An ecological explanation for hyperallometric scaling of reproduction

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Abstract

In wild populations, large individuals have disproportionately higher reproductive output than smaller individuals. We suggest an ecological explanation for this observation: asymmetry within populations in rates of resource assimilation, where greater assimilation causes both increased reproduction and body size. We assessed how the relationship between size and reproduction differs between wild and lab-reared Trinidadian guppies. We show that (i) reproduction increased disproportionately with body size in the wild but not in the lab, where effects of resource competition were eliminated; (ii) in the wild, the scaling exponent was greatest during the wet season, when resource competition is strongest; and (iii) detection of hyperallometric scaling of reproduction is inevitable if individual differences in assimilation are ignored. We propose that variation among individuals in assimilation – caused by size-dependent resource competition, niche expansion, and chance – can explain patterns of hyperallometric scaling of reproduction in natural populations.

Keywords— bioenergetic models, common garden experiments, competitive asymmetry, *Poecilia reticulata*, size-dependent competition, wild populations, Yule-Simpson effect

Introduction

Across animal taxa, larger individuals reproduce more than smaller individuals of the same species (Honěk, 1993; Visman et al., 1996; Kingsolver and Huey, 2008; Lim et al., 2014; Ronget et al., 2018). While many theoretical models assume that reproduction is proportionate to body size (e.g. Roff, 1983; West et al., 2001; Lester et al., 2004; Kooijman, 2010), recent work in marine fishes has shown that larger individuals have disproportionately higher reproductive output: of 342 species, 95% display hyperallometric scaling of reproduction (Barneche et al., 2018). Reproductive hyperallometry – where large individuals produce more offspring per unit body weight than small individuals – appears to be the norm for free-living marine fishes, and has been reported in many other taxa (e.g. freshwater fish (King, 1998), crustaceans and marine invertebrates (Thompson, 1979), true bugs (Valle et al., 1987), turtles (Mueller et al., 1998), and frogs (Gibbons and McCarthy, 1986); reviewed in Marshall & White (2019)). These observations, seemingly at odds with theoretical predictions, beg the question: what process – absent from theoretical models that predict proportionate scaling of reproduction – generates these patterns?

One way to address this question is to consider a simple bioenergetic model of three processes central to any organism: assimilation of energy from the environment, and use of energy for either growth and somatic maintenance, or for reproduction (Fig. 1). Here we describe two versions of this model which both result in hyperallometry of reproduction.

In one version, proposed by Marshall and White (2019), allocation of energy to growth and reproduction is assumed to be size-dependent: individuals allocate an increasing fraction of energy towards reproduction as they grow (Fig. 1A). This increasing investment in reproduction can explain why larger individuals produce disproportionately more or larger offspring. Because a change in energetic allocation would presumably be under endocrinal control, we term this the "physiological model".

An alternative version assumes that the fraction of energy allocated to reproduction is fixed within an individual, but rates of assimilation vary among individuals (Fig. 1B). Individuals with higher rates of assimilation attain both larger sizes and higher reproductive output than those with lower assimilation rates. This is essentially the model proposed by van Noordwijk and de Jong (1986) to explain why the detection of life-history trade-offs often fails at the level of individuals within populations: positive correlations between life-history traits will occur when variance in resource assimilation affects both traits. Following this model, we argue that variation among individuals in assimilation rates will result in reproductive hyperallometry at the level of the population. We term this the "ecological model", because we propose that variance in assimilation rates – and therefore the degree of reproductive hyperallometry – is likely to be driven by the strength of ecological interactions.

Ecological interactions that will influence assimilation rates include resource competition, niche expansion, and the predation risk while foraging for food. A central assumption of the physiological model – that individuals (of different sizes) experience the same environmental conditions (Marshall and White, 2019) – is unlikely to hold true in natural systems, with respect to a key environmental variable: food availability. In wild populations, individuals are rarely equal in their ability to accrue resources, and such differences can drive divergence in realised life histories, generate population dynamics, and determine the strength

