveniles compared to adults we only used data for *A. carolinensis* as it was the largest data set. We ran regressions for juveniles and adults separately of each Log_{10}- transformed trait on Log_{10}-transformed snout-vent length. We recorded the slopes, standard errors, and the R^2 values (Table 4). We next tested whether slopes of the relationships between snout-vent length and each trait differed between juveniles and adults using *t*-tests. Note that in adult males two morphs exist (Lailvaux et al. 2004). These were analyzed together as the morphology~performance slopes do not differ between morphs. Finally, we tested whether individuals of *T. itambere* that survived from 2014 to 2015 differed in bite force from those that did not, and this separately for juveniles and adults.
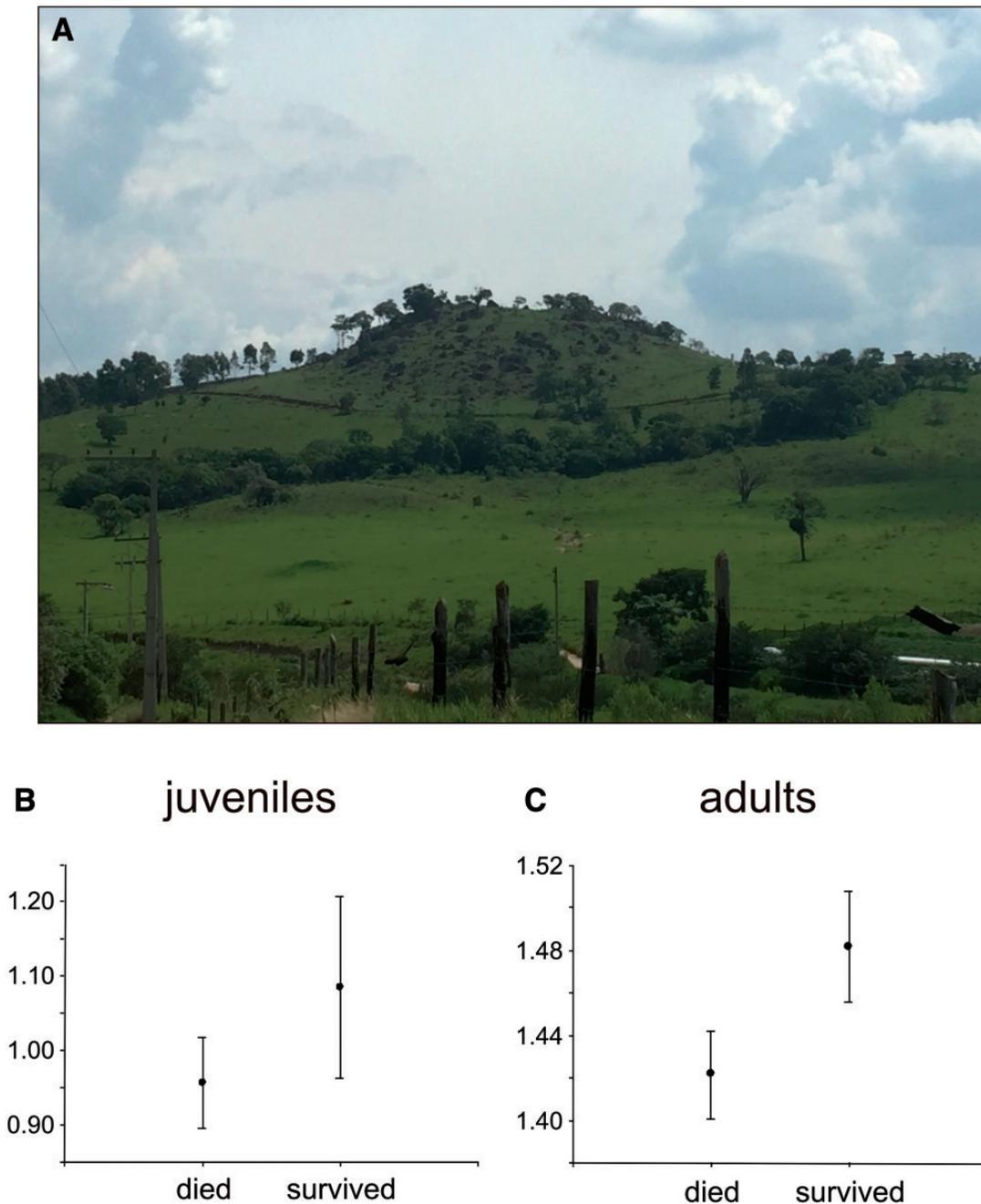
Fig. 1 (**A**) Study site for *T. itambere* (Atibaia, São Paulo, Brazil); (**B**) mean (± standard deviation) Log$_{10}$-transformed bite force for juveniles that survived versus those that did not survive; (**C**) mean (± standard deviation) Log$_{10}$-transformed bite force for adults that survived versus those that did not survive.

