Are Commonly Used Fitness Predictors Accurate? A Meta-analysis of Amphibian Size and Age at Metamorphosis

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Reaching developmental milestones younger and at larger sizes is commonly claimed to reflect increased fitness. However, the amount of fitness gained from being larger and younger at a milestone may vary with several attributes, particularly evolutionary history, life history, and environmental characteristics. We used a meta-analysis to investigate whether these attributes affected the utility of developmental milestones to be used as predictors of future fitness. We chose amphibian size at and time to metamorphosis (SAM and TTM, respectively) as model developmental milestones, because studies have examined SAM and TTM's efficacy for fitness prediction (via post-metamorphic fitness proxies), and they are commonly used in a variety of studies testing ecological and evolutionary theory and more applied research on the effects of anthropogenic stressors. We found variation in the predictive power of SAM and TTM for post-metamorphic performance. SAM was a more consistent predictor of post-metamorphic performance than TTM, but also had a higher sample size. Life history and study design (i.e., laboratory vs. field studies), but not evolutionary history, were important for explaining variation in predictive power for post-metamorphic performance. The correlation between SAM and performance increased with the proportion of time to maturity reached at metamorphosis, suggesting that species can compensate for initial fitness reductions through ontogeny. Because numerous researchers use size and age at developmental milestones to indicate fitness, we urge caution in interpreting their results due to the species- and system-specific nature of fitness surrogates.

P REDICTING an individual's fitness is a great challenge, but a number of correlated traits have been used as proxies for fitness estimates. The size and age at certain developmental milestones in an individual's lifetime are thought to be useful fitness predictors in many organisms (Day and Rowe, 2002; Kingsolver and Pfennig, 2007). These milestones occur at transitions in an organism's life history, including hatching/birth/germination (all organisms), metamorphosis (amphibians and invertebrates), fledging (birds), and maturity (all organisms). Generally, being younger and larger at each milestone is advantageous, because the individual will be more likely to survive and reach the next milestone at a younger age and larger size (though there are certainly trade-offs between growth and development). These advantages should subsequently increase lifetime reproductive success (Roff, 1992; Stearns, 1992), because large body sizes and faster development are under strong selection. In a meta-analysis, Kingsolver and Pfennig (2004) found directional selection for increased body sizes and decreased developmental times in 79% and 84% of studies, respectively, across a range of taxa. The trend of larger body sizes increasing fitness remained when survival, fecundity, and mating success were examined separately. As predictors of future fitness, the size at and time to developmental milestones can be important for examining ecological and evolutionary theory (e.g., Wilbur and Collins, 1973; Dahl et al., 2012) and the impacts of anthropogenic stressors (e.g., Boone et al., 2001; Smith, 2005).

While size and age at developmental milestones have been shown to be effective predictors of future fitness for many organisms, it is likely that species vary in the efficacy of these traits. Because of the utility of studying organisms for shorter amounts of time to infer later performance or fitness, knowledge of when size and age at developmental

milestones are accurate predictors of fitness is immensely valuable. This predictive power could vary with a number of factors, including a species' or population's evolutionary history, environmental characteristics, and life history traits. Phylogenetics and life history characteristics may be especially useful in distinguishing among groups of similar species in how well a developmental milestone predicts future fitness, because different strategies have evolved in response to life history trade-offs and environmental challenges (Hamel et al., 2010; Hector and Nakagawa, 2012).

One potentially informative life history characteristic is the amount of time or growth needed between the measured developmental milestone and maturity or reproduction (Beck and Congdon, 1999), either in absolute or relative terms (i.e., the proportion of time to or size at adulthood attained at the developmental milestone). When individuals of a species (or population) are very close to maturity or reproduction at a developmental milestone, size at and time to the developmental milestone are likely to be accurate predictors of fitness. In this case, the size and timing differences among individuals are very likely to be maintained, and entering adulthood earlier and at a larger size tends to increase fitness (Roff, 1992; Stearns, 1992). Similar trends may occur during carryover and maternal effects, where experiences early in life or due to maternal influence are likely to have stronger effects on short-term rather than long-term performance (e.g., Semlitsch and Gibbons, 1990; Lindholm et al., 2006). As the amount of time lengthens between a developmental milestone and the first reproductive opportunity, individuals may utilize compensatory or catch-up growth and development (Sadeh et al., 2011; Hector and Nakagawa, 2012) to reduce the impact of initial differences at a developmental milestone. Additionally, increased time creates the potential for greater environmental variability that can decrease the correlation between size

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Table 1. Characteristics of studies used in meta-analysis.

Reference	Species	SAM/TTM	Performance metrics	Study design	Significance[a]
Altwegg and Reyer, 2003	*Pelophylax esculenta* (PEES)[b,c]	SAM	Growth, size, survival	Outdoor enclosure	6/9
	Pelophylax lessonae (PELE)[c]	TTM	Growth, size, survival	Outdoor enclosure	1/4
Alvarez and Nicieza, 2002	*Discoglossus galganoi* (DIGA)	SAM	Physical performance	Laboratory	1/1
Beck and Congdon, 1999	*Anaxyrus terrestris* (ANTE)	SAM	Growth, size, survival	Outdoor enclosure	4/6
		TTM	Growth, size, survival	Outdoor enclosure	1/7
Beck and Congdon, 2000	*Anaxyrus terrestris* (ANTE)	SAM	Metabolism, physical performance	Laboratory	2/3
		TTM	Metabolism, physical performance	Laboratory	0/3
Berven, 1990	*Lithobates sylvaticus* (LISY)	SAM	Age at reproduction, size, survival	Field	6/7
		TTM	Age at reproduction, size, survival	Field	0/2
Berven, 2009	*L. sylvaticus* (LISY)	SAM	Age at reproduction, size, survival	Field	2/6
		TTM	Age at reproduction, size, survival	Field	0/6
Berven and Gill, 1983	*L. sylvaticus* (LISY)	SAM	Size, survival	Field	3/4
		TTM	Size, survival	Field	0/2
Boone, 2005	*Anaxyrus woodhousii* (ANWO)	SAM	Growth, size, survival	Outdoor enclosure	0/3
	L. blairi (LIBL)	SAM	Growth, size, survival	Outdoor enclosure	0/3
		TTM	Growth, size, survival	Outdoor enclosure	0/3
	L. clamitans (LICL)	SAM	Growth, size, survival	Outdoor enclosure	0/3
	L. sphenocephalus (LISP)	SAM	Growth, size, survival	Outdoor enclosure	3/3
		TTM	Growth, size, survival	Outdoor enclosure	3/3
Chelgren et al., 2006	*Rana aurora* (RAAU)	SAM	Physical performance	Field	2/4
		TTM	Physical performance	Field	0/2
Davis et al., 2011	*L. clamitans* (LICL)	SAM	Foraging	Outdoor enclosure	0/1
Distel and Boone, 2009	*Anaxyrus americanus* (ANAM)	SAM	Size, survival	Outdoor enclosure	0/2
		TTM	Size, survival	Outdoor enclosure	0/2
Distel and Boone, 2010	*Anaxyrus americanus* (ANAM)	SAM	Size, survival	Outdoor enclosure	0/2
	L. pipiens (LIPI)	SAM	Size, survival	Outdoor enclosure	2/2
Earl and Semlitsch, unpubl.	*Anaxyrus americanus* (ANAM)	SAM	Body condition, size, survival	Outdoor enclosure	2/6
		TTM	Body condition, size, survival	Outdoor enclosure	3/6
	L. sphenocephalus (LISP)	SAM	Body condition, size, survival	Outdoor enclosure	3/6
		TTM	Body condition, size, survival	Outdoor enclosure	4/6
	L. sylvaticus (LISY)	SAM	Body condition, size, survival	Outdoor enclosure	0/6
		TTM	Body condition, size, survival	Outdoor enclosure	2/6
Goater et al., 1993	*Bufo bufo* (BUBU)	SAM	Physical performance	Laboratory	1/4
Howard, unpubl.	*Ambystoma tigrinum* (AMTI)	SAM	Size	Laboratory	1/1
		TTM	Size	Laboratory	0/1
John-Alder and Morin, 1990	*Anaxyrus woodhousii* (ANWO)	SAM	Physical performance	Laboratory	2/3

