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Persistent directional selection on body size and a resolution to the paradox of stasis

Njal Rollinson[1,2] **and Locke Rowe**[1]

[1]*Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St. Toronto, Ontario, M5S 3B2, Canada*

[2]*E-mail: njal.rollinson@gmail.com*

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Directional selection on size is common but often fails to result in microevolution in the wild. Similarly, macroevolutionary rates in size are low relative to the observed strength of selection in nature. We show that many estimates of selection on size have been measured on juveniles, not adults. Further, parents influence juvenile size by adjusting investment per offspring. In light of these observations, we help resolve this paradox by suggesting that the observed upward selection on size is balanced by selection against investment per offspring, resulting in little or no net selection gradient on size. We find that trade-offs between fecundity and juvenile size are common, consistent with the notion of selection against investment per offspring. We also find that median directional selection on size is positive for juveniles but no net directional selection exists for adult size. This is expected because parent–offspring conflict exists over size, and juvenile size is more strongly affected by investment per offspring than adult size. These findings provide qualitative support for the hypothesis that upward selection on size is balanced by selection against investment per offspring, where parent–offspring conflict over size is embodied in the opposing signs of the two selection gradients.

KEY WORDS: Life history, microevolution, offspring size, parent–offspring conflict, trade-off.

Strong selection and abundant genetic variation appear to be widespread in nature (Hereford et al. 2004; Hansen et al. 2011; Houle et al. 2011). We might therefore expect adaptive phenotypic evolution to be common (Lande and Arnold 1983). However, stasis tends to dominate the temporal dynamic of traits in natural populations. This is the paradox of stasis (Hansen and Houle 2004). Additionally, for body size, not only is selection strong (Hereford et al. 2004), it is typically positive (Kingsolver et al. 2001a; Kingsolver and Pfennig 2004; Kingsolver and Diamond 2011b). Thus, for body size, there is an additional dimension to the paradox of stasis: in general, we should expect not only widespread adaptive evolution, but also a trend toward the evolution of larger size (Cope 1896; Kingsolver and Pfennig 2004). Contrary to this expectation, rates of evolution in body size observed over about 1 mya are extremely low (Uyeda et al. 2011).

It is also common to observe stasis in body size at microevolutionary scales (reviewed by Gotanda et al. 2015). For instance, fledgling size in birds is heritable and under persistent directional selection in a variety of species and populations (Kruuk et al. 2001; Merilä et al. 2001a; Charmantier et al. 2004). Yet, microevolution in the direction predicted by the breeder's equation is not observed for fledgling size in collared flycatchers (Kruuk et al. 2001; Merilä et al. 2001a,b), great tits (Garant et al. 2004; Hadfield et al. 2010), blue tits (Charmantier et al. 2004), and possibly snow geese (Cooch et al. 1991; Merilä et al. 2001c). Similar patterns of stasis are observed for body mass of soay sheep (Wilson et al. 2005b, 2007) and red deer (Merilä et al. 2001c).

Stasis is not a new problem. In fact, decades-old theoretical work suggests that some cases of stasis can be explained. Price et al. (1988) demonstrate that a correlation between a heritable trait and fitness can persist when the relationship is mediated by a nonheritable trait that itself covaries with environmental factors (see also Rausher 1992). For example, antler size in red deer is associated with increased breeding success and it is heritable, but this trait does not respond to persistent directional selection (Kruuk et al. 2002). Stasis probably arose because antler size is heavily influenced by nutritional state, and nutritional state is determined primarily by the environment, such that the association between antler size and fitness is mediated through a nonheritable trait. In general, covariance between the environment and fitness will be nontrivial; for instance, Stinchcombe et al. (2002) estimated that approximately 25% of selection estimates for a variety of traits in three plant species were biased by environmental covariances.

Cooke et al. (1990) proposed an alternative theory, where the focal trait is evolving but its phenotypic expression is masked by concurrent changes in the environment. For instance, size might be under positive directional selection, and breeding values for size might increase over time. If a consistent change in the environment occurs over the same period, such as an evolutionary increase in the mean level of competition, this may have the effect of limiting the expression of larger size. In this case, the observer may not detect phenotypic evolution in the direction predicted by the breeder's equation (Merilä et al. 2001b; Garant et al. 2004; but see Hadfield et al. 2010).

Although existing theories have been valuable in understanding patterns of microevolution in the wild (Merilä et al. 2001c), there remain cases in which it is not clear why stasis of body size occurred (Charmantier et al. 2004; Wilson et al. 2007; Hadfield et al. 2010). In contrast to the models of Price et al. (1988) and Cooke et al. (1990), a different literature points to the quantitative genetic theory of parental effects as advancing a possible explanation for stasis of body size (Cheverud 1984; Kirkpatrick and Lande 1989; Thiede 1998; Hadfield 2012). In the present study, we draw on principles of quantitative genetics and life-history theory to underline a potential role for parent–offspring conflict in the evolution of body size, with an emphasis on the classic trade-off between size and number of offspring (Lack 1947, 1954; Williams 1966; Trivers 1974).

