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Density-dependent offspring interactions do not explain macroevolutionary scaling of adult size and offspring size

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Most life forms exhibit a correlated evolution of adult size (AS) and size at independence (SI), giving rise to AS–SI scaling relationships. Theory suggests that scaling arises because relatively large adults have relatively high reproductive output, resulting in strong density-dependent competition in early life, where large size at independence provides a competitive advantage to juveniles. The primary goal of our study is to test this density hypothesis, using large datasets that span the vertebrate tree of life (fishes, amphibians, reptiles, birds, and mammals). Our secondary goal is to motivate new hypotheses for AS–SI scaling by exploring how subtle variation in life-histories among closely related species is associated with variation in scaling. Our phylogenetically informed comparisons do not support the density hypothesis. Instead, exploration of AS–SI scaling among life-history variants suggests that steeper AS–SI scaling slopes are associated with evolutionary increases in size at independence. We suggest that a positive association between size at independence and juvenile growth rate may represent an important mechanism underlying AS–SI scaling, a mechanism that has been underappreciated by theorists. If faster juvenile growth is a consequence of evolutionary increases in size at independence, this may help offset the cost of delayed maturation, leading to steeper AS–SI scaling slopes.

KEY WORDS: Body size, indirect genetic effects, life-history evolution, parent–offspring conflict, parental care, reproductive mode, V_M.

Body size can change remarkably from birth to adulthood, and the forces shaping size along these trajectories are likely to change as well (Roff 2002). Despite the different selective forces acting on adults and juveniles, a common observation is that size at independence from parental care and adult body size exhibit a positive correlated evolution (Caval-Holme et al. 2013). This pattern is usually described as a scaling relationship between species-mean adult size and species-mean size at independence (AS–SI scaling) (Hendriks and Mulder 2008). A comparison of scaling relationships across birds, mammals, reptiles, amphibians, and fishes reveals that major clades exhibit different AS–SI scaling slopes (Blueweiss et al. 1978; Charnov 1993; Visman et al. 1996; Freedman and Noakes 2002; Hendriks and Mulder 2008; Gilbert and Manica 2010; Caval-Holme et al. 2013; Neuheimer et al. 2015; Kasimatis and Riginos 2016; Rollinson and Rowe 2018a). The general mechanism(s) driving AS–SI scaling, and the causes of variation in AS–SI scaling across lineages, has for decades remained an evolutionary puzzle.

The simplest explanation for AS–SI scaling is that it represents a statistical artifact: size at independence must represent some fraction of adult size, and so a scaling coefficient of ≈1 can arise even if all species in a lineage express size at independence as a random fraction of adult size (Nee et al. 2005). Yet, this explanation appears inconsistent with a variety of observations, the most compelling of which is that size at independence is too conserved within lineages to represent a random fraction of adult size (Savage et al. 2006). Numerous adaptive theories have also been advanced to account for positive AS–SI scaling. For example, Moles et al. (2004) argued that AS–SI scaling arises because offspring with relatively high survival, and hence large size, are required to offset the cumulative mortality occurring over the protracted period of juvenile growth necessary to attain large size at maturity. However, Rees and Venable (2007) demonstrated that such high cumulative mortality does not by necessity lead to positive AS–SI scaling, primarily because life histories can evolve along alternative dimensions that likewise offset high juvenile mortality (e.g., increased reproductive lifespan). As another example, Rollinson and Rowe (2015) argue that the ontogenetic persistence of maternal-genetic variation in body size (V_M) could help drive AS–SI scaling. Upward selection on size when V_M is present could result in an evolutionary increase in parental provisioning (Wolf and Wade 2001; Wilson et al. 2005), and hence size at independence, such that size at independence more closely resembles adult size. However, Rollinson and Rowe's verbal hypothesis omits a mechanism that links vital rates of juveniles and adults, which is a general theoretical requirement for AS–SI scaling (Rees and Venable 2007; Venable and Rees 2009), and so it is ultimately unclear whether ontogenetic persistence of V_M alone could result in AS–SI scaling. More generally, none of the models above represent a quantitative theory that explicitly identifies a mechanism driving scaling patterns.

Only two quantitative models have explicitly proposed a mechanism that drives AS–SI scaling, which could in theory account for variation in AS–SI slopes among clades (Falster et al. 2008; Olsson et al. 2016). Both models propose that scaling arise as a consequence of extended periods of density-dependent juvenile competition (henceforth, the density hypothesis). Falster et al. (2008) develop a model where juvenile fitness is initially density independent, but juveniles go on to experience a period of competition beginning when total resource supply in the population matches consumption. An individual's size relative to that of its competitors is the main determinate of survival, and competition results in self-thinning. A larger size at independence is expected to evolve with increasing juvenile biomass entering the population, as higher juvenile biomass results in an earlier onset of competition, which enhances the benefits of a large size at independence. The initial size advantage decreases as juvenile density decreases through the evolution of large size at independence, and ultimately a balance is struck between size and number of offspring (Smith and Fretwell 1974). Evolutionary coordination of adult size and offspring size arises because adult size influences resource availability and the total biomass of juveniles, which in turn influences the size at which juvenile competition begins, ultimately affecting the fitness advantage of larger size at independence. Olsson et al. (2016) develop a similar model inspired by that of Falster et al. (2008). In Olsson et al.'s model, AS–SI scaling is absent when the density-independent juvenile phase is relatively protracted, but AS–SI scaling occurs when the density-dependent phase is relatively long. In sum, theory suggests that AS–SI scaling will arise when there is a protracted period of density-dependent selection for large size at independence beginning at the juvenile stage, provided that the advantage of large initial size reverberates through ontogeny. To date, no empirical study has been conceived with the aim of testing potential mechanisms of AS–SI scaling, and so whether density-dependent juvenile competition helps drive AS–SI scaling remains unclear.