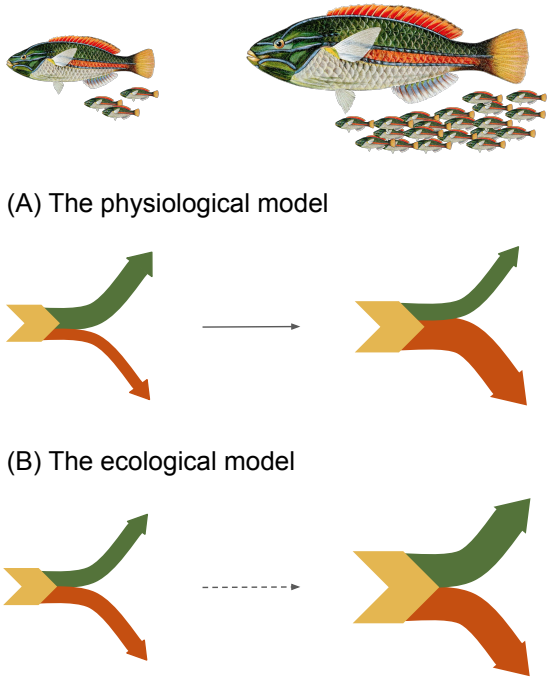

Figure 1: Two versions of a simple bioenergetic model of an organism which both predict hyperallometric scaling of reproduction. The organism is characterised by three energetic fluxes: assimilation of energy into the organism from the environment (yellow arrow), use of energy for growth and somatic maintenance (green arrow), and use of energy for reproduction (red arrow). The magnitude of each flux is depicted by the width of the arrows. In the physiological model (A) allocation to reproduction increases as the organism grows (growth of individual depicted by the solid black arrow). Assimilation increases with body size in absolute, but not relative terms: Marshall and White (2019) assume a size-scaling exponent for assimilation of 0.81, i.e. assimilation $\sim$ size$^{0.81}$. In the ecological model (B) the fraction of energy allocated to reproduction does not change with size (although this fraction will vary among individuals), but individuals with high rates of assimilation have more energy to allocate to both growth and reproduction than individuals with low rates of assimilation. Assimilation rates may increase as individuals grow (dotted arrow), but this is not a prerequisite for hyperallometric scaling of reproduction: variation in assimilation rates among individuals is sufficient for hyperallometric scaling of reproduction at the level of the population. The fish illustration (*Stetholojulis albovittata*) is in the public domain, accessed through the Biodiversity Heritage Library.

of ecological interactions (Bassar et al., 2016; Coulson, 2020; Griffiths et al., 2020; Laskowski et al., 2021).

Evidence for intraspecific competition for resources is widespread among fishes, and larger body size is typically associated with stronger competitive ability (Ward et al., 2006, and references therein). Individuals may become large because their local habitat is rich in food, or because they have certain behavioural or metabolic traits that increase their rates of energy assimilation in a given environment (McCarthy et al., 1992, 1994; Ward et al., 2004; Toscano et al., 2016; Auer et al., 2020). Furthermore, once an individual becomes large, it is likely to experience further size-dependent competitive advantages over smaller individuals, under scenarios of both exploitative and interference competition (Mittelbach, 1981; Post et al., 1999; Ward and Krause, 2001; Potter et al., 2019; Griffiths et al., 2020). In addition, most fish are gape-limited feeders, which has two main consequences for size-dependent resource availability: larger fish can consume a broader range of food items (i.e. size-dependent niche expansion, Scharf et al., 2000), and they are at

lower risk of predation, meaning that they can forage in areas too risky for smaller individuals (Werner and Hall, 1988; Byström et al., 2004; Magnhagen and Borcherding, 2008). As such, big fish inhabit a very different environment – in terms of food availability, past and present – to that experienced by small fish within the same population.

In wild populations, disentangling the causes and effects of resource competition on size and reproduction is extremely challenging. Observational data on size and fecundity alone cannot, for example, directly distinguish (i) whether larger individuals allocate a greater fraction of available energy to reproduction, or (ii) whether they are larger and have greater reproductive output because they have consumed more food than smaller individuals. By contrast, in the lab, the confounding effects of resource competition and niche expansion can be eliminated, allowing direct assessment of these questions.

Here, we assess factors that determine how reproductive output scales with body size in the Trinidadian guppy (*Poecilia reticulata*). Guppies are small, live-bearing, freshwater fish common throughout streams and rivers in Trinidad and Venezuela (Magurran, 2005). Resource competition is asymmetric in guppies, with larger fish being stronger competitors (Bassar et al., 2016; Potter et al., 2019; Griffiths et al., 2020). We compared reproductive scaling exponents from observations of wild populations with those of experimental populations in the absence of the effects of resource competition and niche expansion. Specifically, we assessed how reproduction scaled with female body size (i) for different measures of reproductive output both in the wild and lab, (ii) for wild fish sampled either in the dry or (resource-poor) wet season, and (iii) for lab-reared fish fed either a high-quantity or low-quantity diet. During the wet season in Trinidad, increased water flow and flooding scours the streams of the invertebrates, algae, and detritus that guppies feed on, leading to more intense competition for resources (Kohler et al., 2012; Auer et al., 2012; Zandonà et al., 2015). In the laboratory, fish were housed individually and fed with quantified rations of food equally accessible to all size classes of fish, and so any effects of food level are independent of competitive ability. If larger guppies have disproportionately higher reproduction in both seasons (in the wild) and both food treatments (in the lab), this would support the physiological model, i.e. increasing allocation to reproduction with increasing body size. By contrast, if scaling is hyperallometric in the wild, but not in the lab (in the absence of effects of competition), this would support an ecological explanation for hyperallometric scaling of reproductive output in natural populations.

Methods

Data

The wild data that we used are from an observational study on variation in life histories among natural populations of guppies (Reznick, 1989), supplemented with additional, previously unpublished data. For full details on methodology, we refer the reader to the original study. Briefly, wild guppies were collected from 19 populations in the Northern Range mountains of Trinidad between the years 1981 and 1987 (the previously unpublished data were collected in 1986 and 1987). Sampling took place in both the dry season (in years 1981, 1984-1987) and wet season (1981-1983, 1985), with most populations sampled in more than

1 year (median = 3 years, range = 1-7 years, Table S1). Female guppies were dissected, and developing embryos counted. The weight of adults was recorded to the nearest mg, and the dry weight and lean dry weight of embryos were recorded to the nearest 0.1 mg. In total, the wild dataset included observations of 2547 individuals, of which 1483 contained developing embryos (Table S1).