Table 1. Continued.

Reference	Species	SAM/TTM	Performance metrics	Study design	Significance[a]
Morey and Reznick, 2001	*Spea hammondii* (SPHA)	SAM	Growth, size, foraging	Laboratory, laboratory/outdoor enclosure, fed in outdoor enclosure	17/27
		TTM	Growth, size, foraging	Laboratory, laboratory/outdoor enclosure, fed in outdoor enclosure	2/12
Newman and Dunham, 1994	*Scaphiopus couchii* (SCCO)	SAM	Water conservation	Laboratory	1/2
Nicieza et al., 2006	*D. galganoi* (DIGA)	SAM	Physical performance	Laboratory	1/1
Pfennig et al., 1991	*Spea multiplicata* (SPMU)	SAM	Survival	Laboratory	1/1
Sams and Boone, 2010	*Anaxyrus americanus* (ANAM)	SAM	Size, survival	Laboratory	2/2
Schmidt et al., 2012	*Pelobates fuscus* (PEFU)	SAM	Body condition, reproduction, size, survival	Field	0/8
		TTM	Body condition, reproduction, size, survival	Field	0/10
Scott et al., 2007	*Ambystoma opacum* (AMOP)	SAM	Age at maturity, survival	Field	1/2
Semlitsch et al., 1988	*Ambystoma talpoideum* (AMTA)	SAM	Age at maturity, size, survival	Field	3/5
		TTM	Age at maturity, size, survival	Field	3/6
Smith, 1987	*Pseudacris triseriata* (PSTR)	SAM	Age at maturity, size, survival	Field	4/4
		TTM	Size, survival	Field	0/2
Van Allen et al., 2010	*Agalychnis callidrys* (AGCA)	SAM	Size	Laboratory	1/1
	Pseudacris crucifer (PSCR)	SAM	Size	Laboratory	1/1
Watkins, 2001	*Pseudacris regilla* (PSRE)	SAM	Physical performance, size	Laboratory	2/2
		TTM	Physical performance, size	Laboratory	0/2

[a] Number of significant tests out of the total number of tests examining the relationship between SAM or TTM and post-metamorphic performance that had information available for meta-analysis (see methods section). Note significant tests with the opposite relationship as predicted were counted as non-significant and that significance was not part of our analyses.
[b] Species code is in parentheses (first two letters of genus and first two letters for species).
[c] Analyses for *P. esceulenta* and *P. lessonae* were combined.

at and time to a developmental milestone and future performance or fitness. Although there is circumstantial evidence to support the hypothesis that the accuracy of fitness correlates at developmental milestones should vary with the time to first reproduction and/or adult size (e.g., Goater et al., 1993; Boone, 2005), no formal tests have been conducted.

We explored the importance of phylogeny, life history, and study design for determining the strength of the relationship between size at and time to metamorphosis and post-metamorphic performance (a proxy for fitness; see below) in amphibians. Amphibian metamorphosis is ideal for this research, because there are many studies that have examined the relationship between size at and time to metamorphosis (SAM and TTM, respectively) and post-metamorphic performance (e.g., Semlitsch et al., 1988; Berven, 1990; Schmidt et al., 2012), and this milestone has been used as a frequent predictor of future fitness for a variety of biological studies (e.g., Wilbur and Collins, 1973; Rowe and Ludwig, 1991; Relyea, 2007). In this study, we performed a meta-analysis with the goal of determining how well SAM and TTM predict post-metamorphic performance in amphibians and what factors influence their predictive power. Specifically, we examined whether evolutionary history, life history characteristics (relative time and size between metamorphosis and adulthood), or study type influenced the correlation between SAM or TTM and post-metamorphic performance. Although many studies claim to be testing the correlation between SAM or TTM and fitness, they generally are measuring other fitness proxies (e.g., body size, growth rate) or fitness components (e.g., survival, clutch size in a single season), which we call post-metamorphic performance for clarity in this study.

MATERIALS AND METHODS

An extensive literature search revealed 24 articles, including studies on 20 species in five families of anurans and three species in one family of caudate, which contained sufficient data for this analysis (Table 1). Articles were located by searching Scopus and Google Scholar using search terms "fitness," "amphibian," and either "size at metamorphosis" or "time to metamorphosis." The final search was completed in December 2012. Additional unpublished data were included from R. Howard, Boone (2005), Distel and Boone (2009), and Earl and Semlitsch (2013) to help deal with potential publication bias (Jennions et al., 2013). Several studies that collected data relevant to this study were not utilized because the analysis used a measure of size taken greater than a week after metamorphosis (Capellán and Nicieza, 2007), after feeding metamorphs, or when the information available was insufficient for a meta-analysis (Martof, 1956; Goater, 1994; Relyea and Hoverman, 2003). For each study, we extracted test statistics (e.g., correlation coefficient, F-statistic, t-statistic) used to examine the relationship between SAM or TTM and some measure of post-metamorphic performance (e.g., body size, survival, physical performance), the sample size, the average time individuals spent in their larval period, the time between metamorphosis and the measurement of post-metamorphic performance, the way SAM or TTM was measured and used in the analysis (e.g., continuous variable, categorical variable), the amphibian species, study type (laboratory, field, or outdoor enclosure), and the type of fitness measure. Post-metamorphic performance measures were grouped into eight categories: body

size, survival, age at a developmental milestone (maturity or reproduction), growth rate, body condition, reproduction, metabolism, and physical performance (e.g., endurance, maximum hop distance). For each species, we calculated the proportion of adult size reached at metamorphosis and the proportion of the time to maturity reached at metamorphosis from the articles included in this study and cited averages (Lannoo, 2005). When only limits were available, we used the midpoint. These proportions were square root transformed to meet the assumption of normality and homogeneity of variances. Some of the studies included treatments in the larval stage that altered SAM and TTM. We recognize that these could affect our results, but examination of the several available data sets showed that there was overlap in values of SAM and TTM across treatments.

