Ecology and the diversification of reproductive strategies in

viviparous fishes

Michael Tobler^{1*} & Zachary Culumber²

¹Division of Biology, Kansas State University, Manhattan, KS 66506, USA

²Department of Biological Sciences, University of Alabama in Huntsville, Huntsville, AL 35899,

USA

*Corresponding author: Michael Tobler, Division of Biology, Kansas State University, 106 Ackert

Hall, Manhattan, KS, USA; phone: +1-785-532-6652; email: tobler@ksu.edu

Abstract

Shifts in life history evolution can potentiate sexual selection and speciation. However, we rarely understand the causative links between correlated patterns of diversification or the tipping points that initiate changes with cascading effects. We investigated livebearing fishes with repeated transitions from pre- (lecithotrophy) to post-fertilization maternal provisioning (matrotrophy) to identify the potential ecological drivers of evolutionary transitions in life history. Phylogenetic comparative analyses across 94 species revealed that bi-directional evolution along the lecithotrophy-matrotrophy continuum is correlated with ecology, supporting adaptive hypotheses of life history diversification. Consistent with theory, matrotrophy was associated with high resource availability and low competition. Our results suggest that ecological sources of selection contribute to the diversification of female provisioning strategies in livebearing fishes, which have been associated with macroevolutionary patterns of sexual selection and speciation.

Keywords: life history evolution | natural selection | phylogenetic comparative analysis | Poeciliidae

Introduction

Evolutionary transitions in maternal provisioning strategies represent a primary axis of reproductive life history variation in viviparous organisms (Wourms 1981; Blackburn 1992). Shifts from an ancestral strategy of females providing all resources for embryonic development prior to fertilization (lecithotrophy) to post-fertilization provisioning (matrotrophy) have been associated with the evolution of complex physiological and morphological adaptations, including placental structures of apposed maternal and embryonic tissues that facilitate nutrient transfer (Wooding and Burton 2008). Matrotrophy and placentas have evolved repeatedly in viviparous animals, including multiple invertebrate (Campiglia and Walker 1995; Hart et al. 1997; Korniushev and Glaubrecht 2003; Korneva 2005; Ostrovsky et al. 2016) and vertebrate lineages (Steward and Blackburn 1988; Wourms et al. 1988; Wake and Dickie 1998; Wildman et al. 2006). Transitions along the lecithotrophy-matrotrophy continuum may have far reaching consequences, shaping the evolution of other traits and patterns of biological diversification (Zeh and Zeh 2000; Coleman et al. 2009; Pollux et al. 2014; Furness et al. 2015; Furness et al. 2019). What evolutionary forces shape the evolution of matrotrophy, however, remains unclear (Pollux et al. 2009).

There are two, non-mutually exclusive hypotheses that view matrotrophy as an adaptation to ecological sources of selection: (1) Matrotrophy has been hypothesized to reduce locomotor costs associated with pregnancy (Magnhagen 1991; Shaffer and Formanowicz 1996; Miles et al. 2000). Specifically, lecithotrophic females are expected to suffer from impaired locomotion throughout gestation, while matrotrophic females with initially small embryos should avoid such costs at least in early stages of pregnancy (Miller 1975; Thibault and Schultz 1978). (2) Resource availability may shape evolution along the lecithotrophy-matrotrophy continuum. Lecithotrophy is expected to be adaptive in environments with fluctuating resource availability (Thibault and Schultz 1978), whereas

matrotrophy theoretically maximizes reproductive output when resource availability is high and stable (Trexler and DeAngelis 2003).