One approach to test the density hypothesis is to determine whether AS–SI scaling slopes vary with the potential for density-dependent competition. For instance, variation among closely related species in the extent to which offspring are capable of dispersal prior to, or during, juvenile resource competition should be associated with variation in the degree of density-dependent competition, and so variation in scaling slopes is predicted. However, to date, almost all comparisons of AS–SI scaling relationships have been performed between distantly related phylogenetic groups, such as classes (Rees and Venable 2007; Falster et al. 2008; Hendriks and Mulder 2008) and orders (Blueweiss et al. 1978; Visman et al. 1996; Neuheimer et al. 2015; Olsson et al. 2016). This approach makes it difficult to resolve the mechanistic basis for AS–SI scaling, as such large taxonomic groupings differ in many ways beyond those that determine the intensity of density-dependent competition. Furthermore, with few exceptions, phylogenetic relationships have been ignored in these analyses (but see Gilbert and Manica 2010; Kasimatis and Riginos 2016).

The present study seeks to overcome these difficulties by introducing phylogenetic control into the analyses, by identifying life history variants that are likely to affect the intensity of density-dependent competition, and by then comparing AS–SI slopes between closely related groups of species. To do so, we focus on amphibians and fishes. In amphibians, density-dependent competition is of great evolutionary and ecological importance, as evidenced by frequent observations of high rates of cannibalism and inducible cannibalistic phenotypes in response to high larval competition (Pfennig 1992; Alford 1999). However, density-dependent competition is likely especially strong in species with larval development, as larvae are generally confined to fixed, often small, water bodies where resource competition is intense (Alford 1999; Wells 2010). In contrast, direct-developing amphibians breed terrestrially, and their fully metamorphosed young are able to disperse at hatching, thereby reducing the potential for density-dependent competition. Because evolutionary transitions from larval to direct development have occurred repeatedly in the evolution of anurans and urodeles (Gomez-Mestre et al. 2012), amphibians offer a good opportunity to test the role of density-dependent larval competition in AS–SI scaling. Under the density hypothesis, we predict that direct-developing amphibians should display shallower AS–SI scaling slopes than species with larval development.

Similarly, Perciformes fishes vary in the location in which eggs are laid. Some species produce demersal eggs, which are attached to substrate, and others produce pelagic eggs that are spawned into the water column (Einum and Fleming 2002; Ueberschär and Froese 2002). Despite this difference in egg placement, larval competitive interactions of both life-history variants tend to occur exclusively in the pelagic environment. Under the density hypothesis, species that spawn eggs demersally should feature AS–SI scaling slopes that are similar to species that spawn eggs pelagically, given that larvae of both life-history variants share the same environment where (density-dependent) interactions occur.

Finally, in addition to testing the density hypothesis, another goal of our work is to inform novel hypotheses regarding the evolutionary forces driving AS–SI scaling. To do so, we broadly compare AS–SI scaling slopes between life-history variants (e.g., viviparous vs. oviparous lineages) of closely related species. We therefore compiled additional datasets that include most major vertebrate groups, exhibiting a remarkable range of life-history variation: eutherian mammals, birds, lizards, snakes, and two additional groups of fishes. We use these additional taxa to explore variation in AS–SI scaling, whereas our test of the density hypothesis is restricted to comparisons within amphibians and Perciformes fishes.

Methods

We perform four sets of analyses exploring the correlated evolution of adult size and size at independence (which we define as the size at which juveniles become independent from parental provisioning). First, we estimate AS–SI scaling slopes for major vertebrate clades to assess if previously reported patterns are robust when controlling for phylogenetic nonindependence (see section Testing Overall Patterns). Second, we perform an explicit test of the density hypothesis by comparing AS–SI scaling slopes among groups of amphibians and Perciformes fishes whose life histories differ in ways that affect the intensity of density-dependent larval competition (see section The Density Hypothesis). Third, we explore AS–SI scaling patterns between other sets of closely related species that differ subtly in life-history and ecology (see section Exploration of Life-History Variants). The life-history variants explored are summarized in Table 1, and were chosen as the variants are associated with important axes of variation including offspring size, morphology, and ontogenetic stage at independence, but variants are not systematically associated with variation in adult size. Finally, to generate novel insight into AS–SI scaling patterns, we explore the association between clade-specific AS–SI scaling slopes and their summary characters across all vertebrate clades (see section Generating New Hypotheses).

DATASETS

Amphibia

Data on egg diameter, clutch size, adult snout-to-vent length (SVL), and reproductive mode of frogs and salamanders were compiled by Rollinson and Rowe (2018a,b). For frogs, we converted SVL to weight (g) using family-specific conversions, or when family-level conversions were not available, conversions by lifestyle (arboreal, terrestrial, and aquatic), all provided by Santini et al. (2018). For salamanders, we expanded the Rollinson and Rowe's dataset to include egg diameter data compiled by Oliveira et al. (2017). Data on adult weight of paedomorphic species were collected from Rollinson and Rowe (2018b), and we otherwise converted SVL to weight using family-specific conversions in Santini et al. (2018). When family-level conversions were missing from Santini et al. (2018), we followed Rollinson and Rowe (2018b) where adult weight of species in Hynobiidae and Dicamptodonidae was estimated from the Ambystomatidae conversion factor, and Rhyacotritonidae was estimated from the Plethodontidae conversion factor. Mean egg diameter data were converted to weight assuming eggs are spherical and that volume and weight are equivalent (Einum and Fleming 2002), such that egg weight (g) $= (4/3) \times \pi \times r^3$, where $\pi = 3.14$ and r is the radius in centimeter. In total, we obtained estimates of egg diameter, development mode, and adult SVL for 558 species, representing 80% of known families (44 of 55) and 8.5% of known species (558 of 6584 species) (AmphibiaWeb 2016). For caudatans, we obtained data for 181 species (26.6% of 680 species) comprising all 10 taxonomic families (100% of families) (AmphibiaWeb 2016).