We address two questions. First, why is directional selection on body size so persistent in the first place (Kingsolver et al. 2001a; Kingsolver and Pfennig 2004; Morrissey and Hadfield 2012)? Second, why do microevolutionary studies fail to observe the predicted response of body size to persistent upward selection (Merilä et al. 2001c; Gotanda et al. 2015)? Our thesis arises from the observation that all examples of microevolutionary stasis of body size in wild populations measure size traits of juveniles, such as fledgling size in birds (Merilä et al. 2001a,b; Charmantier et al. 2004; Garant et al. 2004) and birth weight in mammals (Merilä et al. 2001c; Wilson et al. 2005c, 2007). Life-history theory suggests that juvenile fitness increases with juvenile size, and adults affect the size of juveniles by adjusting resource investment per offspring (Lack 1954; Smith and Fretwell 1974; Jørgensen et al. 2011). In the absence of constraint, selection should act to increase both investment per offspring and fecundity, as both traits are generally positively related to fitness (Plants: Stanton 1984; Wulff 1986; Jurado and Westoby 1992; Bonfil 1998; Animals: Kruuk et al. 2000; Garant et al. 2004; Rollinson et al. 2014). However, the energy available for reproduction is finite, leading to a trade-off between investment per offspring and fecundity (Lack 1947; Lim et al. 2014).

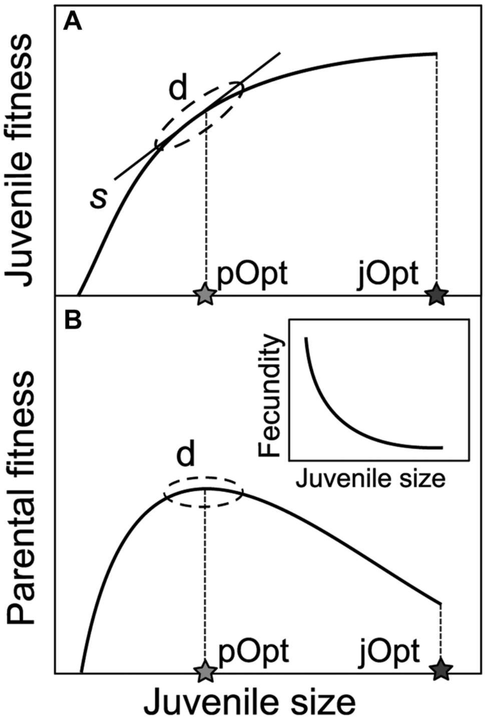

Figure 1. A behavioral–ecological framework for parent–offspring conflict over size. (A) A concave-downward fitness function with respect to juvenile size. (B) Stabilizing selection on juvenile size with respect to parental fitness, the result of a trade-off between juvenile size and parental fecundity (inset). The juvenile size that maximizes parental fitness, *pOpt*, is less than the size that maximizes juvenile fitness, *jOpt*. Given that parents have a strong influence over resource allocation to juveniles, the phenotypic distribution of juvenile sizes, *d*, will more closely match *pOpt* than *jOpt*, such that the selection differential for juvenile size, *s*, will always be positive and will recur in every generation.

The consequences of the size–number trade-off can be understood in different ways, depending on how fitness is assigned (reviewed by Hadfield 2012). A common approach in behavioral ecology is to assign fitness to parents (Smith and Fretwell 1974; Clutton-Brock 1988; Rollinson and Hutchings 2013b), where "parental" fitness includes offspring survival and possibly offspring fecundity. In this paradigm, parents maximize reproductive success by trading off the fitness accrued from an increase in resource investment per offspring against the fitness losses resulting from a reduction in their number (Smith and Fretwell 1974; Einum and Fleming 2000; Johnson et al. 2010). This leads to an expectation of stabilizing selection on investment per offspring from the parental perspective (Fig. 1), and parent–offspring conflict over size arises because the level of investment per offspring that maximizes parental fitness is lower than the level that maximizes juvenile fitness (Fig. 1B).

The evolutionary consequences of the offspring size–number trade-off have long been understood in terms of selection acting through parental reproductive success (Lack 1947; Smith and Fretwell 1974). However, an interesting observation can be made if we consider how selection acts from the perspective of juveniles. Specifically, selection on juvenile size is expected to be positive, and it will recur in every generation (Fig. 1A) despite stabilizing selection on investment per offspring from the parental perspective (Fig. 1B). Whether fitness is assigned to individuals (i.e., juveniles, in this case) or to parents can have important consequences on expected patterns of selection and evolutionary response, and therefore the assignment of fitness must be considered carefully (Cheverud 1984).

Hadfield (2012) suggests that assigning fitness to parents, and hence defining fitness as the product of parental fecundity and offspring survival and/or reproduction, is generally not compatible with the quantitative genetic approach. Fitness should be assigned to the individual and defined as the number of zygotes produced. Under this quantitative genetic definition of fitness, a different framework exists for understanding the trade-off between investment per offspring and fecundity. Given that the individual pays a fecundity cost for increased per-offspring investment (Lack 1947, 1954; Williams 1966), directional selection against investment per offspring likely exists (Cheverud 1984; Hadfield 2012). Selection on size in general, however, can be assumed to be positive (e.g., Kingsolver and Pfennig 2004). In this framework, parent–offspring conflict over size is embodied in antagonistic directional selection across life stages: upward selection on body size, and downward selection on investment per offspring (see qualifications in Hadfield 2012). In the present study, we adopt a quantitative genetic framework and assign fitness to the individual, given that our interest lies broadly in evolutionary response to selection on size.