Livebearing fishes of the family Poeciliidae are an iconic model system for testing hypotheses about the evolution of reproductive strategies at micro- and macroevolutionary scales (Evans et al. 2011). Poeciliids have undergone remarkable diversification in levels of post-fertilization maternal provisioning, with independent origins of matrotrophy in different clades (Reznick et al. 2002; Pollux et al. 2009; Pollux et al. 2014). Research on poeciliid fishes has been instrumental for the advancement of our theoretical and empirical understanding of matrotrophy (Thibault and Schultz 1978; Pollux et al. 2009; Pires et al. 2011), and there is evidence supporting various predictions of both adaptive hypotheses of matrotrophy evolution. Pregnancy in poeciliids has been shown to be associated with locomotor costs (Plaut 2002; Ghalambor et al. 2004; Quicazan-Rubio et al. 2019), and there is evidence that matrotrophy increases streamlining (Fleuren et al. 2018) and may be favored in high predation environments requiring efficient escape responses (Gorini-Pacheco et al. 2017; Hagmayer et al. 2020). At the same time, post-fertilization maternal provisioning also responds to resource availability and female condition (Trexler 1997; Marsh-Matthews and Deaton 2006; Hagmayer et al. 2018), and matrotrophy is associated with significant costs when resources fluctuate (Pollux and Reznick 2011). However, most empirical tests of the potential adaptive function of matrotrophy have been conducted at microevolutionary scales and using just a small number of species, leaving questions about the generalizability of past findings.

Here, we used phylogenetic comparative analyses of matrotrophy evolution across 94 species spanning the family Poeciliidae. Species in this family are broadly distributed throughout the Americas, found in a wide variety of ecological contexts, and have a well-resolved phylogeny (Meffe and Snelson 1989; Hrbek et al. 2007; Reznick et al. 2017), facilitating comparative analyses that contrast hypotheses about the evolutionary origins of matrotrophy. To do so, we first characterized

the evolutionary dynamics of matrotrophy evolution and then used phylogenetic path analysis to test for correlations between ecological variables and variation in matrotrophy.

Methods

Taxon sampling and phylogenetic framework

Our analyses included 94 species (Table S1), encompassing representatives of all major genera in the family Poeciliidae. These species span a geographic range from the eastern United States south to Argentina, including Caribbean islands (Figure S1). The phylogenetic framework used for analyses was established by previous studies with similar taxon sampling (Pollux et al. 2014; Culumber and Tobler 2017). In brief, sequences for six mitochondrial (*12S*, *COI*, *CytB*, *ND2*, *tRNA^{Val}*, and *tRNA^{Leu}*) and 11 nuclear genes (*Beta Actin*, *CCND1*, *ENC1*, *GLYT*, *MYH6*, *RAG1*, *Rhodopsin*, *RPS7*, *SH3PX3*, *T36*, and *XSRC*) were obtained from GenBank, aligned, and maximum likelihood phylogenetic analysis was conducted using RAxML-HPC version 8 (Stamatakis 2014) on the CIPRES computer cluster (San Diego State University, San Diego, CA, USA). The resulting best scoring tree was highly consistent with previously published phylogenetic hypotheses for the family Poeciliidae (Hrbek et al. 2007; Pollux et al. 2014; Reznick et al. 2017). Phylogenetic trees were time calibrated with three calibration points spanning the depth of the phylogeny (see Culumber and Tobler 2017 for details), including a primary fossil calibration associated with the split separating the outgroup (*Fundulus*) from all poeciliids (55-99 Ma; Santini et al. 2009) and a secondary fossil calibration separating *Heterandria formosa* from the genus *Poecilia* (9.3-19 Ma; Ho et al. 2016). In addition, the formation of Laguna de Catemaco (Mexico), a crater lake with several endemic species, was used as a constraint on the age of the endemic *Poeciliopsis catemaco* (0.5-2.0 Ma; Mateos et al. 2002). Even though bootstrap support values of the best scoring tree were generally strong,

phylogenetic comparative methods described below were conducted across 250 trees drawn at random from the bootstrap replicates to account for phylogenetic uncertainty.

Quantifying matrotrophy and sexual selection

Matrotrophy levels for all species included in the analysis were obtained from previously published studies (Pollux et al. 2014; Olivera-Tlahuel et al. 2015). The extent of post-fertilization maternal provisioning was quantified using the matrotrophy index (MI, ln-transformed for all analyses), which is the ratio of offspring mass at birth to the mass of the egg at fertilization (Reznick et al. 2002; Pollux et al. 2009). Offspring of lecithotrophic species typically lose 25-55% of the initial egg mass during development ($MI < 0.75$), while continuous nutrient transfer from mother to offspring during gestation in matrotrophic species leads to $MI > 1$ (Reznick et al. 2002; Pollux et al. 2009).