Cyprinodontiformes fishes

We compiled a life-history database for Cyprinodontiformes fishes, which consists of 10 families (Nelson 2006) and at least 1300 species (Froese and Pauly 2015). Matrotrophic viviparity, which we define as a matrotrophy index greater than a value of 1.0 (see Reznick et al. 2002, with qualifications in Reznick et al. 2007), is observed in three families (Poeciliidae, Anablepidae, Goodeidae), lecithotrophic viviparity in one family (Poeciliidae), and oviparity in all 10 families. We obtained estimates of the matrotrophy index for most Cyprinodonfirmes from Pollux et al. (2014) and Wourms et al. (1988) (Table S2). For 15 species of live bearers, matrotrophy was assumed to be present or absent. Specifically, we assume that all Goodeidae are matrotrophic given that all live-bearing fishes in this family to date have exhibited matrotrophy in controlled experiments (e.g., Wourms et al. 1988), and we assume that *Jenynsia multidentata* is matrotrophic, given that all live-bearers in this family are matrotrophic (e.g., Schindler and

Table 1. Summary of taxa and life-history variants leveraged in the present study.

Clade	Variants compared	Description
Amphibians	Direct development	Terrestrial eggs hatch into terrestrial juveniles
	Larval development	Terrestrial or aquatic eggs produce aquatic larvae
Lizards and snakes	Lecithotrophic Viviparity	Live birth, provisioning consists of yolk
	Oviparity	Eggs, provisioning consists of yolk
Cyprinodontiformes	Matrotrophic viviparity	Embryo provisioned continuously until live birth
Fishes	Lecithotrophic Viviparity	Live birth, provisioning consists of yolk
	Oviparity	Eggs, provisioning consists of yolk
Perciformes fishes I	Matrotrophic viviparity	Embryo provisioned continuously until live birth
	Oviparity	Eggs, provisioning consists of yolk
Perciformes fishes II	Pelagic oviparity	Eggs and larvae spawned into open water
	Demersal oviparity	Eggs attached to substrate, larvae in open water
Birds	Oviparity	Eggs, then parental provisioning
Eutherian mammals	Matrotrophic viviparity	Offspring provisioned before and after live birth

de Vries 1988). We assume that lecithotrophy prevails in *Dactylophallus*, *Girardinus*, *Glaridichthys*, and *Quintana*, all of which are very closely related and none of which show evidence of matrotrophy (Pollux et al. 2014). Finally, we assume all *Gambusia* are lecithotrophic, given that all known species in this genus are lecithotrophic (Table S2).

Size metrics were converted to wet weight using genus-specific or family-specific conversions from published literature, or from raw data we amassed while compiling our data (Table S3). We obtained data on weight at independence and adult weight for 102 species (7.8% of about 1300 species) representing all 10 families in this order, including data on 34 oviparous species from nine families, 39 lecithotrophic viviparous species from one family, and 29 matrotrophic species from three families (Table S2).

Perciformes fishes (I)

To match available phylogenies, we created two separate datasets for Perciformes fishes, one to contrast fishes that differ in provisioning mode, that is, oviparity versus matrotrophic viviparity (this section, I), and one to contrast spawning location, that is, demersal versus pelagic spawners (next section, II). Perciformes is the largest taxonomic order among vertebrates, comprising about 160 families and over 10,000 species. Within this order, matrotrophic viviparity occurs in four families: Embiotocidae features 26 viviparous species and no oviparous species (Froese and Pauly 2015); matrotrophy occurs in approximately 60 of 75 species in the family Clinidae; two of approximately 65 species of Zoarcidae are matrotrophic; and about 21 of 100 Labrisomidae species are viviparous (Wourms 1981; Wourms et al. 1988). Egg size data and data for weight at independence for the Perciformes were collected from primary literature and from previously compiled databases (Freedman and Noakes 2002; Goodwin et al. 2002; Kasimatis and Riginos 2016), and these size metrics were converted to wet weight using genus-specific or family-specific conversions from published literature, or from raw data we amassed while compiling our data (Table S3). Extensive searching revealed no useable life-history information for matrotrophic Labrisomids. In total, data for weight at independence were found for 133 species (1.33% of about 10,000 species) comprising 42 families (26% of about 160) (Nelson 2006). Our dataset comprised 21 of the 88 (24%) matrotrophic species known in the order Perciformes, including the families Zoarcidae (two of two species, 100% of viviparous species represented), Embiotocidae (11 of 24 species, or 46%), and Clinidae (eight of 62 species, or 13%).

For adult size, we used species-specific maximum body weight reported in FishBase (Froese and Pauly 2015), or we converted maximum reported body length to maximum body weight using species-specific or family-specific length-to-weight scaling exponents (Froese and Pauly 2015). Egg diameter data were converted to weight in grams, assuming eggs are spherical and have the same density as water. For viviparous species, birth length was converted to wet weight using family-specific length-weight relationships for birth weight for Embiotocidae, and using length–weight relationships for birth weight from the family Cyprinodontidae for Clinidiae (Table S3); Zoarcidae birth weight was reported as wet weight so no conversion was needed.

Perciformes fishes (II)

Some oviparous Perciformes fishes spawn their eggs directly into the water column and provide no further care, others lay eggs demersally and (typically) guard them until they hatch. To analyze how a change in spawning mode affects the correlated evolution of adult size and size at independence, we used the dataset from Kasimatis and Riginos (2016). We converted adult length to weight using species-specific or family-specific length-to-weight scaling exponents (Froese and Pauly 2015). We excluded species categorized by Kasimatis and Riginos (2016) as "demersal" if they exhibited mouthbrooding (e.g., most Apogonidae), or attachment of ova to parental tissues (e.g., *Syngnathus* sp., Syngnathidae), so that all species categorized as "demersal" laid eggs on the ocean floor. Next, using LarvalBase (Ueberschär and Froese 2002), we excluded all demersal species where larvae are closely associated with the substrate, so that all species analyzed featured pelagic larva but varied in egg placement (demersal or pelagic). After filtering the data, we were left with 24 demersal species and 123 pelagic species (1.5% of species represented) from 33 families (20.6% of families).