Results

Trait variance

When analyzing the residual trait variance in *A. carolinensis*, our data show that juveniles do indeed show a greater variance in both morphology and performance than either adult males or adult females. A notable exception is, however, limb length, with adult females having greater variance in both forelimb and hind limb length than either adult males or juveniles (Table 1). In *Gallotia* lizards the pattern is more variable, however. Whereas adult males had the greatest variance in bite force in all three species, head dimensions showed greatest variance in juveniles of *G. atlantica*, a pattern not identified in the other two species (Table 2). Specifically, head width and depth showed the greatest variance in male *G. caesaris* and head depth showed the greatest variance in male

Table 1 Trait variance in juveniles and adults for *A. carolinensis*

	Juveniles N =118		Adult males N = 152		Adult females N = 50
Head width	**0.000594**	>	0.000396	<	0.000416
Head depth	**0.001112**	>	0.000695	>	0.000654
Close in-lever	**0.002309**	>	0.001094	<	0.001873
Forelimb length	0.000472	>	0.000456	<	**0.000624**
Hind limb length	0.000267	>	0.000222	<	**0.000286**
Bite force	**0.007998**	>	0.006442	>	0.004715
Cling force	**0.010067**	>	0.007604	<	0.008366
Jump acceleration	**0.002760**	>	0.001808	<	0.001874
Jump distance	**0.006045**	>	0.005226	<	0.005584

Notes: Bolded values represent the greatest variance. Table entries are the variance across all individuals of that age class or sex based on the residuals of a regression of the Log_{10} transformed trait on Log_{10}-transformed snout-vent length.

Table 2 Trait variance in juveniles and adults for three species of *Gallotia* lizards

	Juveniles		Adult males		Adult females
Gallotia atlantica					
	N = 27		N = 50		N = 22
Head width	**0.001820**	>	0.000525	<	0.000858
Head depth	**0.002039**	>	0.000960	>	0.000957
Close in-lever	**0.003011**	>	0.001152	<	0.002298
Bite force	0.015846	<	**0.017706**	>	0.012014
Gallotia caesaris					
	N = 24		N = 28		N = 31
Head width	0.000518	<	**0.000993**	>	0.000324
Head depth	0.000416	<	**0.000517**	>	0.000432
Close in-lever	**0.001070**	>	0.000822	<	0.001233
Bite force	0.005569	<	**0.006915**	>	0.006380
Gallotia stehlini					
	N = 49		N = 23		N = 26
Head width	**0.000689**	>	0.000452	<	0.000586
Head depth	0.000633	<	**0.000922**	>	0.000663
Close in-lever	**0.001502**	>	0.000470	<	0.001223
Bite force	0.009295	<	**0.009906**	>	0.004530

Notes: Bolded values represent the greatest variance. Table entries are the variance across all individuals of that age class or sex based on the residuals of a regression of the Log_{10} transformed trait on Log_{10}-transformed snout-vent length.

Table 3 Trait variance in juveniles and adults for *T. itambere*

	Juveniles N = 25		Adult males N = 150		Adult females N = 128
Head width	**0.000703**	>	0.000337	>	0.000318
Head depth	**0.000937**	>	0.000485	>	0.000464
Close in-lever	**0.000354**	>	0.000277	>	0.000241
Bite force	**0.016443**	>	0.015860	>	0.012353

Notes: Bolded values represent the greatest variance. Table entries are the variance across all individuals of that age class or sex based on the residuals of a regression of the Log_{10} transformed trait on Log_{10}-transformed snout-vent length.