Evolutionary dynamics of maternal provisioning strategies

To characterize the evolutionary dynamics of matrotrophy evolution, we conducted ancestral state reconstructions of MI using PHYTOOLS (Revell 2012). To evaluate the directionality of matrotrophy evolution (increases *vs.* decreases in MI) between each node and its descendants, we extracted trait reconstructions for each node of the tree and calculated ΔMI as the observed (tip) or inferred (node) matrotrophy values subtracted from the values of its most recent ancestral node.

Identifying ecological correlates of variation in maternal provision strategies

To test the competing hypotheses for matrotrophy evolution, we assembled a set of relevant environmental predictor variables. According to the locomotor hypothesis, matrotrophy should be associated with environments that favor high locomotor performance, such as habitats with high predation pressure or fast water currents (Reznick et al. 2007; Gorini-Pacheco et al. 2017). Hence,

predictor variables included metrics of hydrology (based on the topography of each species' range) and predation (number of predatory fish species overlapping each species' range). According to the resource availability hypothesis, matrotrophy should be associated with environments where resources are abundant and competition is low (Trexler and DeAngelis 2003). Hence, we quantified climate (including estimates of temporal variability in temperature and precipitation patterns in each species' range), average net primary productivity (NPP), and competition (number of poeciliid species overlapping each species' range). The potential effects of different environmental variables on variation in maternal provisioning strategies was evaluated with phylogenetic path analysis as outlined below.

Quantifying hydrology, climate, and net primary productivity

Assembly of hydrological and climate variables associated with each species' range was based on georeferenced occurrence points. We obtained 73,398 locality points from multiple sources (<http://fishnet2.net/>, <http://gbif.org/>, primary literature), representing the known distributions for all 94 species included in our study. We first removed duplicate points and retained a maximum of 100 randomly sampled localities within the native range of each species, which is sufficient to capture environmental variation even in wide-ranging species (van Proosdij et al. 2015). We further verified that all data points for a given species were at least 1 km apart to match the spatial resolution of environmental data. Any locality that did not meet this criterion was either removed for species with <100 localities or replaced by another randomly drawn locality for species with >100 localities. For all locality records, we then extracted values for three hydrological variables (elevation, slope and compound topographic index; Hydro1k: <https://lta.cr.usgs.gov/HYDRO1K/>), 19 climatic variables (Worldclim: <http://worldclim.org/>), and an estimate of net primary productivity (<https://lpdaac.usgs.gov/>) at a spatial resolution of ~1 km²

(30 arcsec) in ArcMap version 10.2.2 (ESRI Inc, Redlands, CA, USA). For each species, we calculated the median value for all 23 variables. Climatic and hydrological variables were then subjected to separate phylogenetic principal component analyses (pPCA) using a correlation matrix, as implemented in the PHYTOOLS package in R (Revell 2012). In addition to the estimate of net primary productivity associated with each species' range, we retained two pPCA axes accounting for 76% of variation in hydrology (Table S2) and three pPCA axes accounting for 81% of variation in climate (Table S3).

Quantifying competition and predation

Quantifying the actual biotic interactions for a large number of species distributed across the vast geographic scale included in this study is virtually impossible. Hence, we developed two simple, objectively quantifiable metrics to approximate levels of competition and predation. We assumed that competitive interactions for the focal species primarily occur with other species of the family Poeciliidae (Alberici da Barbiano et al. 2010; Torres-Dowdall et al. 2013) and that the intensity of competition is a function of the number of coexisting species. Hence, we first analyzed overlap of distributional ranges to characterize patterns of sympatry (defined as range overlap values greater than zero; Weber et al. 2016). We created geo-referenced distributional range maps for each species by generating a convex hull around each species' known occurrence points (see above) using ArcMap. The resulting species-specific distributions were then intersected to determine the total number of competitor species exhibiting a range overlap with a focal species. Similarly, we created a metric estimating the levels of predation by determining the total number of piscivorous fish species exhibiting a range overlap with each focal species. To do so, we obtained 271,148 locality points (<http://gbif.org/>) of 7,170 species across 1,602 genera and 26 families in the superclass Osteichthyes that coincide with the distribution of poeciliids. Since distributional polygons of some

