

# Reduced burst speed is a cost of rapid growth in anuran tadpoles: problems of autocorrelation and inferences about growth rates

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## Summary

1. It is becoming clear that individual growth rates are optimized to suit local conditions rather than maximized to be as fast as possible. To understand this adaptive variation in growth rates, we need to understand the costs of rapid growth.

2. Recent work in teleost fish suggests that a trade-off between growth rate and critical swimming speed may be common. The current study demonstrates that the trade-off also occurs in anuran tadpoles with regard to burst speed.

3. Individual growth rate and burst speed were compared in *Bufo americanus* and *Scaphiopus hamondi*, representatives of two distantly related anuran families. Path analysis showed that growth rate is negatively correlated with burst speed. Because the trade-off between growth rate and swimming speed occurs in two such distantly related anuran species as well as teleosts, it may be general for all vertebrates.

4. However, identifying costs of rapid growth is complicated by the indirect effects of growth rate on body size which will also often correlate with performance factors. Distinguishing between direct effects of growth rate and indirect effects through body size is difficult because the two necessarily result in collinearity. A randomization test shows just how severe this problem can be.

*Key-words:* *Bufo americanus*, randomization test, *Scaphiopus hamondi*, trade-off

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## Introduction

Two important components of fitness are body size and locomotor ability; in many cases larger (Arendt 1997; Sogard 1997) and faster (e.g. Watkins 1996; Lankford, Billerbeck & Conover 2001) individuals survive and reproduce better than their smaller and slower competitors. Since large body size can be achieved only through growth, it is often assumed that natural selection maximizes growth rate as a life-history parameter, at least during the juvenile stage of the life cycle when there is no trade-off with reproduction. However, evidence has accumulated that juvenile growth rate is not maximized by natural selection. Interspecific comparisons, intraspecific comparisons, selection experiments and genetic engineering experiments all suggest that juvenile organisms have the evolutionary potential to grow faster; the reason they do not is evidently due to trade-offs that make rapid

growth costly (Arendt 1997; Arendt & Wilson 1997; Morgan & Metcalfe 2001). Identifying the costs associated with rapid growth is therefore an important next step for life-history theory. This report identifies a newly recognized trade-off between growth rate and locomotor speed; it may be best to be large and fast, but it may also be difficult to become large without becoming slow.

Kolok & Oris (1995) first reported the trade-off between growth rate and swimming speed in a minnow (*Pimephales promelas*). They expected a positive correlation between growth rate and swimming speed because both traits had been shown to be positively correlated with other physiological factors (enzyme activity and body condition). However, faster-growing individuals turned out to have slower critical swimming speeds (a measure of aerobic swimming). The same trade-off was later demonstrated in studies with Rainbow Trout (Gregory & Wood 1998, 1999) and the Atlantic Silverside (*Menidia menidia*) (Billerbeck, Lankford & Conover 2001). In addition to critical swimming speed, these studies found that rapid growth compromises burst speed (Billerbeck *et al.* 2001) but not endurance swimming (Gregory & Wood 1998). In parallel with these studies of natural variation in

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growth rate are two studies on transgenic salmon carrying extra copies of a growth hormone gene (Farrell, Bennett & Devlin 1997; Stevens, Sutterlin & Cook 1998). These studies were initiated to address concerns that the rapid growth rate of genetically engineered fish would make them superior competitors, threatening wild populations if they should escape from aquaculture settings. These concerns fail to take into account potential costs of rapid growth. When the transgene had a dramatic effect on realized growth rate (a 10-fold increase) the fast-growing fish were clearly poorer swimmers (Farrell *et al.* 1997). However, with more modest increases in growth rate (a two-fold increase) the swimming cost was not significant although there was a clear metabolic cost (Stevens *et al.* 1998). Is there a general trade-off between growth rate and swimming speed for all vertebrates?