The lab data are from an experimental study of rates of senescence in guppies (Reznick et al., 2004, 2005). In summary, guppies were collected from four natural populations and reared for two generations under lab conditions to control for differences in maternal environments. Experimental fish (females) were housed in individual tanks from 30 days of age (mean = 29.6 days, sd = 3.9 days, range = 20-40 days) and fed twice daily with volumetrically quantified rations of brine shrimp nauplii or liver paste. Guppies were assigned to either a high or low food treatment. In both treatments, ration size gradually increased over the first 180 days, and was held constant thereafter. Juvenile females were paired with a mature male to ensure that they were mated as soon as they attained maturity. At each parturition event, females were weighed to the nearest mg, the number, dry weight and lean dry weight of neonates was recorded (to 0.1 mg), and females were re-mated. We calculated the mean somatic growth rate during pregnancy as the change in mass between parturition events, divided by the length of the interval (days) between parturition events. Data were collected over the entire reproductive lifespan of each individual (mean age at final parturition = 722 days, sd = 237 days). The common garden dataset included 4629 observations of 211 individual (Table S2).

We calculated three main measures of reproductive output: fecundity (number of offspring per litter), offspring mass (total dry weight of offspring in a litter, mg), and offspring energy (total energy content of litter, J). We calculated offspring energy by multiplying the total litter protein mass (lean dry weight) and fat mass (dry weight minus lean dry weight) by appropriate energy densities (protein = 17 kJ g^{-1}, fat = 37 kJ g^{-1}). Additionally, for the lab data only we were able to convert each of the three measures of reproductive output into reproductive powers (i.e. output per unit time) by dividing the measure of reproductive output by the interval between births (days).

Models

We used mixed-effects models to address five main questions: (1) How do different measures of reproduction scale with body size in the wild and in the lab, and do environmental differences change this relationship? (2) Do large guppies allocate less energy to growth than small guppies? (3) Do estimates of reproductive scaling change if differences among individuals in assimilation rates are ignored? (4) What factors influence the interval between births in lab-reared guppies? (5) Does probability of pregnancy in wild guppies depend on size and season?

For questions 1-3, we modelled reproduction (R) as an exponential function of size (z), i.e. $R = az^{\beta_1}$. Reproduction is hyperallometric when the scaling exponent $\beta_1 > 1$, isometric (proportionate to body size) when $\beta_1 = 1$, and hypoallometric (smaller individuals have higher reproduction per unit body weight) when $\beta_1 < 1$. We estimated the scaling exponent by fitting linear mixed-effects models where the response was the natural log-transformed measure of reproduction, and the main fixed effect was the natural log-

transformed measure of mass. The parameters a and β_1 are given by the intercept and slope, respectively, of these linear models.

To address question 1, we modelled all three measures of reproductive output for lab and wild data, and all three measures of reproductive power for the lab data. To test the relationship between environmental factors and the scaling exponent β_1, we included either season (wild data) or food treatment (lab data) as fixed effects, interacting with ln(mass). We used appropriate random effects structures to account for non-independence of data (Table S3).

For questions 2 and 3, we chose total offspring energy content per litter as our measure of reproduction, because this measure was available in both lab and wild data and is equivalent to the measure of reproduction used by Barneche and colleagues (2018). To assess whether allocation of energy to growth decreases with increasing size in the lab (question 2), we included an interaction between somatic growth rate and ln(mass) in our model of reproduction (Table S3). Under the physiological model, increased reproduction should be associated with decreased growth, and this effect should be strongest at larger body sizes. This would correspond to a negative main effect of growth and a negative interaction term in this linear model. To address question 3, we modelled reproduction of a cohort of guppies in the lab (aged 200-300 days old) as an exponential function of size, both with and without accounting for differences in food treatment (Table S3).

Questions 4 and 5 concern factors influencing components of reproduction other than output: the duration of the interval between successive births in the lab, and the probability of being pregnant when sampled in the wild, respectively. For question 4, we included ln(mass) and the full interaction between age and food level as fixed effects in our model of the reproductive interval. For question 5, we estimated the probability of a wild-caught individual containing zero developing embryos, as a function of size and season. For this model we fit a logistic regression of the binary response (presence/absence of developing embryos), and included season and the natural log of mass as fixed effects (Table S3).

All analyses were performed using R version 3.5.1 (R Core Team, 2019). We fit our models in a Bayesian framework, using the R package *brms* version 2.14.4 (Bürkner, 2018), which makes use of the probabilistic programming language Stan (Carpenter et al., 2017). In the Gaussian models (Table S3), for the intercept and fixed effect coefficients we specified normal priors with a mean of 0 and standard deviation of 1 (sd = 5 for the intercept). For the standard deviation of random effects and residual variance, we specified cauchy priors with means of 0 and standard deviations of 1. For the correlation of random effects, we specified an LKJ prior with a value of 1, which assumes all correlational structures are equally likely (Bürkner, 2018). For the logistic regression model we used the "get_prior" function in *brms* to obtain appropriate default priors (Bürkner, 2018).

For each model, we ran four Monte Carlo Markov chains, with 2000 samples retained from each chain after a burn-in period of 1000 samples, yielding a combined total of 8000 samples of the posterior distribution. We confirmed that chains had converged by visually checking the trace-plots, and by confirming that scale reduction factors $\hat{R} < 1.01$. Effective samples sizes for all parameters were greater than 10% of the total number of samples.

Figures 2-4 were produced in R using the packages *ggplot2* (Wickham, 2011), *ggridges* (Wilke, 2018) and *patchwork* (Pederson, 2020).