focal species overlapped with marine habitats (particularly in poeciliid species occurring along the Gulf of Mexico and in both island and mainland localities), we first removed species primarily inhabiting marine environments as well as non-native species, retaining 5,019 native freshwater species in 853 genera (Table S4). To identify potential predators, we conducted a genus-level literature search of dietary habits using relevant monographs (Greenfield and Thomerson 1997; Bussing 1998; Boschung et al. 2004; Miller et al. 2005; van der Sleen and Albert 2017), supplemented by the primary literature when necessary. We retained 131 genera that included species with evidence for piscivory (867 species; 73,421 locality points). Values for the number of competitors and predators were square-root-transformed prior to analyses.

Analytical framework

We investigated hypotheses about the hierarchical relationships among abiotic and biotic environmental factors and matrotrophy using phylogenetic path analysis as implemented in the R package PHYLOPATH (van der Bijl 2018). We developed 18 models based on *a priori* hypotheses about the effects of hydrology, climate, NPP, competition, predation, and interactions between predictor variables relevant in the context of the locomotor cost and resource limitation hypotheses of matrotrophy evolution (Figure S2). As with other phylogenetic analyses described above, path analyses were run across 250 random trees. PHYLOPATH implements model selection with covariance inflation criterion, CIC_c (Rodriguez 2005). Models with an average $\Delta CIC_c < 2$ were considered equally supported (Burnham and Anderson 2002). Joint effects of net primary productivity and competition were visualized using non-parametric thin-plate spline regression to create a surface of matrotrophy variation (Arnold 2003). Estimation of matrotrophy surfaces was performed using the FIELDS package in R, with smoothing parameter $\lambda = 0.005$ (Nychka et al. 2007).

Results

Evolutionary dynamics of matrotrophy evolution during diversification of poeciliid fishes

Ancestral state reconstructions (ASR) were used to compare inferred ancestral states of matrotrophy to variation in matrotrophy observed in extant taxa (Figure 1A). ASRs across 250 trees demonstrated that lecithotrophy is not the ancestral provisioning strategy (Figure 1B). The inferred ancestral state was clearly toward the matrotrophic end of the spectrum (with a net weight gain during development) and distinctly above the levels of post-fertilization provisioning observed in most extant taxa (Figure 1B). This does not mean that matrotrophy evolved prior to lecithotrophy, but rather that the common ancestor of extant poeciliids had already evolved some degree of post-fertilization provisioning. Examining the direction of shifts in post-fertilization provisioning strategies between all nodes and their descendants revealed that reductions of post-fertilization provisioning were just as common as increases in matrotrophy (Figure 1C).

Ecological correlates of matrotrophy evolution

We contrasted a series of hypotheses about the hierarchical relationships among different abiotic and biotic environmental variables and matrotrophy using phylogenetic path analysis. Model selection identified two models with average $\Delta\text{CIC}_c < 2$ across the 250 trees (Figure S3), including NPP, competition, and predation as predictor variables for variation in MI (Figure 2A). Both models indicated that NPP positively correlated with competition ($r = 0.325$, 95% CI = 0.324 – 0.326 for both supported models), which in turn was negatively correlated with matrotrophy (top model: $r = -0.030$, 95% CI = -0.034 – -0.025; secondary model: $r = -0.077$, 95% CI = -0.081 – -0.075). In addition, there was a positive relationship between NPP and matrotrophy (top model: $r = 0.024$, 95% CI = 0.022 – 0.025; secondary model: $r = 0.023$, 95% CI = 0.021 – 0.024). Simultaneously visualizing the effects of NPP and competition on matrotrophy indicated that high levels of

matrotrophy occurred when NPP was high and competition was low (Figure 2B). In the best supported model, NPP was also positively correlated with predation ($r = 0.184$, 95% CI = 0.183 – 0.185), which in turn was negatively correlated with matrotrophy ($r = -0.082$, 95% CI = -0.087 – -0.078). Notably, however, the directionality of the relationship between predation and matrotrophy was opposite to the predictions of the locomotor cost hypothesis, which posits that matrotrophy should enhance locomotor performance and be favored in high-predation environments. Although the effects sizes in the path analyses were relatively small, they were significantly different from zero, indicating that ecology has played a role in matrotrophy evolution.