Table 4 Slopes of regressions of morphology and performance on snout-vent length of A. carolinensis

| | Juveniles N = 117 | | | Adults N = 202 | |
	Slope	R^2		Slope	R^2
Head width	0.77 ± 0.027	0.88	<	1.08 ± 0.028	0.88
Head depth	0.75 ± 0.039	0.76	<	1.09 ± 0.035	0.83
Close in-lever	1.19 ± 0.060	0.77	<	1.40 ± 0.052	0.79
Forelimb length	0.90 ± 0.027	0.90	=	0.97 ± 0.031	0.83
Hind limb length	0.85 ± 0.021	0.93	=	0.90 ± 0.022	0.89
Bite force	1.95 ± 0.089	0.81	<	3.38 ± 0.103	0.84
Cling force	2.50 ± 0.157	0.82	>	1.74 ± 0.153	0.52
Jump distance	0.95 ± 0.098	0.45	=	0.96 ± 0.097	0.33
Jump acceleration	0.26 ± 0.067	0.12	=	0.15 ± 0.057	0.035

Note: Bolded traits are those for which the slope is significantly ($\alpha = 0.01$) different between juveniles and adults based on a t-test.

G. stehlini (Table 2). In T. itambere, juveniles showed the greatest trait variance in both performance and morphology (Table 3).

Growth

Growth trajectories showed an interesting pattern with trajectories for limbs and jumping being identical in juvenile and adult A. carolinensis (Table 4). However, this was not the case for head dimensions or bite force, where the slope of the regression of these traits against snout-vent length differed. The slopes in adults were steeper than that observed for juveniles (Table 4). Interestingly, for cling force the slope was greater in juveniles compared to adults (Table 4).

Survival

Of the 10 juveniles of T. itambere captured and re-leased in 2014, two were recaptured in 2015 (20%). Of the 131 adults captured and released, 49 were recaptured in 2015 (37%). When comparing the bite forces of juveniles that survived from 2014 to 2015 with those that did not, no significant differences were observed ($F_{1,8} = 0.88$; $P = 0.375$). However, the mean bite force of those individuals that survived was higher than that of those that did not (Fig. 1B; Table 5). For adults, the difference was marginally non-significant ($F_{1,129} = 3.286$; $P = 0.072$), with those that survived having higher mean bite forces (Fig. 1C; Table 5).

Discussion

A first prediction that follows from the idea that the adult phenotype may reflect selection on juveniles is that trait variance should be greater in juveniles compared to adults. When evaluating the results

Table 5 Mean bite forces of juveniles and adults for individuals of T. itambere that survived versus those that did not

	Survived	Died
Juveniles	12.23 ± 1.75	9.86 ± 4.79
Adults	32.63 ± 11.45	28.90 ± 12.16

Note: Table entries are mean bite forces (N) ± standard deviations.

for A. carolinensis for which we have a large data set this does seem to be the case for most traits except limb length, for which the variance is greatest in adult females. Female and juvenile green anoles use the available habitat in a non-random manner, and adult females have higher levels of jump performance and cling force compared to adult males and juveniles (Irschick et al. 2005a). Possibly, the higher level of performance relative to body size is suggestive of selection on female locomotor performance, which may induce greater trait variance, especially if adult females use alternative strategies to avoid predation (crypsis versus escape). However, this needs to be tested by exploring whether survival is higher in adult females with greater locomotor performance or with alternative behavioral strategies. Alternatively, part of the observed trait variance may be due to phenotypic plasticity a it is known that limb length may respond to variation in substrate usage during the lifetime of an individual (Losos et al. 2000; Kolbe and Losos 2005). However, this would not explain the fact that variance is greatest in females unless their limbs are more plastic than those of males. For the tropidurid T. itambere, juveniles also showed greater variance in head morphology and bite force compared to both adult males and adult females, corroborating the pattern observed in