To address the generality of this trade-off, I compared individual growth rates and swimming speed in tadpoles of two anuran species, a spadefoot toad (*Scaphiopus hammondi*) and the American Toad (*Bufo americanus*). The former is a member of the Pelobatidae, one of the most primitive anuran families, while the Bufonidae is among the most derived families (Ford & Cannatella 1993). As such, these species represent a broad phylogenetic sample from the anuran order. I measured individual burst speed (rate generated from a starting position) which is an anaerobic form of locomotion. Burst speed in tadpoles is important in evading predators (Feder 1983; Watkins 1996) and is likely to be more closely tied to fitness than the aerobic swimming used in most teleost studies.

An important methodological concern when looking for costs of rapid growth is disentangling size and age effects on a performance measure from the direct effects of growth rate. In comparing different growth rates, individuals can be matched at either a common size or a common age, but not both. Because both size and age are likely to correlate with performance measures such as swimming speed, one factor will usually have to be eliminated statistically. This means that studies on growth rate must deal with problems of collinearity. This is further complicated if growth rate is estimated from two size measures at two ages, because growth rate is then necessarily autocorrelated with both measures. A two point estimate of growth rate is common when it is difficult to measure size (especially when size is measured destructively), or in long-lived and slow-growing organisms. The data obtained in this study are used to estimate the effectiveness of partial correlation methods (multiple regression or path analysis) in separating these effects.

### Materials and methods

American Toad tadpoles (*Bufo americanus*) were collected from a pond in Broome County, NY, as hatchlings in 1999 and Western Spadefoot tadpoles

(*Scaphiopus hammondi*) were collected as eggs in Riverside County, CA, and hatched in the laboratory in spring 2000. American Toads were fed flake fish food *ad libitum*. Spadefoot tadpoles were fed *ad libitum* until 4 days posthatch when they were initially weighed and randomly assigned to either a high-food group (100 mg day<sup>-1</sup> with a mixture of rabbit chow, fish food and puppy vitamins) or a low-food group (10 mg day<sup>-1</sup>). This food range was chosen to mimic the range of growth rates typically seen in natural populations of *S. hammondi* (Morey 1994). Tadpoles were raised in 1-l (*Bufo*) or 2-l (*Scaphiopus*) containers with aged tap water, three tadpoles matched for initial size to within 0.4 mg per container (to control for possible Allee effects). Water temperatures were maintained near what each species would experience in nature, 20 °C for *Bufo* (J. D. Arendt, personal observation) and 25 °C for *Scaphiopus* (Morey 1994). Water was changed daily just prior to feeding. Wet mass of tadpoles was taken when initially put into these containers and 14 days later, immediately after the swimming trial, by blotting individuals dry and measuring to the nearest 0.1 mg using an electronic balance. Although absolute growth rates (mg day<sup>-1</sup>) are reported, statistical analyses were conducted on instantaneous growth rate, that is change in ln(mass) over 14 days, for both species. Developmental stage (30–34 for *Bufo*, 34–41 for *Scaphiopus*) was noted following Gosner (1960).