For each analysis, we used one test-statistic as a replicate, but each replicate was weighted by the within-study sample size (i.e., the number of replicates used to calculate the test-statistic) and the study was used as the subject variable in a mixed model to account for non-independence between different measures of post-metamorphic performance from the same study (Rosenberg et al., 2013). We considered any independent data sets within each scientific article (i.e., tests using different sets of individuals) to be different studies. Test-statistics were all converted to Pearson's product moment correlation coefficient (r) using standard conversion formulas (Winfred et al., 2001). Where a positive effect of fitness resulted in a correlation with a different sign (positive or negative), we multiplied r times −1 to be consistent with the other metrics. For example, when examining the correlation between SAM and survival, r would be positive for a fitness gain from a larger SAM, but when examining the correlation between SAM and age at maturity, a fitness gain would be reflected in a negative value of r. In this case, we multiplied the correlation for age at maturity times −1 to make the r-value positive to be consistent with the other values. All r-values were z-transformed for analysis (Rosenberg et al., 2013).

Prior to analysis, we first examined whether the method for measuring SAM or TTM affected the value of r by running a weighted ANOVA (proc MIXED) in PC SAS (SAS Institute, Inc., Cary, NC), where data points were weighted using the sample size used to calculate r (Rosenberg et al., 2013) and the study was used as a subject. We then examined how the post-metamorphic performance measure related to the amount of time between metamorphosis and the measurement of post-metamorphic performance using another weighted ANOVA. Post-metamorphic performance measures with a very short amount of time between metamorphosis and the measurement of post-metamorphic performance (~two weeks) were eliminated from further analyses, because they were unlikely to reflect long-term fitness. All analyses for size at and time to metamorphosis were performed separately. While it would have been advantageous to consider SAM and TTM simultaneously due to potential tradeoffs between the two variables, most studies did not have the information available to do so. However, for the available studies, we did examine the relationship between the SAM-fitness correlation and TTM-fitness correlation using a weighted mixed model with study as the subject.

Next, we determined if there was a phylogenetic signal in the data using phylogenetic meta-analysis (Lajeunesse, 2009). For this analysis, all studies were collapsed into one value per taxonomic unit. For collapsed values, we took
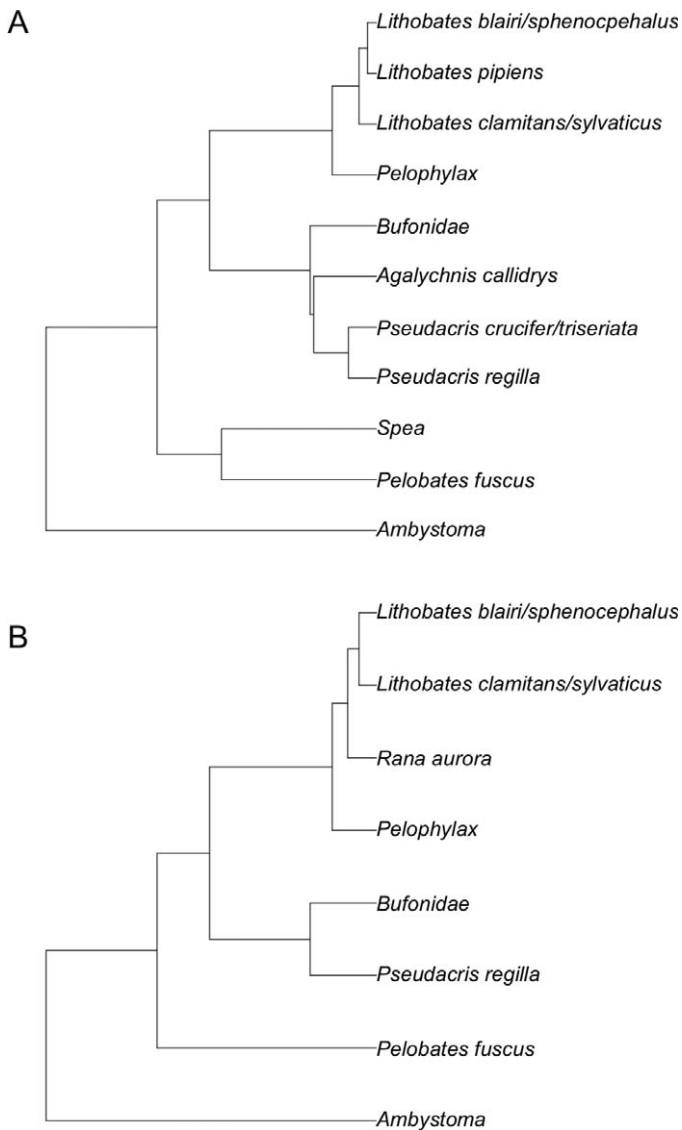
Fig. 1. Proposed phylogeny used in the phylogenetic meta-analysis of the correlation between size at (A) and time to metamorphosis (B) and post-metamorphic fitness.

weighted means of z-transformed r-values using within study sample sizes as weights. We determined the phylogeny for the taxa in the study using Pyron and Wiens (2011) and calculated the distance between branches using the median value of divergence time from timetree.org (Hedges et al., 2006). Unfortunately, divergence times were not available for all species. In such cases, we collapsed taxa into the most basal taxonomic classification possible: species complexes, genera, or family. We used this tree as the hypothesized phylogenetic relationship among taxa in our study (Fig. 1), which was converted into the Newick format for input into phyloMeta 1.3 beta to perform the phylogenetic meta-analysis (Lajeunesse, 2009, 2011). For the analysis, we compared Akaike's Information Criterion (AIC) for a traditional meta-analysis and a phylogenetic meta-analysis (Lajeunesse, 2011) with no other variables in the model. When the traditional meta-analysis had a lower AIC value (indicating a better model fit), we chose to proceed using only the traditional meta-analysis.

To examine the effects of hypothesized factors on the relationship between SAM or TTM and post-metamorphic performance, we used an information-theoretic approach (Burnham and Anderson, 2002). Models were ranked using Akaike's Information Criterion corrected for low samples sizes (AIC$_c$), where the lowest value indicates the best supported model, and any model within three units is considered a competing model (Burnham and Anderson, 2002). Additionally, Akaike weights were computed to examine the relative support for each model and for each variable (Burnham and Anderson, 2002). We first determined the best null model by ranking four null models with AIC$_c$: an intercept only model; a study model containing a categorical variable indicating whether the study was performed in the laboratory, field, or an outdoor enclosure; a methods model containing a categorical variable for the fitness parameter and a continuous variable for amount of time between metamorphosis and the measurement of post-metamorphic performance; and a model containing parameters from both the study and methods model. The best model was used as a component in all candidate models to be ranked: null model, taxonomic family, proportion of adult size attained at metamorphosis (i.e., SAM divided by adult size), proportion of time to maturity attained at metamorphosis (i.e., TTM divided by time to maturity), and all combinations of these variables. For cases with competing models, parameter estimates were made using model-averaging of all candidate models. For models not containing the parameter being averaged, we used an estimate and standard error of zero in the average. All models were implemented in PC SAS using proc MIXED.