We argue that the trade-off between fecundity and investment per offspring, that is, parent–offspring conflict over size, might help explain stasis in both plants and animals. Given that body size is affected by investment per offspring, we hypothesize that upward selection on size (e.g., Kingsolver and Pfennig 2004) is balanced by downward selection on investment per offspring, such that antagonistic selection across life stages of an individual results in a net selection gradient on size that is effectively zero (Cheverud 1984; Hadfield 2012). We acknowledge that determination of whether parent–offspring conflict over size can quantitatively predict stasis of body size requires parameterization of a full quantitative genetic model (Kirkpatrick and Lande 1989; Hadfield 2012). Unfortunately, the parameters of such a model are currently unknown, and development in quantitative genetic theory of parental effects will be required to test whether parent–offspring conflict over size can quantitatively predict stasis (Cheverud 1984; Hadfield 2012). In general, we expect that the full quantitative genetic model will need to partition the variance components associated with size among direct genetic effects (genes belonging to the individual), maternal genetic effects (genes expressed in the mother that affect the individual's phenotype, such as provisioning genes), and the covariance between direct and maternal genetic effects on size across ontogeny (Byers et al. 1997; Thiede 1998; Wilson et al. 2005a,b; Wilson and Reale 2006), in addition to environmental (co)variances.

Nevertheless, some assumptions and predictions of our verbal model can be tested, and we present three such tests in the present study. First, we test the assumption that individuals typically face a size–number trade-off in determining juvenile size by analyzing a newly compiled dataset of phenotypic and genetic correlations between juvenile size and fecundity. This trade-off is well documented at the phenotypic level (Lim et al. 2014), and defining this trade-off phenotypically is important because it avoids conflating selection and inheritance. However, widespread evidence of a genetic trade-off has never been synthesized, and estimates of the genetic correlation between these two traits might provide a more accurate estimate of the trade-off, given that the phenotypic trade-off is more readily obscured by environment-based resource acquisition (van Noordwijk and de Jong 1986; Lim et al. 2014). Second, in all organisms that exhibit a size–number trade-off, parent–offspring conflict over size predicts strong directional selection on size when size is influenced by parental decisions. In the present study, we assume that juvenile size is more strongly influenced by parental decisions than adult size, and we provide two tests to assess whether directional selection on size is relatively strong in juveniles. First, we assemble a new database of selection estimates on juvenile size metrics from the literature (e.g., egg weight, length-at-hatching, birth mass, fledgling mass, etc.) to estimate selection on juvenile size. Second, we use existing data from previous selection reviews (Kingsolver et al. 2001a; Kingsolver and Diamond 2011b; Morrissey and Hadfield 2012; Siepielski et al. 2013) to assess the strength and form of selection on size. Importantly, all recent syntheses of selection estimates—those that have revealed that directional selection on body size is pervasive, positive, and persistent (Kingsolver et al. 2001a; Kingsolver and Diamond 2011b; Morrissey and Hadfield 2012; Siepielski et al. 2013)—are compiled in such a way as to conflate selection on adult body size with selection on juvenile size. If our thesis is correct, then partitioning selection according to ontogeny will reveal that directional selection on size is stronger in juveniles than in adults.

Methods

THE SIZE–NUMBER TRADE-OFF

We tested the assumption that adults face a size–number trade-off in determining juvenile size. In September 2013, we performed a literature search and amassed data on phenotypic (r_p) and genetic (r_A) correlations between juvenile size and adult fecundity. Search terms (Table S1) were designed to extract studies that measured genetic parameters for per-offspring investment (e.g., egg mass, egg diameter, birth weight) and adult fecundity, and a few studies were also gathered opportunistically based on the reference material in selected studies. Our focus was exclusively on animals, given that the databases of phenotypic selection on size that we subsequently employ (see below) were very strongly biased toward animals (e.g., Figs. S1, S2).

Our literature search returned 953 studies, of which 19 studies yielded 46 useable estimates of the genetic correlation (r_A) between investment per offspring and adult fecundity from 16 unique animal species. Estimates were derived from studies employing half-sib analysis (five studies, 10 estimates), dam-daughter regression (five studies, 6 estimates), the animal model (four studies, 6 estimates), and clonal lines (five studies, 24 estimates). Importantly, parent–offspring conflict over size is embodied in the cross-generational genetic correlation between direct genetic effects on fecundity and maternal genetic effects on juvenile size. However, estimating direct—maternal genetic correlations in general is very challenging (Thiede 1998; Wilson et al. 2005a), and only one study by Schroderus et al. (2012) was able to differentiate between direct–direct and direct–maternal genetic correlations between juvenile size and fecundity. For Schroderus et al. (2012), we report the direct–maternal genetic correlation (i.e., $r_{AM} = -0.38$), but we note that all other genetic correlations we report conflate the direct–direct and direct–maternal genetic correlation between juvenile size and fecundity. Phenotypic correlations (r_P) were obtained from a subset of the 19 studies that reported estimates of r_A. In total, we obtained 37 estimates of r_P from 13 studies performed on 12 unique species.

The animals used for our analysis of r_A included four species of terrestrial insect, two crustaceans, one polychaete, two birds, two fish, two mammals, one gastropod, and two reptiles. Notably, data were biased toward crustaceans, as 23 of the total 46 estimates were derived from *Daphnia magna* or *D. pulex*. A phylogenetically explicit meta-analysis of the data would be very challenging because data were derived from a highly heterogeneous grouping of taxa. Instead, sign tests were used to determine whether medians were positive or negative, and all r_A estimates are plotted by taxonomic group in Figure S3. To reduce biases arising from the use of multiple estimates per study and species, data were analyzed as a whole, then analyzed data were reduced either to study medians, or species medians. All tests were two-tailed, and α was set to 0.05.