Results

Parameter values reported in this section are the means of the posterior distribution, with the 95% credible intervals given in brackets. We define reproductive scaling as hyperallometric when the lower bound of the credible interval exceeds 1, as isometric when the interval contains 1, and as hypoallometric when the upper bound is less than 1.

Environmental effects on the scaling of reproduction with body size

In the wild, mean reproductive output across both seasons was hyperallometric when considering offspring mass (β_{1_M} = 1.15 [1.08; 1.23]) and offspring energy (β_{1_E} = 1.14 [1.06; 1.21]), but isometric in terms of fecundity (β_{1_F} = 0.99 [0.92; 1.07]) (Fig. 2Ai).

In the lab, mean reproduction across food treatments scaled hypoallometrically for fecundity (β_{1_F} = 0.93 [0.87; 0.99]), isometrically for offspring mass and energy (β_{1_M} = 0.97 [0.91; 1.02]; β_{1_E} = 0.95 [0.89; 1.01]; Fig. 2A.i), and hypoallometrically for all measures of reproductive power ($\beta_{1_{FP}}$ = 0.48 [0.41; 0.55]; $\beta_{1_{MP}}$ = 0.54 [0.48; 0.61]; $\beta_{1_{EP}}$ = 0.54 [0.47; 0.60]; Fig. 2A.ii). This reduction in how size scales with reproductive power relative to reproductive output corresponded to a linear increase in the interval between births with age: in both food treatments, the interval was ∼40% longer in the oldest fish relative to the youngest (intercept = 25.4 d [23.8; 27.0], β_{age} =0.010 [0.008; 0.013]). There was no clear effect of the natural log of mass, food treatment, or the interaction between age and food on the duration of the reproductive interval ($\beta_{ln(mass)}$ = -0.13 [-1.14; 0.91], β_{food_low} = 0.75 [-0.39; 1.88] , $\beta_{ln(mass):food_low}$ = -0.001 [-0.004; 0.001]).

For the wild populations, reproduction increased disproportionately to body size in both seasons, but the magnitude of hyperallometry was greater in the wet season (offspring energy J, $\beta_{1_{dry}}$ = 1.10 [1.02; 1.18]; $\beta_{1_{wet}}$ = 1.20 [1.10; 1.30]; difference = 0.10 [0.00; 0.20], Fig. 2B.i). In the lab, reproduction scaled isometrically under the high food treatment, but hypoallometrically under the low food treatment (offspring energy J, $\beta_{1_{high}}$ = 1.02 [0.94; 1.09]; $\beta_{1_{low}}$ = 0.89 [0.82; 0.97], Fig. 2B.ii).

Correcting for likelihood of pregnancy in the wild

In the wild, pregnant females were larger on average than females without developing embryos: 337 mg [328;347] vs. 154 mg [141;167] in the dry season, and 420 mg [406; 436] vs. 216 mg [199;233] in the wet season (Fig. 3A). The probability that a wild fish contained developing embryos increased with size, and this effect was stronger in the wet season (logistic regression, intercept = -16.07 [-18.17; -14.12], β_{ln_size} = 3.16 [2.86; 3.50], β_{wet}= -0.87 [-1.20; -0.53], Fig. 3B.i). This meant that for a 200 mg guppy, there was a 45% chance of being pregnant in the wet season, but a 66% chance in the dry season. Accounting for size- and season-dependent pregnancy changed the predicted relationship between size and reproduction in the