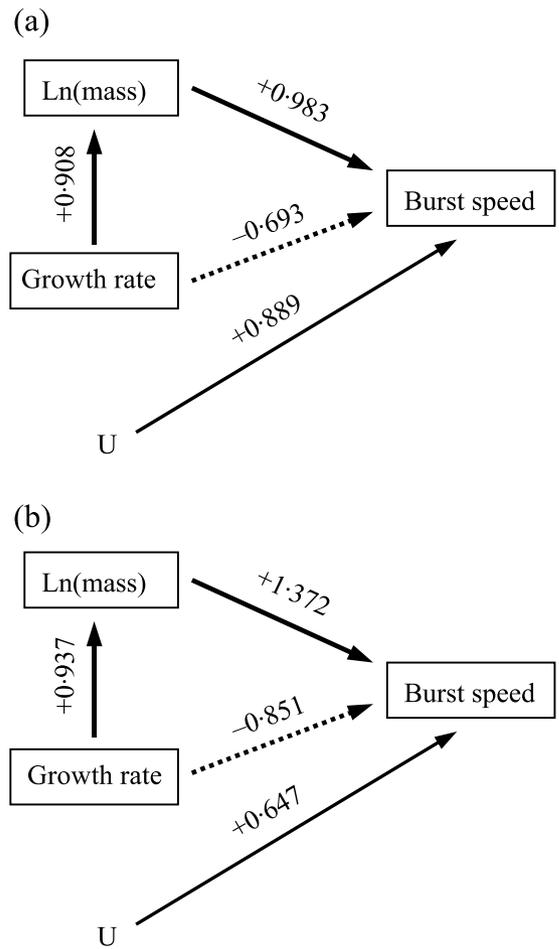
Individual burst swimming speed was measured by placing a tadpole into an aquarium (20 l for *Bufo* and 40 l for the larger *Scaphiopus*) with approximately 2 cm of water, just enough to cover the tadpole and limit swimming to a two-dimensional plane. Tadpoles were allowed to settle for 45–60 s and a startle response was induced by stroking the tail of the tadpole with a blunt probe, a common technique for a eliciting startle response in tadpoles (Brown & Taylor 1995; Van Buskirk & McCollum 2000). This technique simulates a predation attack as predators often target the tail (Blair & Wassersug 2000). Swimming was videotaped overhead at 30 frames s<sup>-1</sup>, and burst speed estimated from the first half second of swimming by measuring position every other frame using the MorphoSys digital imaging system (Meachum & Duncan 1989). Although a full second was measured for all tadpoles, most showed signs of slowing during the second half second (paired *t*-tests comparing first and second half seconds: *Bufo*:  $t_{202} = 12$  *Scaphiopus*  $t_{202} = 21$ ,  $P < 0.001$  for both), usually because they stopped swimming (i.e. tails clearly had stopped beating). Burst speed was estimated during a single trial, but several runs were initiated for each tadpole and only those runs in which tadpoles swam for greater than 1 s without contacting a wall were used in analysis. Immediately after this trial, tadpoles were killed with an overdose of MS-222 and final masses taken. In total, 48 (out of 60) *Bufo* and 63 (out of 66) *Scaphiopus* (31 low food and 32 high food) provided swims of sufficient quality for analysis.

STATISTICAL ANALYSES

Some tadpoles would initiate swimming bouts spontaneously during the acclimation period. The speeds of spontaneous burst swims were compared with induced swimming speeds of the same individual, using a paired *t*-test, to determine whether induced swims really represent a startle response. The relationships among growth rate, body mass and burst speed were determined using path analysis following Sokal & Rohlf (1981). Mean burst speed of several runs (2–6) are reported here rather than the single fastest run for an individual. There was no indication that tadpoles tired as more runs were made. Fatigue was tested with paired *t*-tests comparing first run to second (*Bufo*  $t_{46} = -0.06$ , *Scaphiopus*  $t_{59} = 1.55$ ), second to third (*Bufo*  $t_{46} = 0.34$ , *Scaphiopus*  $t_{50} = -1.24$ ) and third to fourth (*Bufo*  $t_{24} = 0.38$ , *Scaphiopus*  $t_{29} = 1.64$ ;  $P > 0.1$  in all cases), with additional runs being too few to test reliably. Average speed should more accurately reflect likelihood of surviving multiple predation attempts over an individual's lifetime than a single best time. Results for best times were similar to those for average times, although correlations were somewhat weaker. The two species were analysed separately.

The path model used (Fig. 1) is mathematically identical to a multiple regression with body size and growth rate as independent variables, and burst speed as the dependent variable. Conceptually, this model is distinct from multiple regression in that I assume growth rate determines size, but not the reverse (single-headed arrow from growth rate to final body size). Gosner stage was not included in the model because this was not expected to influence swimming speed until near metamorphic climax (see, e.g., Huey 1980; Dudley, King & Wassersug 1991). In addition, I did not include feeding level for *Scaphiopus* in the path analysis as this treatment was used to get the full range of growth rate. Because feeding manipulations had inconsistent effects on trout (Gregory & Wood 1999) and only mattered for one mode of swimming, I did not expect this manipulation to directly affect swimming performance. However, I did test for the effect of these variables using analysis of covariance to confirm that they did not confound the *a priori* path model.