Discussion

Shifts from pre- to post-fertilization maternal provisioning represent a major axis of life history evolution in viviparous organisms (Wourms 1981; Blackburn 1992). Even though life history evolution is generally assumed to progress from oviparity to lecithotrophic viviparity to matrotrophic viviparity (e.g., Furness et al. 2015), our analyses indicated that decreases in levels of matrotrophy were just as common as increases. Such bi-directional evolution along the lecithotrophy-matrotrophy continuum has been documented in other viviparous taxa (e.g., Dulvy and Reynolds 1997; Reznick et al. 2007) and parallels secondary losses of obligate viviparity in fishes and reptiles (Parenti et al. 2010; Recknagel et al. 2018). The standard model of linear life history evolution therefore needs reevaluation to acknowledge that the evolution of these traits is more complex and dynamic than generally appreciated.

Our analyses further suggested that ecological sources of selection are important in driving bi-directional evolution along the lecithotrophy-matrotrophy continuum. Phylogenetic path analysis identified three biotic variables that were associated with variation in matrotrophy (resource availability, competition, and predation), all of which are well-documented drivers of life history

diversification in animals (Stearns 1976; Martin 1995; Wilson 2014). However, the relationship between matrotrophy and predation was opposite to the predictions of the locomotor hypothesis, even though microevolutionary analyses have indicated that matrotrophy can be favored in high predation environments requiring efficient escape responses (Gorini-Pacheco et al. 2017; Hagmayer et al. 2020). Instead, our results provided support for the resource availability hypothesis, demonstrating that high levels of matrotrophy coincided with low competition and high resource availability. This finding is consistent with the predictions of theoretical models, which predict increases in matrotrophy in environments with abundant and stable resources (Trexler and DeAngelis 2003), and empirical observations (Pollux and Reznick 2011). In addition, experimental studies have shown that maternal provisioning strategies in poeciliids respond to resource availability and female body condition (Trexler 1997; Marsh-Matthews and Deaton 2006; Hagmayer et al. 2018).

Our results largely align with previous theoretical and empirical studies; however, there are some caveats that warrant additional consideration. Most importantly, it remains to be tested whether metrics of resource availability, competition, and predation used here to facilitate continental-scale analyses accurately reflect selective regimes experienced by different species. The challenges of quantifying complex variation in biotic interactions across the vast spatial and phylogenetic scales covered in this study highlights the need for microevolutionary analyses and experimental approaches with a broader taxon sampling that allow for a better understanding of causal relationships (Culumber and Tobler 2018). For example, while there is experimental evidence for the fitness costs of matrotrophy under fluctuating resource conditions (Pollux and Reznick 2011), we still lack any empirical evidence indicating that matrotrophy provides fitness benefits over lecithotrophy under high and stable resource conditions (Pollux et al. 2009). In addition, it remains to be experimentally tested how resource availability and competition potentially interact in determining the success of different maternal provisioning strategies, especially because resource

stress and competitive interactions may have non-additive effects (Hart and Marshall 2013; van Egmond et al. 2018).