A. carolinensis. This appears to confirm our hypothesis suggesting that selection does indeed operate on juvenile performance, reducing the trait variance in adults through reduced survival of individuals with lower performance unless individuals with very high levels of performance as adults also experience reduced survival. As a caveat, it should be noted that the greater variance could also be the result of a greater measurement error in juveniles given their smaller body size. However, this is unlikely, as for example in the *Gallotia* lizards adult males often showed the greatest variance. Moreover, the error in performance measurements is not size dependent and as such we should not per se see greater variance in juveniles. The *Gallotia* lizards deviate from the pattern observed in the other two species as they present adult males having a greater variance in bite force and some head dimensions. However, in both *G. atlantica* and *G. stehlini* did juveniles have greater bite force variance than adult females. As these species are extremely dimorphic in head size and head size and bite force determine the outcome of male–male interactions (Molina-Borja et al. 1998; Huyghe et al. 2005), this may induce strong selection on head morphology and bite force in these species. Moreover, alternative reproductive strategies appear to exist in these species with some adult males adopting female coloration and morphology (personal observation). This is relatively common in lizards in general (Miles et al. 2007), and may be driving the higher variance observed in adult males of these species.

If adult phenotypes are purely the reflection of selection on juvenile performance, then growth trajectories can be expected to be identical in juveniles and adults. Our data for *A. carolinensis* bear this prediction out only for locomotion-related traits such as hind limb and forelimb length as well as jump distance and peak jump acceleration. The increase in cling force relative to snout-vent length, on the other hand, was greater in juveniles than in adults. Whereas in juveniles the relationship is positively allometric, in adults the slope did not deviate from isometry. This suggests that juveniles are under strong selection to increase cling force. Given that juveniles occupy perch heights similar to those of adult males and adult females (Irschick et al. 2005a) they may need to rapidly develop their clinging ability. Once adulthood is reached performance increases as expected based on the growth following geometric similarity which is suggestive of relaxed selection on clinging performance. In contrast, head dimensions and bite force increase more rapidly in adults compared to juveniles, suggesting selection on

bite force at the adult stage. This suggests that juveniles may select different prey resources and thus do not need the same level of performance. These patterns are similar to what has been observed for another *Anolis* species (*A. lineatopus*: Herrel et al. 2006; *A. equestris* and *A. garmani*: Herrel and O'Reilly 2006) and the loggerhead musk turtle, *Sternotherus minor* (Pfaller et al. 2010, 2011), although these authors did not specifically test for differences in growth trajectories between juveniles and adults. This is, however, not universally so. For example in the red-eared slider, *Trachemys scripta* (Herrel and O'Reilly 2006) and the African catfish, *Clarias gariepinus* (Herrel et al. 2005), bite forces increase much more rapidly with size in juveniles compared to adults. Interestingly, in both species this change in the ontogenetic trajectory is associated with a dietary switch, suggesting that diet-induced selection may be driving these patterns. Yet, in many species the scaling of bite force appears to be similar in juveniles and adults (Erickson et al. 2003; Huber et al. 2008; Kolman and Huber 2009; Habegger et al. 2011; Habegger et al. 2012; Erickson et al. 2014; Gignac and O'Brien 2016), suggesting that growth trajectories do not change once animals have reached sexual maturity. In this case, and if selection acts to rapidly increase performance in juveniles, adults may show disproportionate levels of performance (see below). In mammals the pattern is radically different, with bite force reaching a plateau at the age of sexual maturity or even diminishing slightly in the oldest individuals (Binder and Van Valkenburgh 2000; La Croix et al. 2011; Chazeau et al. 2013; Thomas et al. 2015).