A complication of this path model is that growth rate and final mass are necessarily autocorrelated because the former is calculated from the latter. Collinearity in general and autocorrelation in particular tend to increase estimated correlations with other variables and may lead to spurious correlations (e.g. Petraitis, Dunham & Niewiarowski 1996; Sheets & Mitchell 2001). One diagnostic for determining the severity of collinearity is the variance inflation factor, which Petraitis *et al.* (1996) recommend should be less than 10. In the present case, variance inflation factors (estimated following Neter *et al.* 1996) were 5.7 for *Bufo* and 8.2 for *Scaphiopus*. Further, ridge regression had little effect on coefficient values for either species,



**Fig. 1.** Path diagrams for (a) *Bufo* ( $N = 48$ ) and (b) *Scaphiopus* ( $N = 63$  with ration levels combined). Solid lines represent positive effects, dashed line is for negative effects. The path coefficients are above each line. U represents residual (unknown) effects not ascribed to either growth rate or body size.

so no adjustments were made to final values. To confirm that the general pattern observed was not merely a by-product of autocorrelation, I also used a randomization simulation to generate a distribution of coefficients that is due entirely to autocorrelation. The simulations were run using MathCad 8 to generate random distributions and calculate correlations. Random values were selected to represent the initial mass and final mass from a distribution having the same means and standard deviations as the actual distributions (*Bufo*: initial  $23.8 \pm 2.7$  (mean  $\pm$  SD) mg, final  $115.0 \pm 27.9$ ; *Scaphiopus*: initial  $212.5 \pm 32.3$ , final  $1494.7 \pm 852$ ). These values were natural log (ln) transformed and then used to calculate growth rate. Simulated burst speeds were derived from the regression of ln(final mass) on burst speed and adding a random error deviation from this regression similar to the residual variation in the original data. For *Bufo* these values were: burst speed =  $26.936 + 4.624 \times \ln(\text{mass})$  with SD of the residuals = 2.9535. For *Scaphiopus* these values were: burst speed =  $1.866 + 0.4368 \times \ln(\text{mass})$  with SD of the residuals = 0.4089. I then calculated the

path coefficients for the simulated data as I did for the real data for 5000 random samples of each species. This many runs of the simulation were required before the variance stabilized (i.e. reached an asymptote). These coefficients were then ranked and the range where 95% of the values occurred determined for comparison with the coefficients from real data.

## Results

Realized growth rates for *Bufo* were  $7.6 \pm 2.1$  mg day<sup>-1</sup> (mean  $\pm$  SD), comparable to those reported for wild populations (Werner & Glennemeier 1999). Realized growth rates for *Scaphiopus* were  $34.8 \pm 9.8$  mg day<sup>-1</sup> for the low-food treatment and  $150.0 \pm 22.9$  mg day<sup>-1</sup> for the high-food treatment. These were also comparable to the minimal and maximal rates seen in wild populations, respectively (Morey 1994).

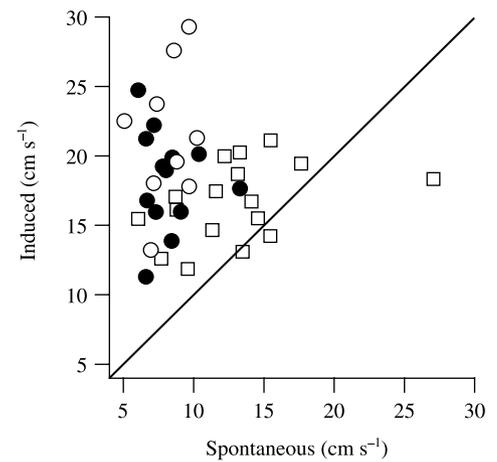
Unlike Gregory & Wood's (1999) finding for critical swimming speed in trout, there was no effect of food ration on the relationship between growth rate and burst speed for *Scaphiopus* after controlling for body size (analysis of covariance with  $\ln(\text{mass})$  as covariate, effect of ration  $F_{1,58} = 0.76$ ;  $P = 0.4$ ). Therefore, these treatments were combined for further analysis of *S. hammondi*. Developmental stage also had no effect on swimming speed once mass was taken into account ( $P > 0.7$  for both species), and was not included in the following model.