We also used a bootstrapping approach to approximate confidence intervals on median r_A and median r_P. We estimated bias-corrected confidence intervals from 10,000 runs, using the *boot* package in R version 3.1.0 (Canty and Ripley 2013; R Development Core Team 2013), and sample size in each run was equivalent to the total number of estimates of r_A or r_P. Publication bias was estimated graphically, by regressing parameter estimates against sample size (Palmer 2000; Kingsolver et al. 2001a).

SELECTION ON JUVENILE SIZE

In all organisms that exhibit a size–number trade-off, our hypothesis predicts strong directional selection on size when size is influenced by parental decisions, and our assumption is that juvenile size is generally more strongly influenced by parental decisions than adult size. We tested this hypothesis using a dataset of variance-standardized selection estimates that were not analyzed in the selection reviews of Kingsolver et al. (2001a), Kingsolver and Pfennig (2004), Siepielski et al. (2009, 2013), or Kingsolver and Diamond (2011b). We used an ISI keyword search in November and December 2013 to locate studies that measured linear (s) and quadratic (c) selection differentials, as well as linear (β) and quadratic (γ) selection gradients on investment per offspring, measured as a juvenile trait (Table S2). A few studies were also gathered opportunistically based on the reference material in selected studies. We did not search within Dryad or within the aforementioned selection databases for estimates of selection on juvenile size. All studies measured viability selection on the size of juveniles, such the mass of an individual at birth, the length of a hatchling, or egg weight; size-related traits such as tarsus length and hindlimb length were avoided. Our focus was exclusively on animals, to increase the comparability of our estimates to those in existing databases (Table S3).

When a study was deemed potentially suitable during our search based on its abstract, it was subsequently examined more carefully. If any estimate of selection or potential estimate of selection (e.g., a figure) was noted during this subsequent examination, the estimate was extracted and included in our database, regardless of whether it would ultimately be included in the final analysis (see below). Where possible, we used DataThief (version 1.6) to extract data from images, and we subsequently calculated variance-standardized s following Lande and Arnold (1983). Where possible, phenotypic distributions before and after selection were used to calculate s, following Lande and Arnold (1983). For these studies, statistical significance of s was determined using Welch's t-test.

Our literature search for estimates of linear and quadratic selection differentials (s and c, respectively) and gradients (β and

γ, respectively) on juvenile size returned 1429 studies, of which 59 studies yielded at least one estimate of s or β (Table S3). After collecting all the data, we systematically examined all studies to determine whether we could use the study in our analysis. One or more datapoints from 45 studies (totaling 205 estimates of s, 105 estimates of β, 152 estimates of c, and 30 estimates of γ) was subsequently excluded from analysis on a priori grounds. We excluded data based on seven possible factors: (1) a problem in parameter estimation (one study); (2) the study reported significant estimates of selection but did not report nonsignificant estimates (three studies); (3) selection was not measured in wild, unmanipulated populations (23 studies); (4) fitness was not measured as juvenile viability (two studies); (5) ontogeny was advanced when selection was measured, such that the study was not measuring investment per offspring (one study); (6) the study already appeared in Kingsolver and Diamond's (2011a) database (10 studies). The seventh reason relates specifically to estimates of c for some studies of fish. Many estimates of selection on size of larval and juvenile fish were based on size distributions before and after selection, where size distributions were estimated using otolith analysis. While estimates of s should on average be accurate using this method, estimates of c will be upwardly biased. This is because estimating initial size from otoliths after growth has occurred is relatively prone to observer error, which has the effect of inflating the variance of estimated initial sizes in the "after selection" sample (see Wilson et al. 2009; Perez and Munch 2010). Therefore, we do not report estimates of c from nine studies that employed otolith analysis ($n = 47$ estimates, median $c = 0.466$, range = –1.16 to 7.85), but these estimates are archived in Dryad, along with all other excluded estimates. After excluding data for reasons 1–7 (above), our main analysis included 106 estimates of s (18 studies), 23 estimates of c (five studies), 12 estimates of β (four studies), and 10 estimates of γ (three studies).

SELECTION ON ADULT SIZE

Recent syntheses of phenotypic selection—those that have revealed that directional selection on body size is pervasive, positive, and persistent (Kingsolver et al. 2001a; Kingsolver and Diamond 2011b; Morrissey and Hadfield 2012; Siepielski et al. 2013)—are not compiled in such a way as to differentiate between selection on adult body size and selection on juvenile size. However, if our thesis is correct, then partitioning selection according to ontogeny will reveal that persistent selection is acting primarily on juvenile body size, not adult size.

Kingsolver and Diamond (2011b) compiled estimates of linear selection for a wide variety of traits by combining the databases of Kingsolver and Diamond (2001a,b) and Siepielski et al. (2009). For the present study, we created the largest possible database of selection estimates by combining records from Kingsolver et al. (2011a,b) with records from a more recent database compiled by Siepielski et al. (2013); we call our new dataset the "K-D Database." In the datasets compiled by Kingsolver and Diamond (2011b) and Siepielski et al. (2013), size-related traits were classified as "other morphology" or "size," and fitness components were classified as "survival," "mating success," and "fecundity." In the present study, only traits that were originally classified as "size" and for which "survival" was measured were included in our K-D Database. We also included records that used principal components analysis to reflect total size of an animal, as long as fitness was measured as survival. In these cases, only the first principal component (PC1) was used, and the original studies were consulted to ensure that PC1 was characterizing total size.