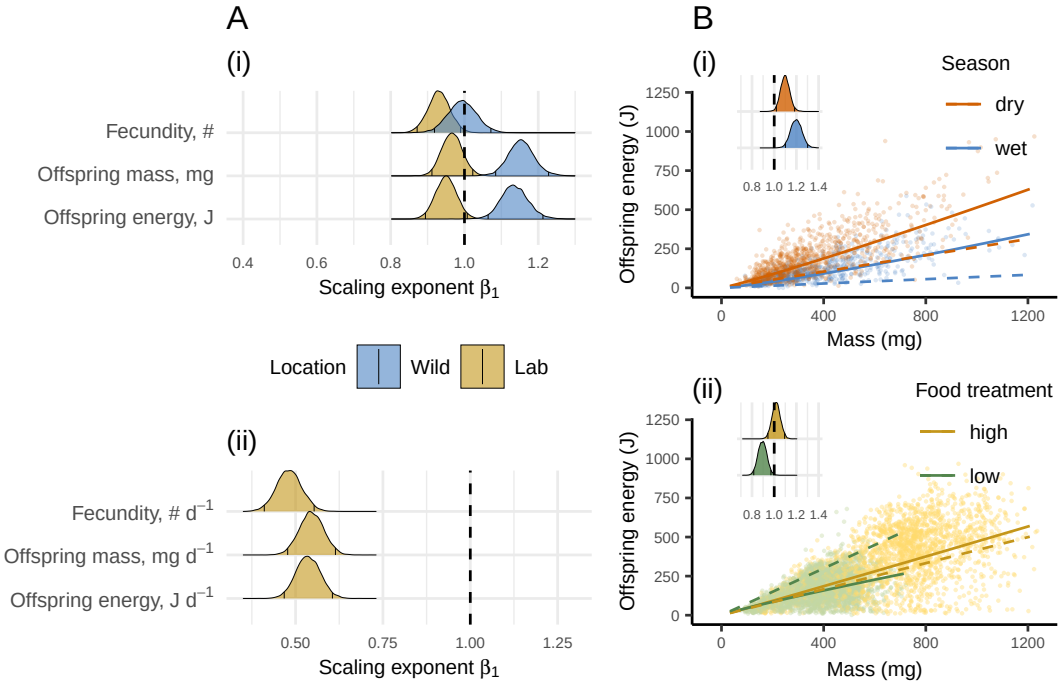

Figure 2: The scaling of reproduction with body size differs between wild and lab-reared populations of Trinidadian guppies, varies by reproductive measure, and is dependent on environmental conditions. (A) shows the posterior distributions of scaling exponents using three measures of reproduction: fecundity, offspring mass, and offspring energy content, expressed (i) per litter, and (ii) per unit time. Vertical black lines denote the 95% credible intervals. Posteriors are given for wild (blue) and lab (yellow) populations. Posteriors are the mean exponent across seasons (wild data) and food treatments (lab data), weighted by the number of observations in each season/food treatment. Measures of reproduction per unit time were not available for wild populations. (B) shows reproductive energy content per litter by body size in (i) wild guppies in the dry season (red) and wet season (blue) (1485 datapoints, one per individual), and (ii) guppies reared in the lab under high (yellow) or low (green) food treatments (4629 datapoints, from 211 individuals). Insets show the posterior distribution of the scaling exponents β_1. Solid lines show predicted reproduction given the estimated scaling exponents. Dashed lines show predicted reproduction assuming isometric scaling of reproduction, i.e. $\beta_1 = 1$.

wild: large fish had an even greater relative advantage over small fish in terms of reproduction (Fig. 3B.ii). Accounting for the probability of being pregnant, the mean reproductive output (total energy content per litter) of a 200 mg fish was 19.2 J in the dry season, but only 5.3 J in the wet season; for a 1000 mg fish, mean reproductive output in the dry season was 503.9 J, and 263.9 J in the wet season. Per unit body weight, the reproductive output of a 1000 mg guppy was 5.2 times higher than that of a 200 mg guppy in the dry season, and 10.0 times higher during the wet season.

Potential mechanisms underlying reproductive hyperallometry

In the lab, we found no evidence that larger fish allocate relatively more energy to reproduction over growth: when we included growth rate interacting with size in our model, the main effect of growth was negative (β_G = -0.63 [-0.84; -0.44]), but the interaction with body size was positive ($\beta_{G:z}$ = 0.10 [0.07; 0.13]), meaning that growth rate and reproduction co-varied negatively in small individuals, but positively