Snakes and lizards

Data for adult weight and both birth and hatching weight were obtained from the reptile database compiled by Scharf et al. (2015). We excluded from this dataset five species in the genus Chalcides and one species of Leiolopisma, as these species are known or suspected to exhibit matrotrophic viviparity (Blackburn 1992), and additional literature searches failed to yield additional size data for these matrotrophic groups. The remaining species in our analysis exhibited lecithotrophic viviparity or oviparity. For lizards, birth/hatching weight data were obtained for 442 species (7.2% of 6145 species) comprising 31 families (79% of 39) (Uetz et al. 2019). For snakes, our dataset comprised 10 families (36% of 28 families) and 204 species (5.7% of 3567 species) (Uetz et al. 2019).

Birds and mammals

All life-history data were obtained from Myhrvold et al. (2015). Weaning weight data were obtained from eutherian mammals from 26 orders (62% of orders of 29 recognized orders) representing 102 families (47% of 156 recognized families) and 812 species (11% of 5416 known species) (Wilson and Reeder 2005). For birds, fledging weight data were available from eight orders, representing 36 families and 154 species. This comprises about 20% of orders (eight of 40), 15% of families (36 of 239), and 1.5% of species (154 of 10,612) (Gill and Donsker 2015).

PHYLOGENETIC ANALYSES

Species-level phylogenies were obtained from the literature for amphibians (Pyron and Wiens 2013), two groups of Perciformes fishes (Kasimatis and Riginos 2016; Betancur et al. 2017), Cyprinodontiformes fishes (Pollux et al. 2014), reptiles (Pyron and Burbrink 2014), and mammals (Bininda-Emonds et al. 2007). All phylogenies were already time calibrated, with the exception of Cyprinodontiformes fishes (Pollux et al. 2014), which we calibrated using penalized likelihood (Sanderson 2002), using the value of lambda that maximized the cross-validation criterion. Phylogenetically least square (PGLS) analyses were performed in the R environment (R Core Team 2017), primarily by implementing the packages *ape* (Paradis et al. 2004), *phytools* (Revell 2012), and *geiger* (Harmon et al. 2008). PGLS regression parameters and phylogenetic signal were estimated simultaneously, using Pagel's λ (Pagel 1999). Quantitative traits were $\log_{10}$ transformed prior to analysis to linearize allometric relationships.

The phylogeny used in the analysis of Perciformes (I) was species poor with respect to the availability of life-history information for matrotrophic fishes (16 matrotrophic species represented in phylogeny) (Betancur et al. 2017). We made use of available life-history data for matrotrophic species by simulating more species-rich phylogenies that were constrained against the existing phylogenetic backbone. We generated 100 phylogenies in which missing species were added to randomly generated tips within the clade containing the other members of their genus, using the function *add.species.to.genus* in *phytools* (Revell 2012). This allowed us to increase the sample of matrotrophic species from $n = 13$ to $n = 21$, with additional data added to tips within the genus Embiotocidae ($n = 3$), Clinidae ($n = 4$), and Zoarcidae ($n = 1$). Species without their genus represented in the phylogeny were not added to the phylogeny; further, in no case did the focal life-history variant (i.e., matrotrophy vs. oviparity) in the analysis differ within a genus. A PGLS regression was then run for each of the 100 phylogenies, and mean parameter estimates were calculated from the 100 runs. Confidence intervals were calculated assuming the overall mean parameter obtained from all simulation runs was estimated with error, and that each parameter estimate in each of the 100 simulations was also estimated with error. The former error term was estimated from the upper and lower 2.5% of parameter estimates in our simulations, and this error was added to the latter error term, which was estimated using Equation 3C in Martins (1996). We present the mean *P*-value in results tables, as all *P*-value distributions were unimodal.

The phylogeny for Cyprinodontiformes fishes (Pollux et al. 2014) was also species poor relative to the available data. We made use of additional life-history data for by simulating 100 phylogenies in which missing species were added to randomly generated tips within their genus, as above. This allowed us to increase sample size from $n = 86$ to $n = 102$ species, with additional data added to tips within the genus Fundulus ($n = 11$), Rivulus ($n = 3$), and Epiplatys ($n = 2$).

We estimated the PGLS slope of fledgling weight over adult weight in birds by generating 1000 species-level phylogenies using the Ericson backbone provided by Jetz et al. (2012). Phylogenetic error was incorporated by performing a PGLS regression using each of the 1000 phylogenies (see Jetz et al. 2012), and both means and errors were calculated as above.

TESTING OVERALL PATTERNS

First, we fit PGLS regressions for each major clade, ignoring life-history variants, to estimate AS–SI scaling slopes within each major group.

TESTING THE DENSITY HYPOTHESIS

To test the density hypothesis, we performed two comparisons in the Amphibia and one comparison in Perciformes fishes. Using our datasets on Anurans, Urodeles, and Perciformes fishes (II), we fit PGLS regressions with weight at independence as the dependent variable and an interaction between the life-history variant and adult weight (Table 1).

EXPLORATION OF LIFE-HISTORY VARIANTS

We leveraged our datasets on lizards, snakes, Perciformes fishes (I), and Cyprinodontiformes fishes to explore how subtle differences in life history are associated with AS–SI scaling. We fit a separate PGLS model for each major group with weight at independence as the dependent variable and an interaction between the life-history variant and adult weight.

GENERATING NEW HYPOTHESES

With the analyses above, we estimated an AS–SI slope for birds, mammals, and each life-history variant within anurans, urodeles, snakes, lizards, Perciformes, and Cyprinodontiformes fishes. We used these estimates to visualize how the AS–SI slope varied as a function of mean size at independence. To give context to the strength of these associations, we used linear regression. We caution that *P*-values for these regressions are not strictly correct as we could not account for the broad phylogenetic structure in the data, but these analyses are nevertheless informative as we gain insight into how the AS–SI slope varies with size metrics.