A third corollary of the idea that the adult phenotype may be biased by selection on juvenile performance is the idea that adults should be over performers. Indeed, if selection is strong on juveniles, and given that juveniles are small and thus show low levels of absolute performance, this should push juveniles to increase their performance rapidly during growth. If during the adult stage growth continues along the same lines, then adults may end up having extremely high levels of performance, higher then what they need in their ecological context. One example of this is the bite force of *Gallotia* lizards. In a paper published in 1999, Herrel and co-authors showed that both male and female *Gallotia galloti* lizards had bite forces that exceeded the forces needed to crush even the hardest prey in their environment. This is in stark contrast with data for smaller lizards and bats, where animals eat prey of the size and hardness that perfectly match their bite force capacity (Herrel et al. 2001; Verwaijen et al. 2002;

Aguirre et al. 2003). Alternatively, the high bite forces in female *Gallotia* may also be due to the strong selection on fighting capacity and bite force in males, simply dragging females along as bite force is likely a polygenic character (see Lande 1980). In animals with continuous growth, like lizards, growth trajectories often differ dramatically from those observed in animals like mammals or birds, which stop growing once they have reached the adult stage. In ectotherms, adults thus commonly show levels of performance that exceed what they need. This idea may also shed light on the peculiar patterns observed with lizard sprint speeds. Indeed, many lizards run in the field at only a fraction of their maximal sprint capacity as measured in the laboratory (Irschick et al. 2005; Husak et al. 2006). If the adult phenotype is indeed the result of strong selection on juvenile performance, then adults may in fact be considered ''over performers'' capable of higher levels of performance than they typically need. A nice illustration of this idea is provided by the work of Jerry Husak who measured selection on sprint speed in collared lizards. He first showed that juveniles were under strong directional selection for speed (Husak 2006b). However, maximal sprint speed did not predict adult survival in either males or females suggesting that sprint speed is not under selection in adults (Husak 2006b). Adults in the field moreover used speeds that were significantly lower than the maximal sprint speeds as measured in the lab (Husak et al. 2006) consistent with the idea that adults may be ''over performers.'' Interestingly, juveniles that survived had sprint speeds that were slightly above the average speed used by adults in the field (Husak 2006a) further confirming that adults kept increasing performance even above the threshold level needed to survive. Further studies on selection on performance traits in the field will be needed to test the generality of these observations, however.

Our final prediction was that survival should be non-random with respect to on juvenile performance but not dependent on performance in adults. Our data for *T. itambere* show that both juveniles and adults that survived from 2014 to 2015 had, on average, greater bite forces than those that did not. However, the difference in bite force between those that survived and those that did not were not significant, largely due to our small sample size. The next sample period in 2016 should allow us to test whether this pattern is confirmed or not, as our sample size will be much greater. In any case, our results do not confirm our predictions, and suggest that in both adults and juveniles animals with higher bite forces may survive better. However, the higher mean bite forces observed in adults that survived may be due to differential survival of adult males relative to adult females. Indeed, only 27% of the adult females were recaptured in 2015, whereas 45% of the adult males were recaptured. Given that adult males bite harder than adult females, this may skew our results. Clearly more data are needed to test the survival of each age group and sex separately. Studies on selection on performance and survival in the field are rare (but see e.g. Jayne and Bennett 1990; Le Galliard et al. 2004) and to our knowledge few have compared trait-dependent survival in juveniles versus adults (but see Husak 2006b for an excellent example on locomotor performance). Further field studies quantifying selection on performance are clearly needed in order to address the question of whether selection is stronger and non-random in juveniles compared to adults.

Conclusion

Our data provide partial support for the idea that trait variance should be greater in juveniles, suggesting that adult phenotypes may encompass only a subset of the potential juvenile phenotypes. Growth patterns are similar for juveniles and adults for some traits but not others, suggesting that selection is trait specific. In ectothermic vertebrates characterized by continuous growth, patterns are very different from those observed in mammals and can show (1) no difference, (2) more rapid increases in adults, and (3) slower increases in performance with size in adults. In some cases, adults are over performers and show levels of performance that exceed their ecological needs. However, this may not always be the result of selection on juvenile performance, as observed in species where sexual selection acts directly on performance traits. Finally, our preliminary data suggested that survival may indeed be dependent on performance in juveniles and adults alike. However, additional data are needed to test this idea. In summary, we believe that the evaluation of patterns of growth and selection for different life-history stages separately may be extremely insightful in understanding the evolution of adult phenotypes at a macro-evolutionary level.

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