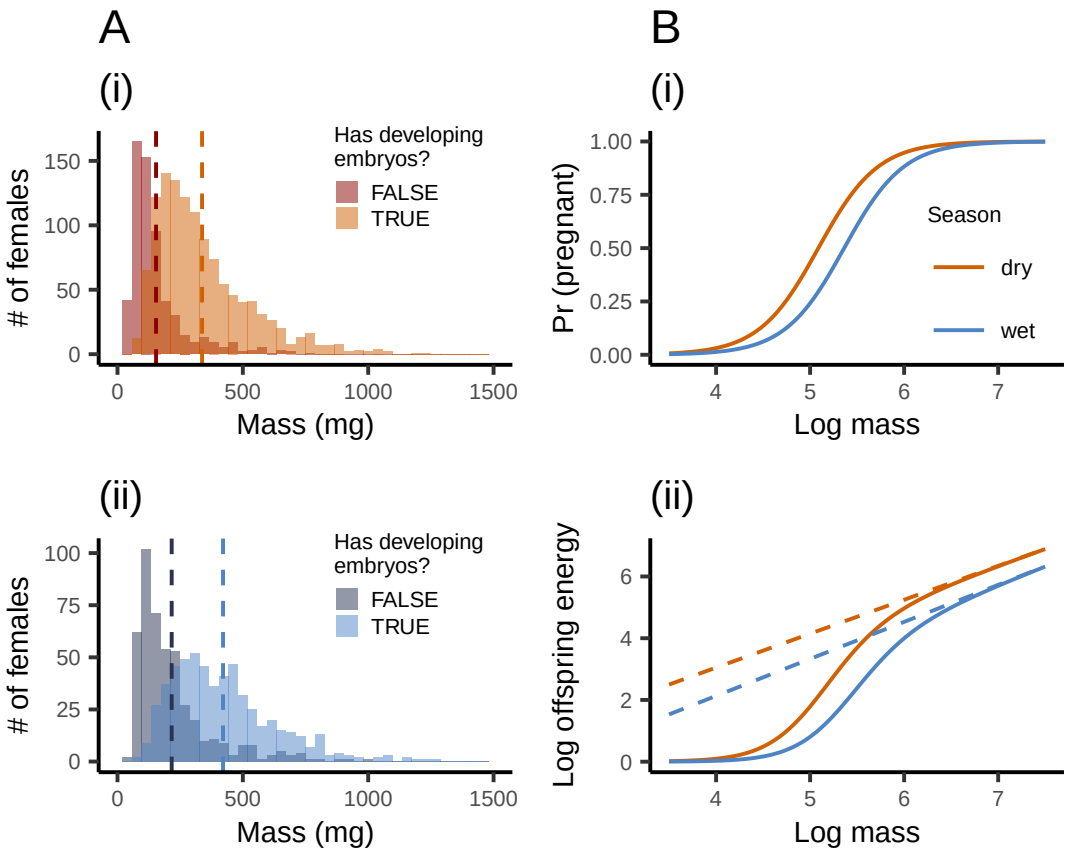

Figure 3: In wild populations, the probability of an individual being pregnant depended on size and season. (A) Histograms showing the size distribution of sampled fish that contained no developing embryos (dark) and those that contained at least one developing embryo (light) in (i) the dry season and (ii) the wet season. Dashed lines indicate the means of the distributions. (B.i) Probability of a wild fish containing developing embryos as a function of size (natural log of mass) in the dry season (red) and the wet season (blue). (B.ii) Log reproduction as a function of log size, when incorporating the probability of pregnancy by size (solid lines) in the dry season (red) and the wet season (blue). Dashed lines show the relationship between ln(size) and ln(reproduction) given that an individual is pregnant. The solid lines were calculated by multiplying the pregnancy probability function (B.i) by the season-specific log-linear function (dashed lines).

in large individuals.

Guppies reared under the high food treatment grew to larger sizes and had higher reproductive output than those in the same age cohort in the low food treatment (Fig. 4). Although reproduction scaled isometrically at high food ($\beta_{1high} = 0.71$ [0.36; 1.05]) and hypoallometrically at low food ($\beta_{1low} = 0.62$ [0.25; 0.98]), reproduction was hyperallometric when calculated across both food treatments ($\beta_{1high/low} = 1.30$ [1.17; 1.43], Fig. 4).

Discussion

What mechanism can explain the patterns of reproductive hyperallometry that are so widespread among wild populations? We propose that such patterns emerge from differences among individuals in their

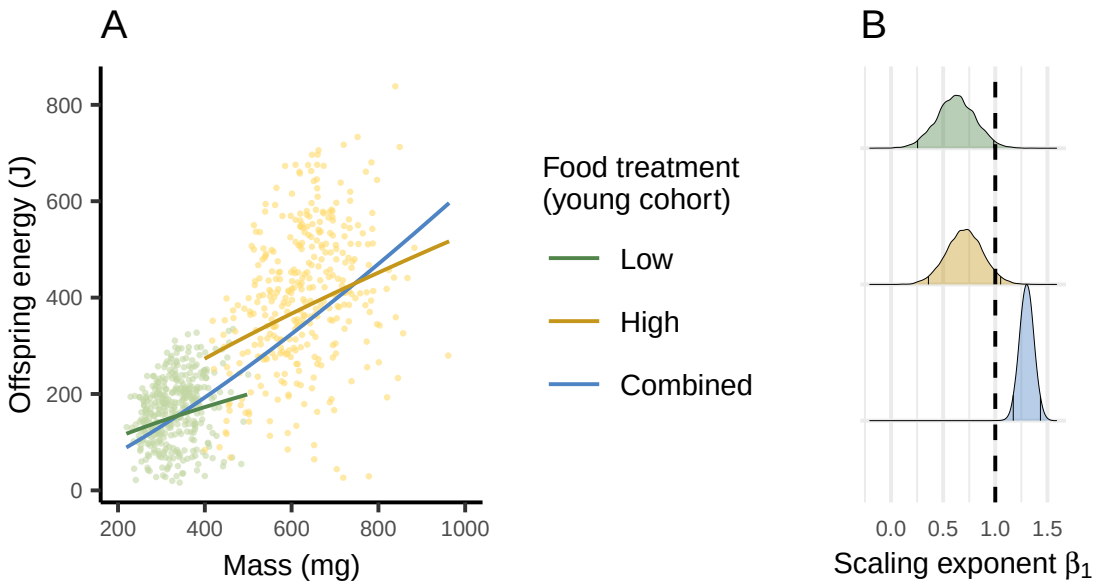

Figure 4: Hyperallometric scaling of reproduction was detected when differences in food availability within a cohort were ignored. (A) The relationship between reproduction (offspring energy content per litter, J) and body size (mass, mg) for a cohort of lab-reared guppies between the ages of 200 and 300 days old (total N = 729), reared under experimental treatments of either low (green) or high (yellow) levels of food availability. Lines show predicted reproduction when differences in food treatment are explicitly modelled (green and yellow) and when they are not (blue). (B) The reproductive scaling exponent β_1 was greater than 1 when data from both food treatments were combined (i.e. reproduction appeared hyperallometric), but mean values of the exponents were less than 1 when differences in food availability were included in the model.

history of energy assimilation (i.e. the ecological model, Fig. 1B), rather than as a consequence of an ontogenetic shift in allocation of resources within individuals (i.e. the physiological model, Fig. 1A (Marshall and White, 2019)). Our argument is supported by three main findings. First, in wild populations the strength of reproductive hyperallometry was environmentally dependent: large guppies had an even greater reproductive advantage over small guppies during the wet season, when resource competition was strongest (Fig. 2B.i, Fig 3). Second, in the lab, in the absence of the effects of resource competition and niche shifts, we found no evidence that large individuals allocated a greater fraction of available energy to reproduction: reproduction was either proportionate or less-than proportionate to body size (Fig. 2A, Fig 2B.ii). Third, we demonstrate that detection of reproductive hyperallometry is inevitable if differences in energetic assimilation are not taken into account (Fig. 4). We expand on these points in the following sections.