Publication bias can occur when the studies in a meta-analysis are not representative of all studies performed. This frequently happens when studies that have non-significant results are less likely to be published (Jennions et al., 2013). We tested for publication bias using three methods: the relationship between effect size and sample variance, Egger's linear regression and the failsafe number. For the relationship between effect size and sample variance, we examined Spearman's and Kendall's correlation between the standardized effect size and the sample variance (Jennions et al., 2013). The significance of these correlations indicate publication bias. Egger's linear regression is based on the regression of the standard normal deviates versus precision (inverse of variance). The significance of the intercept indicates funnel plot asymmetry, another measure of publication bias (Jennions et al., 2013). These two measures are likely to indicate bias in our results for many reasons besides studies missing from the meta-analysis, including the inclusion of both observational and experimental studies, different taxa, uneven sampling of different taxa and habitats (particularly a strong North American bias), and differences in the time to study termination (Jennions et al., 2013). We also calculated the failsafe number, which is the number of non-significant studies not included in the meta-analysis that would cause the effect size to be non-significant (i.e., not different from zero). We used Rosenberg's N$_+$ with a t-distribution computed using the fail-safe calculator (http://www.rosenberglab.net/software.html#FailSafe). Unpublished studies are unlikely to affect the results if N$_+$ is greater than the robust failsafe number (5N+10; Jennions et al., 2013).

RESULTS

The proportion of adult size attained at metamorphosis and proportion of time to maturity attained at metamorphosis were significantly correlated (r = 0.56, P = 0.009, n = 21; Fig. 2A). These variables also varied by taxonomic family

(proportion of adult size attained at metamorphosis: $F_{4,16}=$ 11.13, $P = 0.0002$; proportion of time to maturity attained at metamorphosis: $F_{5,16}= 3.96$, $P = 0.02$), though Tukey's pairwise comparison revealed no significant differences among pairs of families in proportion of time to maturity attained at metamorphosis. The proportion of adult size attained at metamorphosis was highest in ambystomatids and lowest in bufonids, with hylids, ranids, and pelobatids intermediate (Fig. 2B). As expected, the proportion of adult size attained at metamorphosis was correlated with SAM ($r = 0.77$, $P < 0.0001$, $n = 21$; Fig. 3A), and the proportion of time to maturity attained at metamorphosis was highly correlated with TTM ($r = 0.93$, $P < 0.0001$, $n = 21$; Fig. 3B). We found no correlation between the SAM-fitness correlation and the TTM-fitness correlation ($F_{1,27} = 2.13$, $P = 0.16$), but only six studies on eight species had information on both SAM and TTM for the same group of individuals examining the same parameter.

Size at metamorphosis.—The method of measuring SAM did not affect the correlation between SAM and fitness ($F_{2,1} = 4.44$, $P = 0.32$). In the SAM data set, the different ways of measuring fitness varied in amount of time between metamorphosis and the measurement of post-metamorphic performance (the time since metamorphosis when they were measured; $F_{9,25} = 6.48$, $P < 0.0001$; Fig. 4). Post-metamorphic foraging, metabolic rate, physical performance (e.g., maximum jump distance, endurance), and water conservation were all measured shortly after metamorphosis (around two weeks; Fig. 4). Thus, we excluded them from further analysis, as they were less likely to reflect long-term fitness. From the remaining studies available, 11 taxa had enough phylogenetic information available for a phylogenetic meta-analysis (Fig. 1A). However, the traditional meta-analysis had much higher support than the phylogenetic meta-analysis (traditional AIC = 64.48, phylogenetic AIC = 82.52).

For the SAM meta-analysis, we utilized a data set including 24 articles and 19 species from five taxonomic families (Table 1). The best null model was the study model (AIC$_c$ weight = 0.86; Table 2), so its parameters were included in all candidate models. The best overall model included the proportion of time to maturity attained at metamorphosis, the proportion of adult size attained at metamorphosis, and the type of study with no competing models (AIC$_c$ weight = 0.71; Table 3). Parameter estimates indicated that the correlation between SAM and post-metamorphic fitness increased with increasing proportion of time to maturity attained at metamorphosis (Fig. 5), and that correlations were lower in less controlled (field or outdoor enclosure) than more controlled (laboratory or enclosures with supplemental food) studies (Table 4).

For size at metamorphosis, we detected publication bias with the relationship of the standardized effect size to variance and Egger's linear regression, but not with the failsafe number. For the relationship of the standardized effect size to variance, the Spearman ($\rho = 0.35$, $P = 0.0006$) and Kendall ($\tau = 0.24$, $P = 0.0007$) correlation coefficients were significant. This indicates that the effect size increases with increasing variance (or decreasing sample size). Egger's linear regression indicated significant funnel plot asymmetry ($t_{1,24} = 2.65$, $P = 0.009$). However, Rosenberg's N$_+$ (1682) was much larger than the robust failsafe number (135), indicating that the addition of missing studies is unlikely to affect the overall result of the meta-analysis.

Time to metamorphosis.—The method of measuring TTM did not affect the correlation between TTM and fitness ($F_{2,10} = 1.81$, $P = 0.21$). There was also no difference among post-metamorphic fitness measures in amount of time between metamorphosis and the measurement of post-metamorphic performance ($F_{6,6} = 1.74$, $P = 0.26$). From the studies available, eight taxa had enough phylogenetic information available for a phylogenetic meta-analysis (Fig. 1B). However, the traditional meta-analysis had much higher support than the phylogenetic meta-analysis (traditional AIC = 33.98, phylogenetic AIC = 50.28). Thus, further analyses were performed using traditional meta-analysis.

For the TTM meta-analysis, the data set included 16 articles and 14 species from five taxonomic families (Table 1). One of the families (Pelobatidae) was represented by only one species (*Pelobates fuscus*). The best null model was the intercept-only model (AIC$_c$ weight = 0.62; Table 2) with the methods/study model competing. Because almost all parameters in the competing model had confidence intervals that did not overlap zero, we included all its parameters in all candidate models. The best overall model was the global model with two competing models (Table 3). Model-averaging of parameter estimates identified two parameters with confidence intervals that did not include zero (Table 4). The correlation between TTM and post-metamorphic body condition and body size was stronger than other measures of fitness.