If we initially ignore potential complications of autocorrelation, all path coefficients were significant ( $P < 0.05$ ). For both species there was a trade-off between growth rate and burst speed (i.e. a negative path coefficient leading from growth rate to burst speed, Fig. 1). Not surprisingly, faster-growing tadpoles were also larger, and larger tadpoles had a faster raw burst speed than smaller tadpoles (positive path coefficients in Fig. 1). The direct effect of growth rate explained 20% and 34% of the variation in burst speed (partial coefficients of determination) for *Bufo* and *Scaphiopus*, respectively. This is comparable to the 20–37% reported for critical swimming speed in teleosts (Kolok & Oris 1995; Gregory & Wood 1998, 1999). However, the autocorrelation between growth rate and body size makes interpretation of the relative strengths of coefficients unreliable (Petraitis *et al.* 1996).

Induced swims were significantly faster than spontaneous swimming speeds of the same individual (*Bufo*  $t_{16} = 3.4$ ; *Scaphiopus*  $t_{22} = 20.9$ ;  $P < 0.001$  for each species, Fig. 2), suggesting that induced swims truly were startle responses. Spontaneous speeds of high- and low-fed *Scaphiopus* did not differ, but the much smaller *Bufo* had significantly faster spontaneous speeds ( $t_{38} = 4.9$ ;  $P < 0.01$ ).

## SIMULATED EFFECTS OF AUTOCORRELATION

Because the results of the randomization simulation are derived from randomly selected values, the simu-