The K-D Database comprised 1183 estimates of selection from 39 studies (Table S3). Next, we revisited each of these 39 studies and determined whether viability selection was estimated on adult size or juvenile size, thereby creating an "Adult Dataset" and a "Juvenile Dataset." A study was assigned to the Juvenile Dataset if size traits reflected a measure of investment per offspring, such as birth weight, egg size, or fledging size; all other studies were assigned to the Adult Dataset. Therefore, the Juvenile Dataset contained only estimates of selection on juvenile size, whereas the Adult Dataset contained estimates of viability selection on body size of adults and subadults.

Previous reviews of the strength of phenotypic selection have consistently observed that median estimates of linear selection are positive, and that nonlinear components of size selection are negative (Kingsolver et al. 2001a; Kingsolver and Pfennig 2004; Kingsolver and Diamond 2011b). To confirm that this same pattern exists in our K-D Database, we bootstrapped medians, as above, using all estimates in the K-D Database. Next, we quantified differences in linear selection on adults and juveniles by bootstrapping the median (separately for s and β) of the Adult Dataset and the Juvenile Dataset, and we calculated the median difference in each of 10,000 runs. In this comparison, confidence intervals were obtained from the upper and lower 2.5% of bootstrapped differences, and two-tailed P-values were calculated as two times the quotient of the bootstrapped differences greater than zero divided by the total number of bootstrap replicates. Although we did not formally account for phylogeny in our analyses, all selection estimates are plotted with respect to taxonomic group in Figures S1, S2.

Results

THE SIZE—NUMBER TRADE-OFF

Our analyses revealed evidence for both a phenotypic (r_P) and genetic (r_A) trade-off between investment per offspring and adult fecundity. In our dataset, 33 of the 37 estimates of r_P were

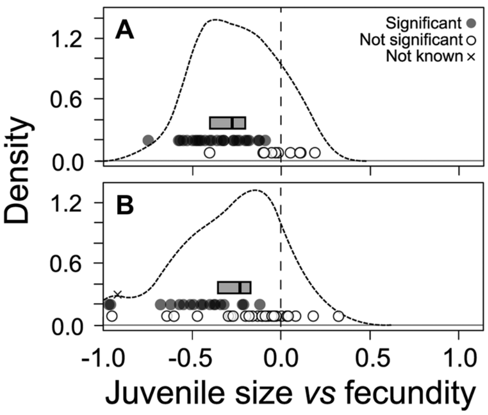

Figure 2. **The distribution of (A) phenotypic and (B) genetic correlations between a measure of investment per offspring (e.g., egg weight, birth weight) and a measure of fecundity, as estimated by kernel density. The boxplot is the median with bootstrapped 95% confidence intervals estimated across all data.**

negative (89%), and 27 of 37 estimates (73%) were significantly negative (Fig. 2A). A sign test revealed r_P was negative more often than expected by chance ($n = 37$, median = –0.27, $P < 0.001$). This conclusion was robust whether we considered only the median estimate per study ($n = 13$, median = –0.24, $P < 0.001$) or the median estimate per species ($n = 12$, median = –0.220, $P = 0.006$). Bias-corrected 95% confidence intervals from bootstrap analysis across all r_P estimates did not overlap zero (Fig. 2A).

For genetic correlations, we found that 40 of the total 46 estimates (87%) were negative. Statistical significance could be determined for 45 of these estimates, and 19 of these 45 estimates (42%) were significantly negative (Fig. 2B). A sign test revealed r_A was negative more often than expected by chance ($n = 46$, median = –0.24, $P < 0.001$) or this finding was robust whether we considered only the median estimate per study ($n = 19$, median = –0.32, $P < 0.001$) or the median estimate per species ($n = 16$, median = –0.34, $P < 0.001$). Bias-corrected 95% confidence intervals from bootstrap analysis across all r_A estimates did not overlap zero (Fig. 2B). There was no indication of publication bias in the trade-off datasets we compiled (Fig. S4).

SELECTION ON JUVENILE SIZE

We found evidence of positive directional selection on juvenile size (Fig. 3): 85% of s estimates in our J-S Database were positive (90 of 106), and sign tests showed that s was positive more often than expected by chance (median s for all data = 0.262, $n = 106$, $P < 0.001$; median s per study = 0.278, $n = 18$, $P < 0.001$; median s per species = 0.335, $n = 17$, $P = 0.002$). Estimates of quadratic differentials (c), linear gradients (β), and quadratic gradients (γ) were too scant to perform formal statistics, although median c was negative (median c = –0.0970, $n = 23$ estimates from five studies, Fig. 3), median β was positive (median = 0.221, $n = 12$ estimates from four studies, Fig. 3), and median γ was negative (median = –0.0225, $n = 10$ estimates from three studies, Fig. 3).

Finally, we note that our quality control procedure, namely the exclusion of over 300 estimates of selection on juvenile size, had no effect on our central findings: an examination of excluded data revealed patterns that are consistent with our main conclusions (median excluded $s = 0.0962$, $n = 205$; median excluded $c = –0.0306$, $n = 152$; median excluded $\beta = 0.113$, $n = 105$; median excluded $\gamma = –0.0473$, $n = 30$). There was no indication of publication bias in our J-S Database (Fig. S5).