For TTM, we detected some publication bias, but it is unlikely to affect the major results. For the relationship of the standardized effect size to variance, both the Kendall ($\tau = -0.31$, $P = 0.005$) and Spearman ($\rho = -0.41$, $P = 0.001$) correlation coefficients were significant. Egger's linear regression indicated funnel plot asymmetry ($t_{1,60} = 3.02$, $P = 0.004$). The meta-analysis showed that the average effect size was not different than zero (see the intercept value in Table 3), and thus, no additional nonsignificant studies would make the results nonsignificant.

DISCUSSION

We found extensive variation in the predictive power of amphibian SAM and TTM for post-metamorphic performance among studies, indicating that size at and time to developmental milestones are not universal predictors of future fitness. We found evidence that study type, life history, and the performance metric could alter the correlation strength, but results were different depending on whether SAM or TTM was the measure used. Also, SAM appears to be a better predictor of fitness for amphibians than TTM, as shown by the significance of the intercept in the best SAM model but not in the best TTM model. However, the sample size was lower for TTM than SAM, so additional data would improve our ability to assess the relationship between TTM and fitness. There was no evidence that evolutionary history (i.e., phylogeny) was important in either analysis.

Size at and time to developmental milestones are commonly used as surrogates of fitness. The use of SAM and TTM are particularly widespread fitness surrogates for amphibians (e.g., Rowe and Ludwig, 1991; Boone et al., 2001). Our findings suggest that caution should be used when interpreting results using these fitness surrogates, particularly regarding the use of TTM in all species and SAM in species with large amounts of time between metamorphosis and reproductive maturity. Because the proportion of
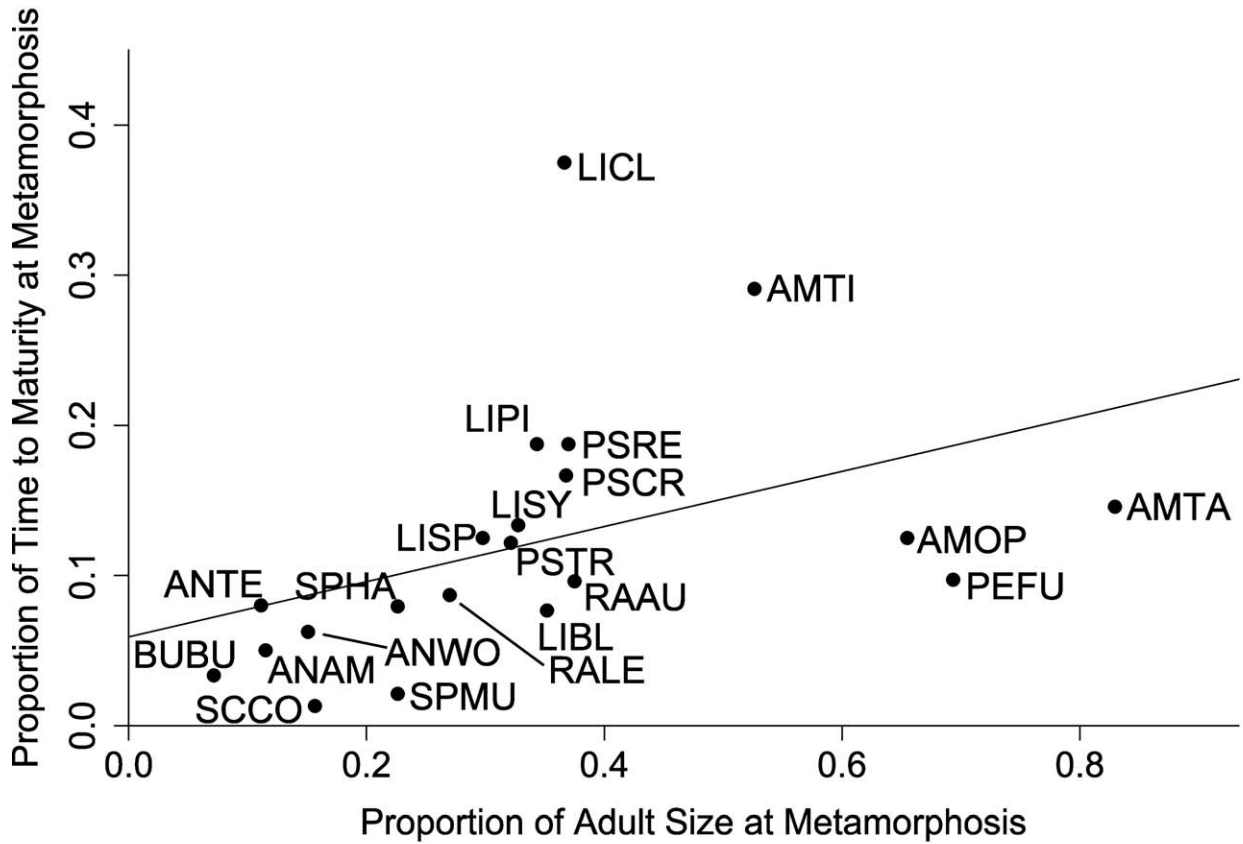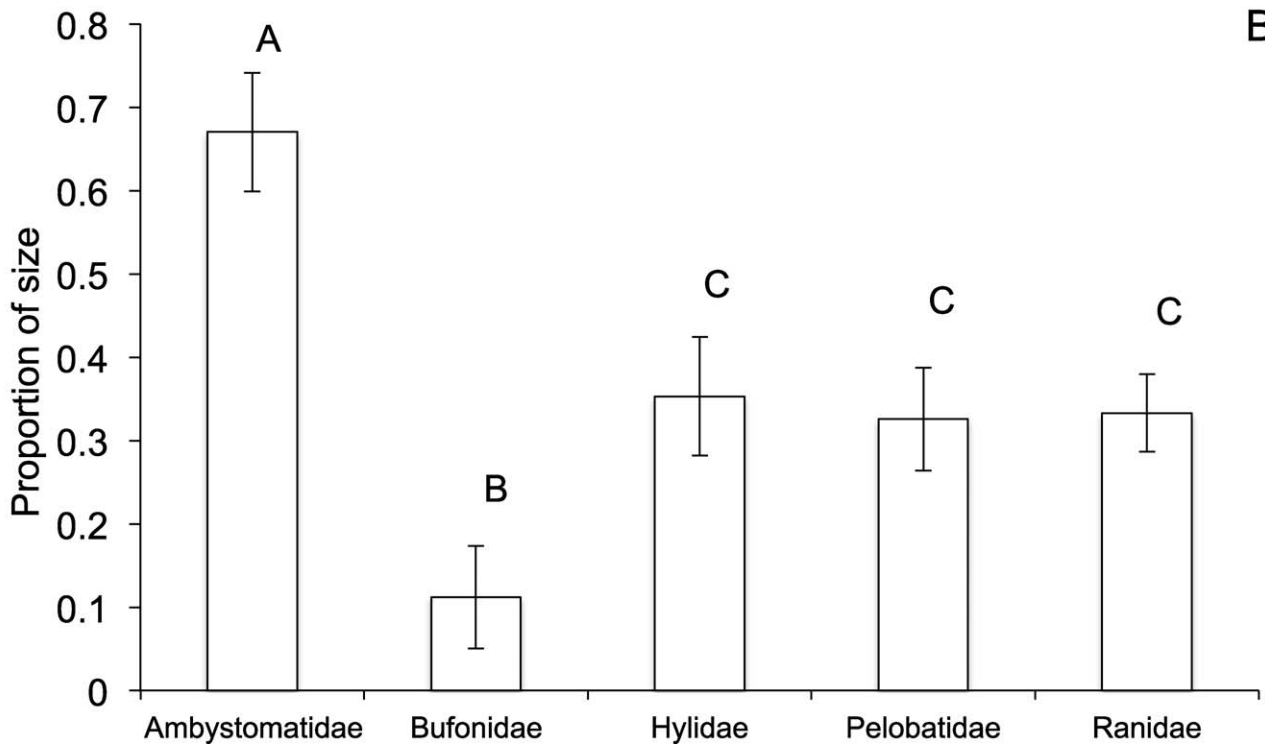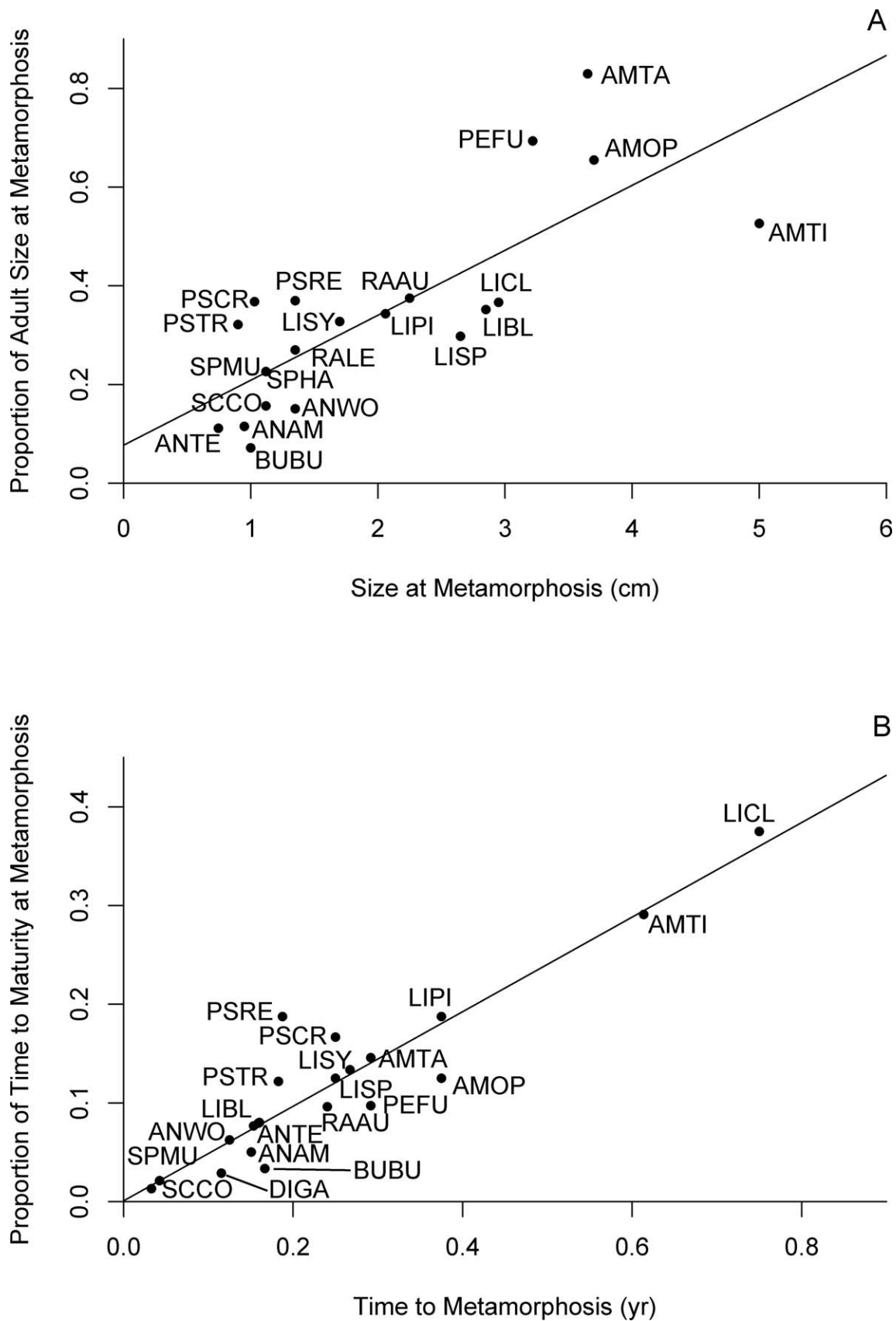
Fig. 2. Correlation among the proportion of adult size and time to maturity attained at metamorphosis (A) and differences among taxonomic family in the proportion of adult size attained at metamorphosis (B). Both analyses used square root transformed proportions. Each point represents a species, and the species code labels each point (A). Different letters indicate significant differences with Tukey's pairwise comparisons (B). Error bars represent standard error (B).