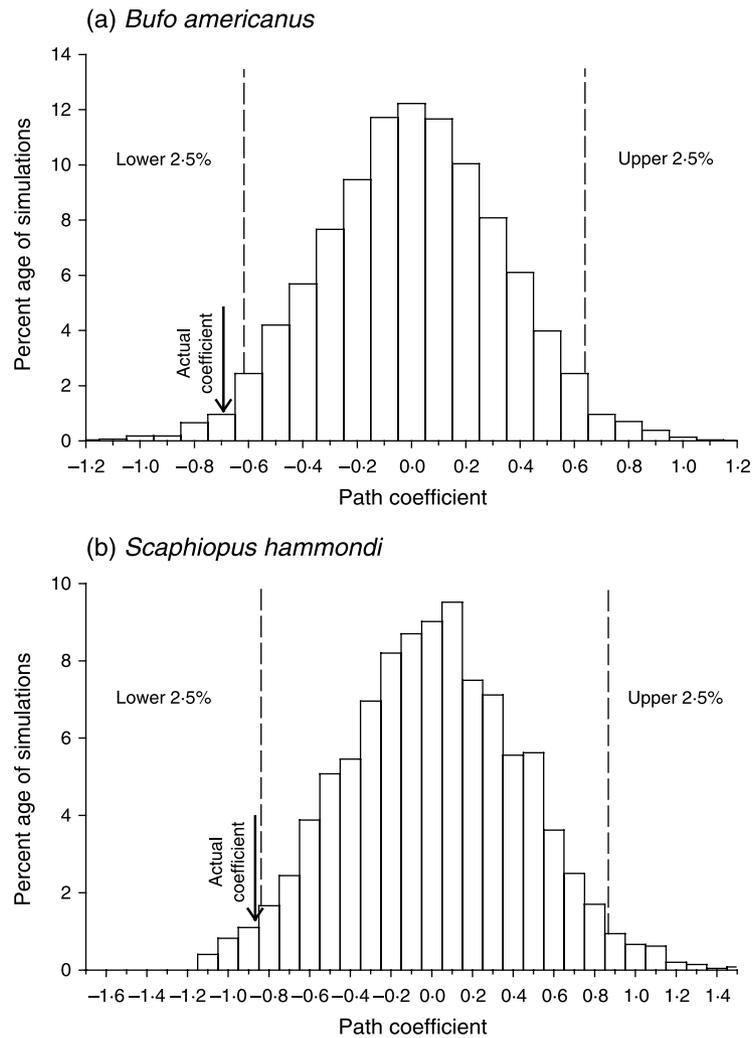


**Fig. 2.** Effectiveness of induced swims as a startle response. Each point represents the mean spontaneous swimming speed and the mean induced swimming speed for the same individual. Diagonal line represents equal speeds. Induced swimming speeds were faster than spontaneous speeds (above the diagonal) with the exception of three *Bufo*. □ *Bufo americanus*; ● *Scaphiopus hammondi* on low ration; ○ *S. hammondi* on high ration.

lated path coefficients between growth rate and swimming speed should be entirely due to autocorrelation between final mass and growth rate. Path analysis appears to be able to remove the effects of autocorrelation as the average simulated coefficients from growth rate to speed are near zero (Fig. 3). However, as expected when collinearity is present (Petraitis *et al.* 1996), the range of values around the mean are quite large. Clearly, with such large confidence intervals spurious correlations are likely to be common. For both species, the actual path coefficients for the effect of growth rate on swimming speed do, nonetheless, fall outside the two-tailed 95% range. I therefore conclude that the trade-off between growth rate and swimming speed is real and not merely a statistical aberration. However, it is clearly not advisable to try to draw inferences on the relative strengths of growth rate or body size on swimming speed.

## Discussion

This report extends the number of vertebrate species showing a trade-off between intrinsic growth rate and swimming speed to a total of five (six, if transgenic salmon are included). Importantly, it shows that this trade-off is not peculiar to teleosts, but also occurs in larval anurans. In addition, I have measured a swimming mode, burst speed, which has been measured in only one other study that relates locomotion to growth rate (Billerbeck *et al.* 2001). Burst speed is an anaerobic form of locomotion distinct from the aerobic 'critical swimming speed' already reported for teleosts. Interestingly, tests of endurance, a third swimming mode, do not appear to show the same trade-off in trout (Gregory & Wood 1999). The difference in swimming



**Fig. 3.** Distribution of simulated path coefficients for the direct effect of growth rate on swimming speed for model in Fig. 1 for (a) *Bufo* and (b) *Scaphiopus*. All simulated coefficients are derived entirely from the autocorrelation between growth rate and size. Actual coefficients calculated from data, indicated by arrows, fall beyond 95% of the values around the mean, indicated by dashed lines.

mode may also explain why I failed to find an effect of ration level on burst speed in contrast with that found by Gregory & Wood (1999) for critical swimming speed in trout. The existence of a trade-off between growth rate and swimming speed in such distantly related anuran species as well as teleosts suggests that it may be true for vertebrates in general. It remains to be seen if the trade-off also applies to terrestrial modes of locomotion. Klukowski, Jenkinson & Nelson (1998) found an increase in sprint speed in male lizards with reduced growth rate when they experimentally elevated testosterone levels. However, it is difficult to tell if growth rate and sprint speed in this study are directly related or only indirectly connected through steroid effects.

The current study also shows that stimulated swimming is typically faster than spontaneous swimming speeds in anuran tadpoles. Curiously, *B. americanus* showed significantly faster spontaneous swimming speeds than did *S. hammondi*, although the latter was capable of much faster speeds when startled. This may

reflect differences in feeding patterns (*Bufo* are generally very active during feeding), social behaviour (*Bufo* are also gregarious feeders) or relative cover in breeding ponds. *Scaphiopus* generally breed in ephemeral ponds with little cover and general inactivity may decrease detection by potential predators, although other species of *Scaphiopus* are noted for having especially active tadpoles (e.g. *S. couchii*; Dayton & Fitzgerald 2001).