Environmental conditions affect how reproduction scales with body size

Our results add to the list of examples of reproductive hyperallometry in wild populations (Barneche et al., 2018; Marshall and White, 2019). Differences in reproductive output per unit body mass in wild guppies were driven by larger individuals producing disproportionately larger offspring, rather than through disproportionately higher fecundity (Fig. 2A.i). We show that the strength of hyperallometry was dependent

on environmental conditions: big guppies had an even greater reproductive advantage over small fish during the wet season (Fig. 2B.i). Increased levels of competition during the wet season lead to declines in recruitment and populations size (Reznick et al., 2019). When individuals are not equal competitors – which is the case in natural populations of guppies (Griffiths et al., 2020) – an increase in the intensity of resource competition will by definition result in increased variance in assimilation rates. Under the ecological model (Fig. 1B), increased variance in assimilation rates explains the increased value of the scaling coefficient β_1 in wild guppies during the wet season.

Not only did reproductive output decrease in pregnant guppies during the wet season, but the size-dependent probability of pregnancy also changed: when we accounted for the probability of wild fish being pregnant, the effects on reproduction of size and season increased drastically (Fig. 3B.ii). Although this measure of hyperallometry is not directly comparable with standard values of β_1 (our reproduction function was non-linear on the log scale), across a typical range of adult sizes, the pregnancy-corrected estimates corresponded to values of β_1 of $\sim$5 and $\sim$10: the reproductive output of large (1000 mg) guppies per unit body weight was five times that of a small (200 mg) guppy in the dry season, but ten times greater in the wet season. This degree of reproductive hyperallometry far exceeds those reported in other species (Barneche et al., 2018; Marshall and White, 2019), and highlights the strong effect of seasonality on the relationship between size and reproduction in wild guppies.

No evidence for increased allocation to reproduction with increased body size

The physiological model could explain the increased value of β_1 in the wet season if large individuals allocate even more energy to reproduction under conditions of resource limitation. Given that per-capita food availability is reduced in the wet season (Kohler et al., 2012; Auer et al., 2012), large fish may respond by allocating an even greater fraction of assimilated energy towards reproductive efforts. Our results in the lab demonstrate that this is not the case: under conditions of low food reproductive output scaled hypoallometrically, i.e. smaller fish had higher reproductive output per unit body weight (Fig. 2B.ii). At high food, reproduction was proportionate to body size in lab-reared guppies (Fig. 2B.ii). However, when we considered measures of reproductive power (i.e. reproductive output per unit time), reproductive scaling was strongly hypoallometric in the lab (Fig. 2A.ii). This suggests that guppies became increasingly food-limited as they grew, and compensated for the increasing costs of somatic maintenance that come with larger body size by diverting energy away from reproduction. As such, this implies that energetic allocation is not fixed (as assumed in the ecological model), but here the direction of change was opposite to that predicted by the physiological model.

We detected a trade-off between somatic growth and reproduction in small fish, but these traits were positively correlated in large fish. Under the physiological model, we would expect the trade-off to be stronger in larger individuals, as they are assumed to allocate more energy to reproduction over growth. Instead, small fish that grew slowly had higher reproduction, but big fish that grew faster also had higher reproduction. This positive correlation in large fish was likely due to individual differences in assimilation rates (even within food treatments) due to differences that we could not control in the lab, e.g. individual

variation in digestive efficiency. Because variation in digestive efficiency would have a cumulative effect on body size, size differences become more pronounced with time, such that the underlying trade-off between growth and reproduction becomes increasingly obscured by variation in assimilation rates (e.g. as in van Noordwijk and de Jong, 1986).

The expression of life-history traits in guppies is often highly dependent on food availability (Felmy et al., 2021). As such, it was unsurprising that guppies in the high food treatment grew to larger sizes and had higher reproductive outputs than those of the same in age in the low food treatment (Fig. 4A). Within food treatments, mean values of the reproductive scaling exponent β_1 were less than 1 (Fig. 4). However, when estimated across both treatments, β_1 was greater than 1 (Fig. 4). This illustrates how reproductive hyperallometry can be detected at the level of the population if differences among individuals in assimilation rates are not taken into account.

Causality and competition

The change from $\beta_1<1$ to $\beta_1>1$ shown in Figure 4, and more generally the explanation for positive correlations among life-history traits (van Noordwijk and de Jong, 1986), exemplify the Yule-Simpson effect: a change in a covariance conditional on a third factor (Yule, 1903; Simpson, 1951). Yule-Simpson effects are common in regression analyses, occurring when covariances are estimated over aggregated data structured by a third variable (Blyth, 1972; Pearl, 2014). In such cases, the covariance captures a non-causal association between the two variables of interest, which is in fact conditional on a third variable. Here, the variables of interest were size and reproduction, and the third variable was resource assimilation. The physiological model (Fig. 1A) assumes a causal effect of size on reproduction: bigger individuals allocate more energy to reproduction. By contrast, the ecological model (Fig. 1B) assumes a causal effect of assimilation on both growth and reproduction: individuals that assimilate more energy grow larger *and* produce more offspring.