Fig. 3. Correlation between size at metamorphosis (SAM) and the proportion of adult size attained at metamorphosis (A) and between time to metamorphosis (TTM) and the proportion of time to maturity attained at metamorphosis (B). Each point represents a species, and the species code labels each point. Both analyses used square root transformed proportions.
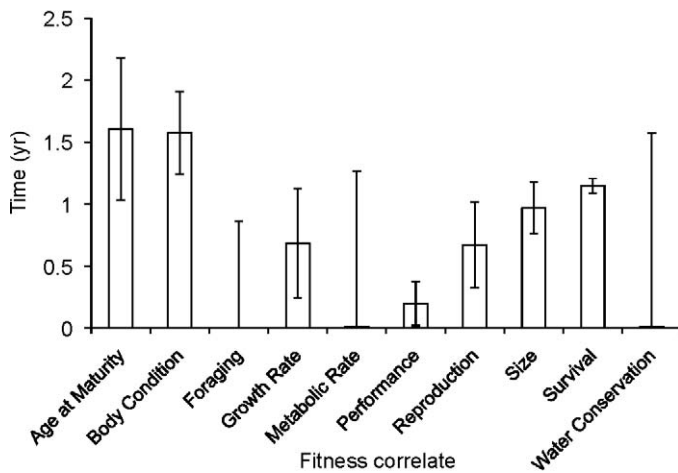
Fig. 4. Difference among fitness correlate measures in the time since metamorphosis when the measurements were made. Analysis used square root transformed time variable.

time to maturity attained at metamorphosis was highly positively correlated with TTM, it may be easier for researchers to use a species or population's average TTM as a predictor of how well SAM will predict fitness. However, the predictive power of the proportion of time to maturity attained at metamorphosis for fitness exhibited considerable variation around the regression line, so species or population-specific information is likely to be the most reliable. Also, it is likely that these relationships vary with trade-offs between SAM and TTM and environmental conditions. More research into such questions will help determine the utility of these guidelines.