Results

TESTING OVERALL PATTERNS

Our initial phylogenetically informed analysis of the entire data set confirmed a general positive AS–SI scaling in vertebrates, but with considerable variation among the vertebrate clades. Notably, clades with postpartum provisioning (birds and mammals) showed stronger correlated evolution of weight at independence and adult weight than those where postpartum provisioning is absent (Fig. 1, Table S1).

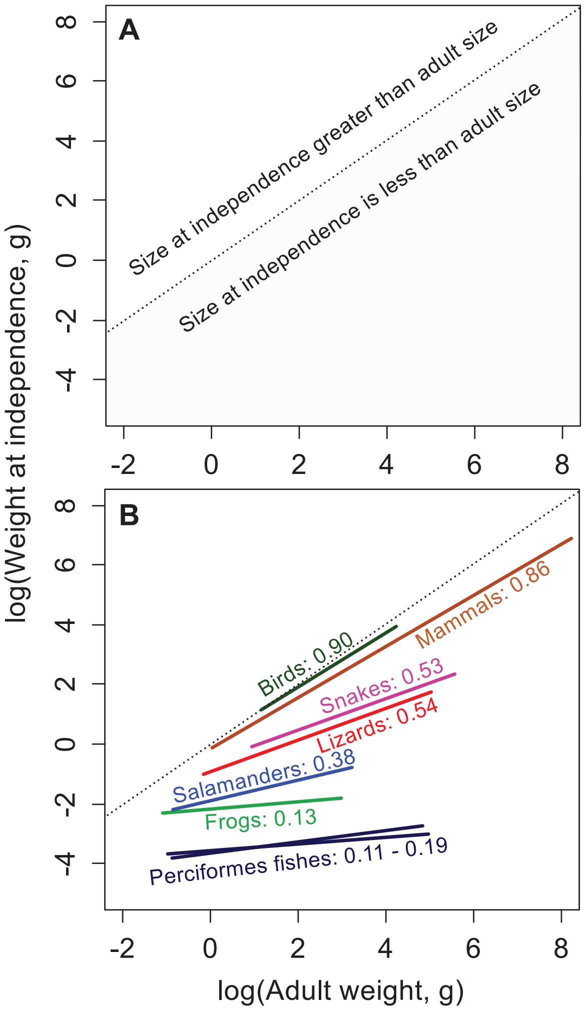

Figure 1. Correlated evolution of log weight at independence and log adult weight. (A) Shaded area is the distribution of plausible values for weight at independence, with the dashed line representing equivalent weight of adults and individuals at independence. (B) Lines are fits from phylogenetically least square regressions (PGLS), and clade-specific values are PGLS slopes (see Table S1 for model summaries) fitted for all available data, regardless of life-history variation within clades. Cyprinodontiformes are omitted for clarity.

TESTING THE DENSITY HYPOTHESIS

Direct developing Anurans exhibited a significantly steeper AS–SI slope than did Anurans species with larval development. This is opposite to what would be expected if larval competition were driving AS–SI scaling, because we would expect less opportunity for competition in direct developers. For Urodeles, the AS–SI slope did not differ between life-history variants (Fig. 2, Table 2).

Perciformes fishes that spawn demersally and have pelagic larvae exhibited a steeper AS–SI slope than pelagic-spawning Perciformes that also have pelagic larvae (Fig. 2, Table 2). This seems inconsistent with the density hypothesis, as larval interactions in the pelagic environment should be similar regardless of where eggs are initially placed.

EXPLORATION OF LIFE-HISTORY VARIANTS

Cyprinodontiformes fishes with matrotrophic viviparity exhibited a steeper AS–SI slope than did either lecithotrophic viviparous