SELECTION ON ADULT SIZE

Using the K-D Database, which is a database compiled from the studies of Kingsolver and Diamond (2011) and Siepielski et al. (2013), we first confirmed previous findings that linear selection on body size is positive and quadratic estimates of selection are negative. Median estimates of viability selection in the K-D Database were indeed positive for β and negative for both c and γ; in no cases did bootstrapped 95% confidence intervals overlap zero. The median estimate of s was positive but bootstrapped confidence intervals overlapped zero (Fig. 3).

As we demonstrate below, however, linear selection on body size observed in the K-D Database is largely due to viability selection on juvenile size, whereas median linear viability selection on adult size is near zero. When we focus only on studies in the K-D Database that reported selection on juvenile size (the "Juvenile Dataset"), median estimates of β and s were positive and confidence intervals did not overlap zero; this finding is consistent with the results for our J-S Database (Fig. 3). Conversely, when we consider only studies that estimated selection on adult body size (the "Adult Dataset"), 95% confidence intervals for β and s overlapped zero (Fig. 3). Finally, the median difference in β between the Adult Dataset and the Juvenile Dataset was significant (median difference = 0.17, UCI: 0.25, LCI: 0.11, $P < 0.001$, n = 10,000 bootstrap comparisons), as was the median difference in s (median difference = 0.027, UCI: 0.050, LCI: 0.010, $P = 0.012$, n = 10,000 bootstrap comparisons), indicating that median directional selection on body size was significantly larger in the Juvenile Dataset.

Discussion

Persistent directional selection on size is widely observed in nature (Kingsolver and Pfennig 2004; Kingsolver and Diamond 2011b; Morrissey and Hadfield 2012). Yet, evolutionary response is generally not in the direction predicted by the breeder's equation (reviewed by Gotanda et al. 2015), and stasis dominates the temporal dynamic of size over macroevolutionary timescales (Uyeda

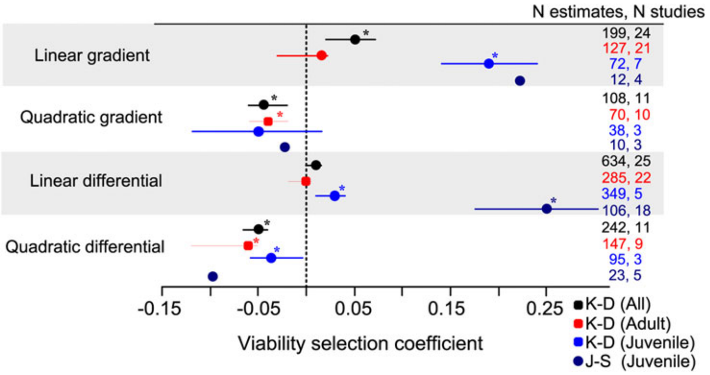

Figure 3. **Median estimates of viability selection on body size and 95% bootstrapped confidence intervals. Previously compiled data are presented first (K-D Database), and these data represent a mixture of juveniles and adults. Selection coefficients from the K-D Database are subsequently separated based on whether selection was measured on adult viability (K-D Adult, red) or juvenile viability (K-D Juvenile, light blue). Selection coefficients from a novel database of viability selection on juvenile size (J-S Database) are also presented (dark blue). Asterisks indicate that confidence intervals do not overlap zero. No confidence intervals appear on some estimates from the J-S Database, as sample sizes are small.**

et al. 2011). In the present study, we help resolve this paradox by suggesting that the observed selection for larger size is balanced by selection against investment per offspring (see also Cheverud 1984; Hadfield 2012).

Two main findings support this resolution. First, we observed that phenotypic and genetic correlations between investment per offspring and fecundity are overwhelmingly negative in the animal species that we examined (Fig. 2). This trade-off suggests the presence of selection against investment per offspring, as individuals pay a fecundity cost to increased investment (Cheverud 1984; Hadfield 2012). Second, we observed that positive directional selection on juvenile size is pervasive in wild animal populations, and most importantly, directional selection is stronger in juveniles than in adults. This result is expected because juvenile size is more strongly affected by investment per offspring than adult size, and selection against investment per offspring will result in relatively strong upward selection on juvenile size. Finally, we also found that selection on juvenile size exhibits a positive directional component and a negative-quadratic component. This pattern of selection is consistent with theories of offspring-size evolution, which assume a concave-downward fitness function for juvenile size (Smith and Fretwell 1974; Einum and Fleming 2000; Rollinson and Rowe 2015).

We emphasize that our results provide only qualitative support for the focal hypothesis, and that estimating all parameters of a full quantitative genetic model would be required to test whether stasis is quantitatively predicted by antagonistic selection on size across life stages. Furthermore, we acknowledge that the patterns of selection we observed might not be caused by parent–offspring conflict. A different interpretation of our results is that relatively strong upward selection on size exists when organisms are small (e.g., size-dependent predation exists), but selection on size becomes weaker as organisms grow along a trajectory toward a larger adult size (e.g., Milner et al. 1999; Blanckenhorn 2000; Pelletier et al. 2007). Further tests are therefore required to directly implicate parent–offspring conflict in the evolution of size. As an example, the model we propose predicts that species exhibiting the strongest trade-off between juvenile size and fecundity should also exhibit the strongest selection on size, as juveniles or as adults. Unfortunately, not enough data exist at present to test this prediction. Although we are not able to directly implicate parent–offspring conflict in the evolution of size, we underline that parent–offspring conflict is broadly expected and supported (Lack 1947; Smith and Fretwell 1974; Trivers 1974; Godfray and Parker 1991; Godfray 1995; Einum and Fleming 2000; Hadfield 2012; Rollinson and Hutchings 2013a). Based on our findings, we suggest parent–offspring conflict plays an important role in body–size evolution.