In wild populations, the causal relationship between size and assimilation rates is more nuanced than that: large size may cause increased rates of assimilation (e.g. through increased competitive ability and niche shifts, as described in the Introduction), resulting in a positive feedback loop between assimilation rates and body size. In this case, size has an indirect causal relationship on reproduction, through size-dependent increases in assimilation. Furthermore, competition for finite resources is a zero-sum game: the assimilation rate of a focal individual (and subsequently its growth and reproduction) depends on the assimilation rates of its competitors. Here, size is key: in lab-based competition trials, large guppies suppressed the somatic growth rates of smaller individuals to a greater extent than vice-versa (Potter et al., 2019); in the wild, the growth and survival of individuals depended on their size relative to those of their competitors (Griffiths et al., 2020).

While size-dependent competitive ability will act to enhance the effect of reproductive hyperallometry, it is not a necessary condition. Differences in resource assimilation across a population could result from stochastic processes and environmental heterogeneity, without the need for resource competition among individuals. Nevertheless, given that size-structured competitive interactions are common in fish (Ward

et al., 2006), the strength of resource competition is likely to be a key determinant of the magnitude of reproductive hyperallometry in wild populations.

Limitations, generality, and alternative explanations

Our study considered a single species. As such, whether reproductive scaling exponents are consistently higher in the wild than in the lab (i.e. under conditions that limit competition) remains to be tested. However, a recent aquaria based study of the European sea bass (*Dicentrarchus labrax*) reported hypoallometric scaling of reproduction ($\beta_1 = 0.84$) under constant food availability (Sadoul et al., 2020), whereas wild populations of this species show hyperallometric scaling of reproduction ($\beta_1 = 1.34$, Barneche et al., 2018). The same study demonstrated that, under the framework of dynamic energy budget theory (Kooijman, 2010), differences within a population in food availability or ambient temperature can generate patterns of reproductive hyperallometry (Sadoul et al., 2020). These empirical observations and theoretical predictions are consistent with our findings here.

The vast majority (98%) of data used by Barneche and colleagues (2018) were from wild populations. Without any additional information on relevant ecological and environmental conditions, we argue that one cannot infer the cause of reproductive hyperallometry from such data. Interestingly, the most extreme values of hyperallometric scaling reported by Marshall and White (2019) do not come from observations of wild populations: they come from a lab-based study on the effects of experimental "crowding" on the growth and reproduction of leafhoppers (Valle et al., 1987). This scenario – where scaling exponents were measured across multiple groups differing in the intensity of resource competition – is precisely where the ecological model (and the Yule-Simpson effect) would predict the greatest degree of reproductive hyperallometry.

In our study there were, of course, many differences between the lab-reared and wild populations besides the effects of competition. One potential contribution to the observed difference in scaling exponents was selection bias in the wild-caught samples: while we obtained data from a random sample of individuals over their full lifespan in the lab, large individuals in the wild are rare, and likely represent a non-random subset (in terms of attributes) of the population as a whole. Indeed, in the wild dataset we observed very few large guppies (>800 mg) with low reproduction (<150 J per litter), compared to in the lab (48% of large lab-reared individuals (N = 60) had at least 1 litter with low reproductive output, compared to 15% of large wild guppies (N = 66), Fig. 2B). Nevertheless, this difference between lab and wild populations emphasises the role of ecological interactions in determining reproductive hyperallometry in natural populations: it is likely that those lab-reared large guppies with low reproduction (and presumably low assimilation/digestive efficiencies) would not have attained a large size under competitive conditions in the wild.

Conclusions and broader implications

Our results demonstrate that variation in assimilation rates among individuals cause patterns of reproductive hyperallometry at the level of the population. However, we also found evidence that the fraction

of energy allocated to reproduction was not fixed: large individuals in the lab allocated less energy to reproduction, presumably to cover increasing somatic maintenance costs while available food levels remained constant. We cannot rule out that the opposite may be true – large individuals with excess energy may allocate more towards reproduction. Nevertheless, differences in assimilation rates ultimately drive differences in both size and reproductive output among members of a population.

What can we infer from observations of how reproduction scales with size in natural populations? The simplest interpretation is that it tells us how resource assimilation rates vary by size. For example, rare cases of hypoallometric scaling in the wild, as in Arctic cod (*Boreogadus saida*, reported in Barneche et al., 2018), indicate that large fish are more food-deprived than smaller individuals. Given that reproductive hyperallometry is the rule in wild populations of fishes, rather than the exception (Barneche et al., 2018; Marshall and White, 2019), this implies that in most natural populations, small individuals are resource-limited relative to larger conspecifics. Although we cannot infer causality of size on assimilation rates from such observations – differences in assimilation rates may be due to chance – size-dependent asymmetric competition favouring large individuals will increase the strength of reproductive hyperallometry.

In natural populations, it is inevitable that individuals will differ in their rates of resource acquisition and assimilation. Whether through trait-mediated differences or chance, two individuals in a wild population will never have equivalent amounts of assimilated energy with which to fuel their metabolism and contribute to somatic growth, and with which to invest in reproduction. The effects of differences in food availability among individuals are non-trivial: resource-dependent expression of life-history traits often exceeds the effect of evolved differences between locally-adapted populations (Felmy et al., 2021), and trait-dependent differences in assimilation rates can flip predictions about life-history evolution (Laskowski et al., 2021) and generate eco-evolutionary dynamics (Coulson, 2020). Understanding how and why individuals differ in rates of resource assimilation is central to understanding variation in demographic rates that underpin ecological and evolutionary dynamics in wild populations.

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