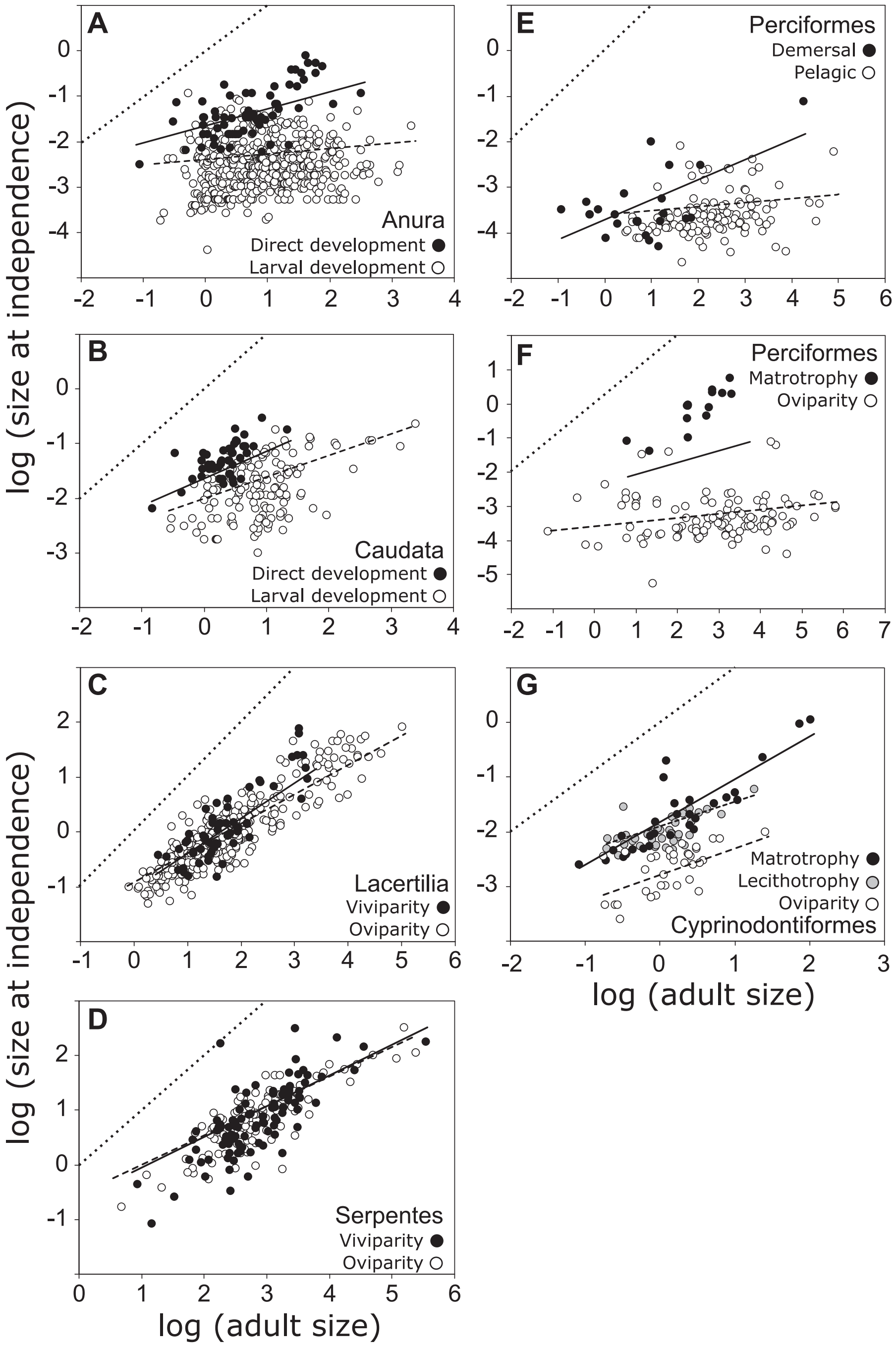

Figure 2. Correlated evolution of weight at independence and adult weight in relation to life-history variation for (A) frogs and toads, (B) salamanders and newts, (C) lizards, (D) snakes, and (E–G) fishes. Dotted upper line is the 1:1 line. Parameter estimates are presented in Table 2, and linear fits are phylogenetically controlled.

or oviparous species. Lecithotrophic and oviparous Cyprinodontiformes did not differ in AS–SI scaling (Fig. 2, Table 2). In Perciformes fishes (Perciformes I), matrotrophic viviparity was associated with a sight and nonsignificant increase in the scaling of AS–SI (Fig. 2, Table 2), compared to (lecithotrophic) oviparity. In these Perciformes, it is notable that the difference between phylogenetically informed versus a phylogenetically naïve analysis is substantial (Fig. 2). Finally, in lizards and snakes, oviparity versus lecithotrophic viviparity was not associated with different patterns of AS–SI scaling (Fig. 2, Table 2).

GENERATING NEW HYPOTHESES

In sum, of nine comparisons (2 × amphibians, 3 × Cyprinodontiformes fishes, 2 × different groups of Perciformes, 2 × reptiles),

Table 2. PGLS estimates for models testing whether correlated evolution of log size at independence and log adult size and differs between life-history variants in six different clades.

Clade	λ, N	Parameter	Estimate	SE	P
Anura	$\lambda = 0.889$,	Intercept	−1.72	0.286	0.005
	$N = 558$	Log adult weight	0.377	0.0993	0.002
		Life history [Larva]	−0.678	0.126	<0.001
		Weight × life history [Larva]	−0.255	0.106	0.017
Caudata	$\lambda = 0.867$,	Intercept	−1.69	0.235	<0.001
	$N = 181$	Log adult weight	0.499	0.140	0.005
		Life history [Larva]	−0.353	0.145	0.016
		Weight × life history [Larva]	−0.105	0.154	0.50
Cyprinodontiformes[1]	$\lambda = 0.657$,	Intercept	−1.86	0.146	<0.001
	$N = 102$	Log adult weight	0.752	0.0877	<0.001
		Life history [Ovi]	−0.966	0.154	<0.001
		Life history [Leci]	−0.0881	0.0903	0.32
		Weight × life history [Ovi]	−0.290	0.169	0.043
		Weight × life history [Leci]	−0.308	0.138	0.022
Perciformes I[1]	$\lambda = 0.884$,	Intercept	−2.42	0.576	<0.001
	$N = 133$	Log adult weight	0.339	0.120	0.051
		Life history [Ovi]	−1.21	0.555	0.01
		Weight × life history [Ovi]	−0.203	0.191	0.25
Perciformes II	$\lambda = 0.737$,	Intercept	−3.67	0.233	<0.001
	$N = 145$	Log adult weight	0.443	0.100	<0.001
		Life history [pelagic]	0.164	0.227	0.47
		Weight × life history [Pelagic]	−0.374	0.110	<0.001
Lacertilia	$\lambda = 0.877$,	Intercept	−0.914	0.116	<0.001
	$N = 442$	Log adult weight	0.527	0.0232	<0.001
		Life history [Ovi]	0.111	0.107	0.30
		Weight × life history [Ovi]	−0.103	0.0660	0.12
Serpentes	$\lambda = 0.762$,	Intercept	−0.570	0.232	0.015
	$N = 204$	Log adult weight	0.543	0.0523	<0.001
		Life history [Ovi]	−0.0294	0.228	0.90
		Weight × life history [Ovi]	0.0132	0.0755	0.86

Square brackets indicate comparison to the reference category within clades.

[1] Parameters are mean estimates from 100 simulations, and *P*-values are mean values from simulations; approximate SEs computed from upper and lower 95% of parameter distributions.

there were four in which a subtle difference in life history corresponded with a significant difference in the AS–SI slope (1 × amphibians, 2 × Cyprinodontiformes fishes, 1 × Perciformes, 0 × reptiles). More broadly, across all clades and life-history variants, there appeared to be a positive association between the AS–SI slope and mean size at independence, where mean size at independence is specific to a particular life-history variant within a given group ($r^2 = 0.52$, $P < 0.001$, Fig. 3).