We found much stronger support for SAM than TTM as a predictor of fitness. This may, in part, be due to strong selective pressure in some species to optimize time to metamorphosis in relation to pond drying (Morey, 1998). Many amphibians breed in temporary ponds, and thus face severe time constraints for larval growth and development (Morey, 1998). This is taken to the extreme by some members of Pelobatidae, such as *Spea multiplicata*, which can metamorphose in as little as 14 days (Pfennig et al., 1991). Such severe time constraints act to lower the variation in time to metamorphosis among individuals (Morey and Reznick, 2004). It is likely that any variable that lowers the variation in time to or size at a developmental milestone will lower the predictive power of time to or size at a developmental milestone in relation to fitness, because smaller differences in

size or time should be easier to recover from than larger differences. Further, larval constraints (e.g., pond drying, short growing seasons, limited resources) may be better predictors of fitness than characteristics at developmental milestones. De Block and Stoks (2005) found that larval constraints were better predictors than SAM or TTM of lifetime reproductive success in damselflies, which suggests that larval or juvenile experience is not completely represented by characteristics at developmental milestones in all species. Other measures, such as fat stores, may prove to be better predictors than SAM or TTM in some species (De Block and Stoks, 2005; Scott et al., 2007).

Life history affected the correlation between SAM and post-metamorphic performance. The correlation increased with the proportion of time to maturity attained at metamorphosis. Thus, SAM was a better fitness predictor in species where metamorphosis and adulthood (or maturity) were closer together in time than species where these milestones were farther apart. Similarly, in carryover and maternal effect research, experiences early in life or due to maternal influence are likely to have stronger effects on short-term rather than long-term performance (e.g., Bernardo, 1996; Lindholm et al., 2006). These trends agree with the general recommendation that fitness proxies covering a larger portion of the life cycle are likely to be more accurate (Hunt and Hodgson, 2010). This commonality highlights a general phenomenon that is evident in life history: the ability of experiences or performance metrics to predict later performance diminishes with increasing time between those measurements. It is likely that the amount of time between performance measurements (such as developmental milestones or carryover effects) affects the potential for catch-up growth and development, which takes some minimum time to achieve (Hector and Nakagawa, 2012). Additionally, increased time is generally associated with increased environmental variability, causing greater variance in performance of individuals. Such information is critical for improving the utility of current and future fitness correlates, as relationships that are useful for predicting future fitness will aid researchers in studies of ecological and evolutionary principles (e.g., Kingsolver and Pfennig, 2004; Dahl et al., 2012), as well as the effects of anthropogenic stressors on various taxa (e.g., Boone et al., 2007).

Another result of our study was that study design altered the correlation between SAM and post-metamorphic performance. The correlation was strongest in more controlled laboratory research and was weakest in less controlled field studies. Study type (laboratory, outdoor enclosure, or field) is analogous to an

Table 2. Model ranking for best null model for the traditional meta-analysis.

Model	K	AIC_c	ΔAIC_c	ω_i
Size at metamorphosis				
Study	5	74.5	0	0.864
Study/methods	11	78.4	3.9	0.123
Methods	7	82.8	8.3	0.014
Intercept only	1	99.9	25.4	0.000
Time to metamorphosis				
Intercept only	1	−9.7	0	0.623
Study/methods	11	−8.6	1.1	0.359
Study	5	−2.3	7.4	0.015
Methods	7	1.6	11.3	0.002

Table 3. Results of the traditional meta-analysis to determine the best model for predicting the strength of the relationship between SAM or TTM and post-metamorphic fitness. For both SAM and TTM, all models contain a variable for the type of study (four and two parameters, respectively). For TTM, all models also contain a categorical fitness variable (six parameters), and the time since metamorphosis when the fitness parameter was measured (continuous variable). Proportion of time = the proportion of time to maturity attained at metamorphosis; proportion of size = the proportion of adult size attained at metamorphosis.

Model	K	AIC$_c$	ΔAIC$_c$	ω_i
Size at metamorphosis				
Proportion of time and size	7	66.5	0	0.709
Global	11	70.0	3.5	0.123
Proportion of time	6	70.3	3.8	0.106
Proportion of time, family	10	73.5	7.0	0.021
Null	5	74.5	8.0	0.013
Proportion of size, family	10	75.0	8.5	0.010
Family	9	75.3	8.8	0.009
Proportion of size	6	75.4	8.9	0.008
Time to metamorphosis				
Global	16	−13.9	0	0.448
Proportion of size, family	15	−12.0	1.9	0.173
Proportion of time, family	15	−12.0	1.9	0.173
Family	14	−10.1	3.8	0.067
Proportion of time and size	12	−9.5	4.4	0.050
Proportion of time	11	−8.8	5.1	0.035
Proportion of size	11	−8.6	5.3	0.032
Null	10	−7.8	6.1	0.021
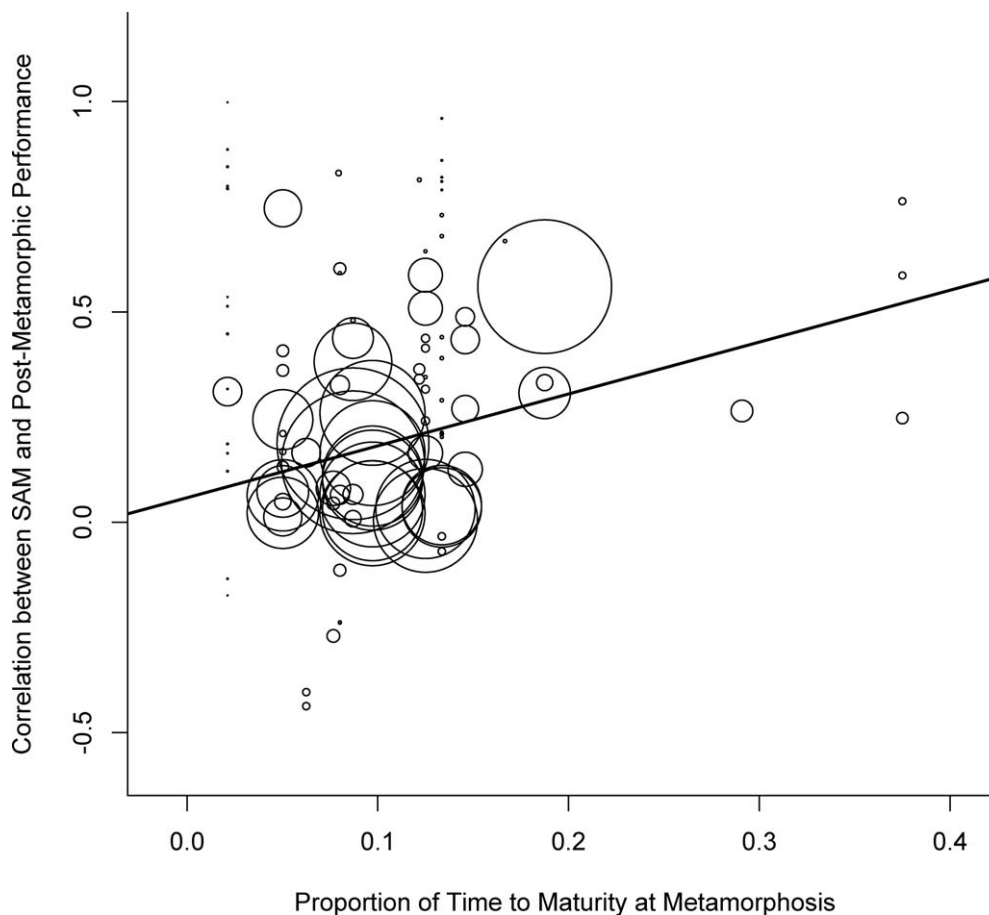
Fig. 5. Effect of the proportion of time to maturity reached at metamorphosis on the correlation (r) between size at metamorphosis (SAM) and post-metamorphic fitness. Size of circles indicates sample size of correlation.