Provided that parent–offspring conflict over size exists, a general insight from the present study is that persistent directional selection on size is expected to occur when size is influenced by investment per offspring. While the conceptual framework for our study was grounded in the size–number trade-off, our findings should also apply to species that produce only one juvenile per reproductive episode (e.g., many ungulates). Here, the relevant trade-off is that of current versus future reproductive success (Williams 1966; Creighton et al. 2009), and provided that the individual retains residual reproductive value, selection against investment per offspring is expected (see also Clutton-Brock 1984).

Our findings might also provide some insight into why upward selection on size in microevolutionary studies generally does not result in the evolution of larger size (reviewed in Gotanda et al. 2015). All microevolutionary studies documenting stasis in wild populations have been performed on birds or mammals, presumably because these groups are amenable to long-term evolutionary study. Yet, these groups also exhibit high investment per offspring and protracted periods of parental care: birds often provision offspring over days or weeks, and mammals provision offspring throughout gestation and over weeks or months following parturition. Juvenile body size at independence is typically predictive of adult body size in birds and mammals, probably because of extended care (Clutton-Brock 1988; Clutton-Brock et al. 1992; Schluter and Gustafsson 1993; Perrins and McCleery 2001; Wilson et al. 2005b). In a quantitative genetic framework, genetic variation in investment per offspring is subsumed by maternal genetic variation for size. Under the simplifying assumption that maternal genetic effects on size are caused only by maternal genes that affect investment per offspring, and ignoring any direct–maternal genetic correlation for investment per offspring, the extent to which body size is constrained by investment per offspring likely depends on the extent to which maternal genetic variation exists for adult size. The logic is that any maternal genetic contribution to adult size may not respond to upward selection, as it is constrained to a degree by the trade-off between investment per offspring and fecundity.

For birds and mammals, indirect genetic effects (e.g., maternal and paternal genetic effects) on size are suspected to play a role in stasis (e.g., Wilson et al. 2007), but modeling these effects is challenging (Thiede 1998; Wilson et al. 2005a; Head et al. 2012). Indirect genetic effects generally have not been considered in microevolutionary studies that document stasis (Merilä et al. 2001a,b,c; Charmantier et al. 2004; Garant et al. 2004; Wilson et al. 2005c; Hadfield et al. 2010; but see Cooke et al. 1990; Wilson et al. 2007). It seems likely that microevolutionary stasis is due in part to the difficulty in accounting for indirect genetic effects on size in general, especially given that these effects become increasingly important and complex when parents actively provision juveniles (Wilson and Reale 2006; Head et al. 2012). While acknowledging that indirect genetic effects in general play an important role in the evolution of size (Wilson et al. 2005a; Wilson and Reale 2006), we specifically suggest that the negative direct–maternal genetic correlation between fecundity and investment per offspring plays a central role in constraining the evolution of body size, especially in birds and mammals. This suggestion is supported by studies documenting a strong correlated evolution of juvenile size and adult size in birds and mammals, where investment per offspring likely affects adult size, but a weak correlated evolution of these traits in groups where maternal genetic effects on adult size seem less likely, such as amphibians and fish that generally exhibit larval stages (Fig. 4).

Interestingly, we found that selection on adult body size features an important negative-quadratic component, but median linear selection on adult size is near zero (Fig. 3). Stabilizing selection on adult size is consistent with long-term stasis of size (Estes and Arnold 2007; Uyeda et al. 2011), but the apparent absence of directional selection on adult size must be regarded cautiously. Although upward selection is generally expected for juvenile size under our hypothesis, we also expected upward selection on adult size in some taxonomic groups, particularly in birds and mammals, where variation in investment per offspring