Discussion

Our phylogenetically informed tests confirm that positive AS–SI scaling is common to vertebrates and varies a great deal among major clades (Fig. 1). However, we found no support for current theory, the density hypothesis, which aims to account for variation in AS–SI scaling among taxa. Our study, nevertheless, provides significant insight into patterns of AS–SI scaling. For example, having rejected the density hypothesis, we went on to show that variation in AS–SI scaling can be pronounced even across groups of closely related species (Fig. 2), and that scaling tends to become steeper as size as independence becomes larger (Fig. 3). Our analyses therefore question current theory while providing significant new insight into a common yet unexplained life-history phenomenon, and below we outline how our findings motivate new formal theory.

The density hypothesis posits that large adults with high reproductive output effect density-dependent competition that can drive AS–SI scaling, provided the competitive advantage of large

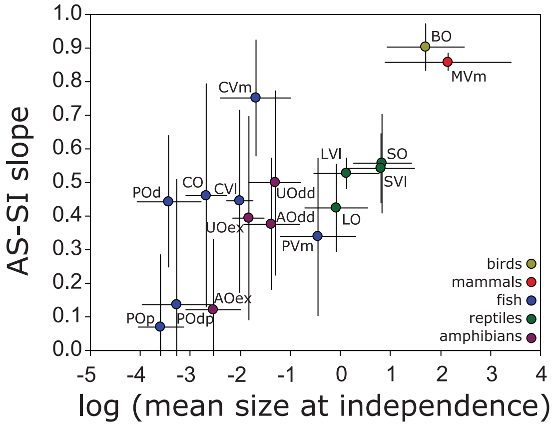

Figure 3. AS–SI slope ± 95%CI versus mean size at independence ±SD. Each life-history variant within each group contributes an estimate. The first letter of each label describes the clade (P = Perciformes, C = Cyprinodontiformes, A = Anura, U = Urodele, L = Lizard, S = Snake, B = Bird, M = Mammal), the second letter describes the life-history variant (O = oviparous, V = Viviparous), and subsequent letters further distinguish between variants (d = demersal spawning, p = pelagic spawning, dp = demersal and pelagic, ex = exotrophic larvae, dd = direct developing, m = matrotrophic, and l = lecithotrophic).

size at independence persists throughout a protracted period of density dependence (Falster et al. 2008; Venable and Rees 2009; Olsson et al. 2016). Although we acknowledge that this hypothesis is difficult to test quantitatively, our study does not support the proposition that it is major driver of AS–SI scaling. In amphibians, repeated evolutionary transitions to a life-history that is expected to decrease juvenile competition (Gomez-Mestre et al. 2012) did not result in a reduction in AS–SI scaling. Larval amphibians are generally confined to ponds or pools, where competition for resources is intense (Alford 1999; Wells 2010). In contrast, direct-developing amphibians breed terrestrially, and their young hatch from ova and are able to disperse, thus providing opportunities to escape juvenile competition. Yet, in two major clades of amphibians, we found that the transition from aquatic larvae to direct-developing offspring did not result in shallower AS–SI scaling slopes. In fact, among the Anura, we found the opposite effect: direct-developing species exhibited a significantly steeper AS–SI scaling slope. Second, we found that AS–SI scaling was stronger in demersal-spawning teleost fish, compared to pelagic spawners, even though we ensured that only egg placement, and not larval life histories, differed systematically between these groups (Einum and Fleming 2002). Given that the conditions experienced during the larval stage are similar between groups, the density hypothesis is unlikely to account for the steeper AS–SI scaling slope observed in demersal spawners. The result for Perciformes fishes is similar to that of Kasimatis and Riginos (2016) and Thresher (1988), where demersal spawning fish exhibited a stronger correlated evolution of adult size and size at independence, although in the present study the result persists even after carefully accounting for differences in the larval environment.

The density hypothesis also appears inconsistent with patterns of AS–SI scaling not examined herein. For instance, there is a strong correlated evolution of egg size and adult size in turtles (Elgar and Heaphy 1989; Iverson et al. 1993), such that the density hypothesis predicts strong juvenile competition. Yet, turtle life histories are typified by extreme egg depredation prior to hatching (e.g., Spencer 2002), leading to few recruits per annum and little opportunity for density-dependent competition (Brooks et al. 1991). Indeed, turtle longevity is hypothesized to have evolved in conjunction with extremely low annual reproductive success, where recruitment and population growth depend critically on protracted reproductive lifespans of adults, whereas egg and juvenile survival are extremely low (Heppell 1998). The sum of evidence therefore suggests that density-dependent juvenile competition may be, at best, of relatively minor importance to AS–SI scaling.

The question that remains, then, is why do large-bodied species produce large-bodied offspring? We suggest the broad analysis presented herein provides some new insights. Among the vertebrates we studied, the evolution of large size at independence is often associated with strong AS–SI scaling. This association is present even within groups where size at independence is a small fraction of adult size, and more generally across the enormous range of offspring sizes among clades that we have analyzed (Fig. 3). Our results also suggest that AS–SI tends to be stronger in vertebrates that exhibit egg guarding or other forms of parental care. Indeed, ectothermic groups that generally protect eggs and embryos, such as direct-developing frogs (Gomez-Mestre et al. 2012), demersal-spawning fishes (Kasimatis and Riginos 2016), and viviparous animals in general (Jørgensen et al. 2011), tended to exhibit stronger correlated evolution of adult size and size at independence compared to groups that provide no protection, such as most frogs with free-swimming larvae and pelagic-spawning fishes. Theory and data suggest that large size at independence precedes the evolution of parental care (Nussbaum and Schultz 1989; Summers et al. 2006), because large size is associated with long development time (Gillooly et al. 2002), and care decreases offspring mortality during a relatively protracted period of development (Shine 1978; Sargent et al. 1987). Strong AS–SI scaling in birds, mammals, and the vertebrate groups examined herein is associated both with large size at independence and parental care, and it will therefore be difficult to disentangle the effect of these correlated traits (if any) on AS–SI scaling, at least empirically.