Table 4. Parameter estimates for best models for traditional meta-analysis predicting the strength of the correlation between size at or time to metamorphosis and post-metamorphic fitness. The parameters for time to metamorphosis are model-averaged. Note that stronger correlations are more positive for size at metamorphosis and more negative for time to metamorphosis. Asterisks indicate parameters with confidence intervals that do not include zero. Proportion of time refers to the proportion of time to maturity attained at metamorphosis, and proportion of size refers to the proportion of adult size attained at metamorphosis.

Parameter	Estimate	Standard error
Size at metamorphosis		
Intercept	1.86	0.69*
Field study	−1.57	0.68*
Laboratory study	−1.42	0.68
Laboratory/enclosure study	−1.41	0.70
Enclosure study	−1.79	0.68*
Enclosure (food added) study	0	—
Proportion of time	1.42	0.48*
Proportion of size	−0.71	0.35
Time to metamorphosis		
Intercept	0.08	0.41
Ambystomatidae	0.08	0.24
Bufonidae	−0.002	0.15
Hylidae	0.24	0.13
Pelobatidae	0.33	0.19
Ranidae	0	—
Age at maturity	−0.21	0.16
Body condition	−0.43	0.08*
Growth	−0.17	0.14
Metabolism	−0.37	0.26
Performance	−0.16	0.11
Size	−0.31	0.07*
Field study	0.14	0.13
Laboratory study	−0.04	0.16
Enclosure study	0	—
Proportion of time	0.35	0.52
Proportion of size	−0.24	0.61
Post-metamorphic time	−0.11	0.07

extreme classification of habitat, where this continuum of less to more controlled studies is similar to gradients of variability or stress in natural habitats. Size and time to developmental milestones may be less reliable predictors of fitness in more variable environments, because more variable or stressful habitats have so much stochasticity that performance becomes a more random process and less influenced by individual characteristics. This effect is similar to more general carryover effects where different habitat characteristics in a later environment can alter the expression of carryover effects (e.g., James and Semlitsch, 2011) or potentially overwhelm variation from an earlier life stage (e.g., Earl and Semlitsch, 2013).

The time since metamorphosis when measurements were taken (i.e., study length) varied by the type of study. Field studies were longer than both laboratory and outdoor enclosure studies, which were not different from each other. However, study length was never an important variable, suggesting that the importance of study design in the model results is not due to study length. Understanding whether natural habitats show similar trends to our results will be vital to understanding how anthropogenic stressors affect natural

populations and how well size and age at a developmental milestone predict future fitness in different environments.

Another factor that may affect whether the size and time to a developmental milestone can predict fitness is the correlation between these two measures. A variety of studies have shown that size and time to maturity can be positively, negatively, or uncorrelated in a range of organisms (Roff, 1992; Stearns, 1992), and the same is true for amphibian SAM and TTM (e.g., Semlitsch et al., 1988; Berven, 1990; Schmidt et al., 2012), which reflect different trade-offs between growth and development under different environmental conditions. The correlation between SAM and TTM can also vary within amphibian species under different environmental conditions (Pfennig et al., 1991). When size and time to a developmental milestone are positively correlated, individuals can either have the benefit of being large or reaching a milestone early, either of which may nullify the other, leading to alternative life history pathways that result in similar fitness payoffs (Schmidt et al., 2012). Under this line of reasoning, size and time to developmental milestones may be better predictors of fitness when they are negatively or uncorrelated, though there is currently not enough data available to test this hypothesis.

There was no evidence that evolutionary history was important in explaining the relationship between SAM or TTM and post-metamorphic performance. For both SAM and TTM, the traditional meta-analysis model provided a much better model fit than the one including a phylogenetic covariance matrix. Others have found that phylogeny is quite important in meta-analyses and can change the results in about half of fixed effect analyses (Chamberlain et al., 2012). However, an evolutionary signal might have been evident if data from more species were available (Chamberlain et al., 2012). Our final data set included 19 and 14 species (for SAM and TTM, respectively), though the number of taxa in the phylogenetic analysis was even lower. This made the sample size low enough that phylogeny was unlikely to have a large effect. A better test would include data from more species and families with greater taxonomic resolution and a wider geographic range, although such data are currently unavailable.

Studies using captive model organisms have shown that fitness surrogates, such as body size, are weak to modest predictors of future fitness relative to long-term measures of adult survival and fecundity (Pekkala et al., 2011). There is clearly a methodological trade-off between the effectiveness of fitness surrogates and the time and effort required to collect such data (Hunt and Hodgson, 2010). Our study shows that there is variation among species in the efficacy of specific fitness surrogates as well. These results will be extremely important in interpreting the many studies using developmental milestones as endpoints thought to reflect future fitness. Additionally, our results have direct implications for understanding the evolution of body size and developmental timing, which is under strong selection in a wide range of species (Kingsolver and Pfennig, 2007). Many other species groups have developmental milestones used to predict future fitness, most notably size and time to maturity, which has been studied in a variety of organisms. Future complementary studies should include meta-analyses and targeted comparative studies of other developmental milestones and other taxonomic groups. Further tests of how size and age at developmental milestones predict fitness and how this predictive power varies could aid in

the design of studies to help researchers choose reliable fitness predictors and thus lead to a broader understanding of ecological and evolutionary phenomena.

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