The simulations suggest that it may be difficult to detect costs of rapid growth when costs are also influenced by body size. Given a path diagram such as that in Fig. 1, it is tempting to try to estimate the relative importance of different factors on a target variable. In this case, one might ask what the net effect of growth rate is on swimming speed. Even though rapid growth has a negative direct effect, fast-growing individuals may still be faster swimmers than slow-growing individuals of the same age because they are larger. Unfortunately, because of the autocorrelation between growth rate and body size, such an estimate would not

be reliable (Petraitis *et al.* 1996). The real path coefficients, independent of autocorrelation, may be close to zero or nearly twice as large as calculated. In truth, the fitness consequence of rapid growth will depend as much upon local ecology as it does on the physiological relationships described here. For anurans, some predators (fish and insects) will not take tadpoles above a certain size (e.g. Richards & Bull 1990; Tejedo 1993), while other predators (birds and mammals) target larger tadpoles (e.g. Crump & Vaira 1991). In the former case, large size and inactivity appear to be the most important antipredator strategies and a rapid intrinsic growth rate should be favoured even if this occurs at the expense of speed (Van Buskirk & McCollum 2000). In the latter case, large size offers little advantage in itself and rapid burst speed may be more important for evading terrestrial predators. In addition, differences in perceived risk of predation can have profound effects on competitive interactions within populations (e.g. Reinhardt 1999; Relyea 2000), which will feedback into realized growth rates dependent upon food intake. Within a population, this trade-off may serve to maintain genetic variation for growth rate and size within a population because fast-growing but slow-swimming individuals may have the same fitness as slow-growing but fast-swimming individuals (Mangel & Stamps 2001).

What causes the trade-off between growth rate and swimming speed? Growth rate may limit metabolic scope, reducing the energy available for locomotion (Billerbeck *et al.* 2001; Conover & Schultz 1997). It has also been suggested that the reduction in protein turnover correlated with rapid growth could reduce swimming efficiency (Morgan, McCarthy & Metcalfe 2000). In addition, developmental characteristics may limit swimming speed. A trade-off between growth rate and skeletal development has been found across bird species (Starck 1994) and within one species of fish (Arendt & Wilson 2000). A stiff skeleton is important in determining how efficiently muscle contraction is translated into locomotion (McHenry, Pell & Long 1995). However, most tadpoles, including *Scaphiopus* (Hall & Larsen 1998), show little mineralization until metamorphic climax, so skeletal development cannot explain the results reported here. Muscle development is also influenced by growth rate (Arendt 2000) and preliminary data suggest this partially explains variation in *Bufo* swimming speeds (J. D. Arendt, unpublished observation). Given that growth rate and locomotor speed are both composite traits, it is likely that a combination of factors may underlie the trade-off, and the particular combination may vary from species to species.

It makes sense that the growth processes should influence performance variables (Arendt 1997; Gotthard 2000; Mangel & Stamps 2001), and biologically it is growth rate that determines size at a given age. Unfortunately, growth rate cannot be measured directly and must be estimated from size. How can we avoid the

complications of autocorrelation? Estimating growth rate from a trajectory (i.e. size measured at three or more ages) should decrease the autocorrelation although it is unlikely that collinearity can be eliminated entirely. Alternatively, individuals can be subsampled from a large population so that they have similar final sizes but different initial sizes. This necessitates using animals of different ages, which may introduce an additional complicating variable into the analysis. In conclusion, two point estimates of growth rate as described here represent a worst-case scenario for studying costs of rapid growth and should be avoided whenever possible. Nonetheless, it is possible to show that costs of rapid growth exist in general, and that this study shows rapid growth compromises burst speed in particular. The implication of this trade-off is that it matters not only how large one is, but how one gets to be that size.

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