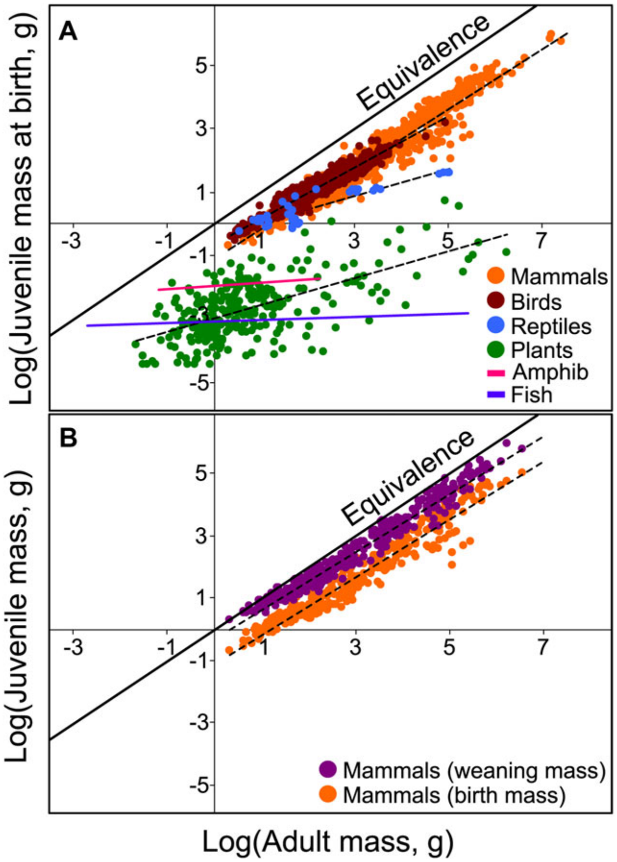

Figure 4. (A) Interspecific relationships between species-mean adult mass and mean weight at birth (mammals), mean egg weight (birds, reptiles, amphibians, fish), or mean seed weight (plants). For comparability, values for plants were converted to wet weight (g) by multiplying dry mass values by 1.8, all other groups are wet weight (g). Slopes, coefficients of determination (r^2), and number of species (n) are as follows: mammals (slope = 0.95, $r^2 = 0.95$, $n = 816$), birds (slope = 0.81, $r^2 = 0.92$, $n = 713$), reptiles (slope = 0.83 $r^2 = 0.42$, $n = 36$), plants (slope = 0.42 $r^2 = 0.38$, $n = 281$), amphibians (slope = 0.10, $r^2 = 0.02$, $n = 61$), and fish (slope = 0.05, $r^2 = 0.01$, $n = 153$). (B) Size at weaning closely corresponds with final adult size in mammals, suggesting that parental effects on adult size are common. Regression lines are drawn for birth weight ($y = 0.932x - 1.12$, $r^2 = 0.94$, $n = 371$) and for weight at weaning ($y = 0.934x - 0.320$ $r^2 = 0.97$, $n = 371$). Species and sample sizes are identical for birth weight and weaning datasets. Data sources are as follows: mammals (Ernest 2003), birds (Lislevand et al. 2007), plants (Falster et al. 2008), reptiles (Blueweiss et al. 1978), and regression lines drawn for amphibians and fish were estimated by Visman et al. (1996).

may affect variation in adult size. A preliminary examination of how selection on adult size differs among taxonomic groups suggests relatively strong upward selection in mammals, but no clear directional trend in birds or other groups, although sample sizes are generally small (Fig. S1). The relatively protracted period of gestation and care in mammals suggests that parental influences on adult size are perhaps most likely in this group (see also Reinhold 2002), and this would be consistent with our observation that upward selection on adult size occurs only in mammals. Yet, our supplementary analysis considers only viability selection, not selection on size via fecundity or total fitness. More detailed and phylogenetically explicit investigations into patterns of selection on size are warranted, and future meta-analytic work might also benefit from the accumulation of more selection gradients estimated in wild populations, as understanding selection on size of juveniles and adults in diverse taxa may prove important in resolving the paradox of stasis for size.

The present work focuses exclusively on the size–number trade-off, and so far we have ignored many elements involved in parent–offspring interactions. But other forms of parent–offspring conflict might also limit the evolution of body size. In species with parental care, for instance, an individual can affect its own size and the size of its siblings by competing directly for parental resources, and by manipulating parental allocation (Godfray and Parker 1991; Godfray 1995). At face value, the effect of parental manipulation on body–size evolution is conceptually similar to the effect of the size–number trade-off: individual fitness can be relatively high when it manipulates parents, but fitness of the same individual as a parent is highest when manipulation is absent (Godfray and Parker 1992). Yet, the individual is also related to its parents and siblings, and therefore the individual is expected to act selfishly only when the benefit to the individual is greater than the cost to the other parties, weighted by relatedness (Hamilton 1964; Trivers 1974). When Hamilton's rule is considered, it is possible that upward selection on size might also be balanced by selection against selfish behavior. We emphasize that the extent to which kin selection can help explain stasis must also be assessed in a full quantitative genetic model (Cheverud 1984; Kirkpatrick and Lande 1989), and that estimating the relevant parameters of such models will probably prove challenging.

In conclusion, the paradox of stasis for body size involves two related observations. The first is that persistent upward selection on body size in contemporary populations seems incongruent with low rates of macroevolution. We suggest that the missing part of this evolutionary puzzle is that the observed upward selection on size is balanced by selection against input per offspring. In support of this, we demonstrate that linear selection on juvenile size is stronger than selection on adult size, and that juvenile size and adult fecundity trade-off. The second part of the paradox is that contemporary examples of microevolutionary stasis are frequently observed in wild birds and mammals. We provide insight into this problem by suggesting that investment per offspring is likely to affect adult size in these groups, such that the trade-off between investment per offspring and fecundity might result in a relatively strong evolutionary constraint on adult size.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1: Linear selection coefficients plotted for each phylogenetic group for the J-S database, and for the K-D database separated into the Juvenile Dataset and the Adult Dataset.
Figure S2: Quadratic selection coefficients plotted for each phylogenetic group for the J-S database, and for the K-D database separated into the Juvenile Dataset and the Adult Dataset.
Figure S3: Genetic correlations between size and fecundity are plotted for each taxonomic group.
Figure S4: Estimates of the (a) phenotypic correlation (rP) and (b) genetic correlation (rA) between a measure of investment per offspring (e.g., egg weight, birth weight) and fecundity are plotted against log sample size.
Figure S5: Estimates of (a) linear selection and (b) quadratic selection are plotted against log sample size.
Table S1: Search string used for ISI Web of Science search to identify studies measuring the genetic correlation between propagule size and fecundity.
Table S2: Search string used for ISI Web of Science search to identify studies measuring selection on juvenile size.
Table S3: Summary data for estimates of linear (*s*) and quadratic (*c*) differentials as well as linear (β) and quadratic (γ) gradients in the offspring-size database compiled for the present study (J-S Database) and from Kingsolver and Diamond.s (K-D) database.