We suggest that the positive correlation between the extent of AS–SI scaling and large size at independence may be of considerable interest, particularly because a factor not considered in formal theories of AS–SI scaling is rate of offspring growth. Juvenile growth rate tends to be positively related to size at independence within species (Einum and Fleming 1999; Marshall and Keough 2008; Cameron et al. 2016) and across related species (Case 1978; Metcalf et al. 2006). Presumably, this association arises because larger organisms use energy more efficiently (Pettersen et al. 2018) and can acquire energy more easily, both in terms of movement energetics (e.g., Reynolds number in aquatics systems) and foraging efficiency (e.g., gape size). Further, life-history theory suggests that, within populations, variation in juvenile growth will be a strong determinate of size at maturity, with fast early growth tending to increase the benefits of delaying sexual maturity and increasing adult size (Stearns and Koella 1986; Day and Rowe 2002). New theory is needed to determine if a similar pattern can emerge across related species, and the present study suggests that such a theory could be conditioned, in part, on a positive correlation between size at independence and rate of early growth.

Although variation in prematuration growth may be a fruitful avenue of inquiry, variation in patterns of postmaturation growth seem to provide little insight into patterns of AS–SI scaling. On the one hand, Gilbert and Manica (2010) demonstrate a strong AS–SI scaling of approximately $b = 0.95$ across insect species, a scaling coefficient that rivals those observed in birds and mammals ($b \approx 0.90$). We point out that birds, mammals, and insects (typically) exhibit determinate growth, whereas clades with indeterminate growth often exhibit shallower AS–SI scaling slopes, such as fishes, amphibians, and reptiles (Heino and Kaitala 1999). This limited observation suggests that the strength of AS–SI scaling is perhaps related to patterns of growth that occurs postmaturity, rather than prior to maturity. On the other hand, Neuheimer et al. (2015) demonstrate that both marine crustaceans and elasmobranches, which have indeterminate growth, also have AS–SI coefficients close to $b \approx 0.90$, although size was estimated differently in Neuheimer et al.'s study than in the present study and that of Gilbert and Manica (2010). Patterns of postmaturation growth do not, therefore, appear to be associated with patterns of AS–SI scaling. Yet, the possibility of an association should not be completely disregarded until a single study estimates AS–SI scaling across patterns of postmaturation growth, while keeping size metrics in a common currency.

Although the density hypothesis represents the only quantitative theory to explain AS–SI scaling, verbal models also exist. For instance, Rollinson and Rowe (2015) proposed that the ontogenetic persistence of maternal-genetic variation in body size (V_M) could help drive the scaling of AS–SI. Under the V_M hypothesis, maternal genes that affect body size of individuals in the next generation are largely attributable to maternal provisioning genes (Hunt and Simmons 2002; Maestripieri and Mateo 2009; Hadfield 2012). Then, if size is generally under positive directional selection prior to maturity (Rollinson and Rowe 2015), an increase in the ontogenetic persistence of V_M increases the scope of size-at-age in which upward selection on size will elicit and evolutionary response in both adult size and investment per offspring. It is argued that the slope of AS–SI scaling will be positively associated with the extent of ontogenetic persistence of V_M. Although maternal effects on adult size are not uncommon in mammals, some fishes, and insects (Kruuk et al. 2000, 2015; Hunt and Simmons 2002; Rauter and Moore 2002; Wilson et al. 2005; Casellas et al. 2009; Wilson and Festa-Bianchet 2009), the present study does not provide clear support to the V_M hypothesis. In part, this is because the V_M hypothesis is verbal and generates only vague predictions. More fundamentally, however, we found that reptiles and demersal-spawning Perciformes fishes exhibit moderate AS–SI slopes, but there is no evidence to our knowledge that V_M is persistent in reptiles (see, e.g., Madsen and Shine 2000). It also seems unlikely that V_M would be persistent in demersal-spawning Perciformes fishes, where AS–SI scaling is moderate (Fig. 2E), and individuals are tiny at hatch but can go on to become enormous over their long lifespan (Freedman and Noakes 2002; Froese and Pauly 2015). So, although V_M may play some role in AS–SI scaling, it seems difficult to reconcile with some of our observations.

In sum, the present study suggests that the mechanism(s) underlying AS–SI scaling have yet to be formally recognized, but our broad synthesis and analysis sheds some new light on potential avenues of inquiry. Perhaps most importantly, variation in life-history that is associated with a larger size at independence (and, by association, parental care) typically correspond to stronger scaling. These transitions appear to be independent of an increase in offspring competition and changes in the ontogenetic persistence of maternal effects, suggesting that some unknown factor promoting greater offspring investment also promotes a stronger correlated evolution of adult size and size at independence. We suggest that this unknown factor may be prematuration growth. We emphasize that it is particularly intriguing that large size at independence is indeed positively correlated with prematuration growth (Case 1978), and that classical life-history theory predicts an intraspecific association between fast prematuration growth and large adult size (Stearns and Koella 1986).

AUTHOR CONTRIBUTIONS

N.R. designed the study, collected, and analyzed the data. All authors contributed ideas and wrote the manuscript.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Scaling relationships between log weight at independence and log adult weight fit in PGLS for all clades in the main text.
Table S2. Estimates of the matrotrophy index (MI) collated from the literature for live-bearing Cyprindodontiformes in our analysis.
Table S3. Conversions used to build datasets for fishes (SL standard Length; TL total length; BL Length at birth; all weight (wt) measurements are wet weight (g) unless otherwise noted).