Conclusions

The role of ecological sources of selection as key drivers in life history evolution is well established at microevolutionary scales (Partridge and Harvey 1988; Reznick et al. 1990). Our study revealed that ecology also correlates with maternal provisioning strategies at macroevolutionary scales, suggesting that adaptation to resource availability and competition could explain life history diversification in livebearing fishes and potentially in other viviparous taxa (Wourms 1981; Blackburn 1992). Our findings do not exclude the possibility that other evolutionary forces are also at play. For example, variation in maternal provisioning strategies has been associated with parent-offspring conflict (Schrader and Travis 2008; Ala-Honkola et al. 2011; Pollux et al. 2014), potentially leading to antagonistic coevolution between maternal and embryonic traits that impact nutrient transfer during pregnancy (Crespi and Semeniuk 2004; Furness et al. 2015). Further studies will consequently need to explore how ecological sources of selection might interact with parent-offspring conflict to shape the evolution of matrotrophy. Disentangling the drivers of matrotrophy evolution will be particularly interesting because changes in female provisioning strategies can potentiate (or impede) sexual selection and speciation (Zeh and Zeh 2000; Zeh and Zeh 2008) and explain broad-scale patterns of diversification in viviparous taxa (Furness et al. 2019).

Data Accessibility

Data used to conduct this study will be archived on Dryad upon acceptance of the manuscript.

Acknowledgments

This research was supported by the National Science Foundation (IOS-1557860 to MT). We thank members of the K-State Evolution Journal Club for constructive feedback on the manuscript.

References

- Ala-Honkola, O., E. Friman, and K. Lindström. 2011. Costs and benefits of polyandry in a placental poeciliid fish *Heterandria formosa* are in accordance with the parent–offspring conflict theory of placentation. *Journal of Evolutionary Biology* 24:2600-2610.
- Alberici da Barbiano, L., J. Waller, and C. Gabor. 2010. Differences in competitive efficiency between a sexual parasite and its host provide insight into the maintenance of a sperm-dependent vertebrate species. *Journal of Freshwater Ecology* 25:523-530.
- Arnold, S. J. 2003. Performance surfaces and adaptive landscapes. *Integrative and Comparative Biology* 43:367-375.
- Blackburn, D. G. 1992. Convergent evolution of viviparity, matrotrophy, and specializations for fetal nutrition in reptiles and other vertebrates. *American Zoologist* 32:313-321.
- Boschung, H. T., R. L. Mayden, and J. R. Tomelleri. 2004. *Fishes of Alabama*. Smithsonian Books, Washinton, D. C.
- Burnham, K. P. and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York, NY.
- Bussing, W. A. 1998. *Peces de las Aguas Continentales de Costa Rica - Freshwater Fishes of Costa Rica*. Editorial de la Universidad de Costa Rica, San José.
- Campiglia, S. S. and M. H. Walker. 1995. Developing embryo and cyclic changes in the uterus of *Peripatus (Macroperipatus) acacioi* (Onychophora, Peripatidae). *Journal of Morphology* 224:179-198.

Coleman, S. W., A. Harlin-Cognato, and A. G. Jones. 2009. Reproductive isolation, reproductive mode, and sexual selection: empirical tests of the viviparity-driven conflict hypothesis. *American Naturalist* 173:291-303.

Crespi, B. and C. Semeniuk. 2004. Parent-offspring conflict in the evolution of vertebrate reproductive mode. *American Naturalist* 163:635-653.

Culumber, Z. W. and M. Tobler. 2017. Sex-specific evolution during the diversification of live-bearing fishes. *Nature Ecology & Evolution* 1:1185-1191.

Culumber, Z. W. and M. Tobler. 2018. Correlated evolution of thermal niches and functional physiology in tropical freshwater fishes. *Journal of Evolutionary Biology* 31:722-734.

Dulvy, N. K. and J. D. Reynolds. 1997. Evolutionary transitions among egg-laying, live-bearing and maternal inputs in sharks and rays. *Proceedings of the Royal Society B* 264:1309-1315.

Evans, J. P., A. Pilastro, and I. Schlupp, eds. 2011. *Ecology and Evolution of Poeciliid Fishes*. The University of Chicago Press, Chicago, IL.

Fleuren, M., E. M. Quicazan-Rubio, J. L. van Leeuwen, and B. J. A. Pollux. 2018. Why do placentas evolve? Evidence for a morphological advantage during pregnancy in live-bearing fish. *PLoS ONE* 13:e0195976.

Furness, A. I., K. R. Morrison, T. J. Orr, J. D. Arendt, and D. N. Reznick. 2015. Reproductive mode and the shifting arenas of evolutionary conflict. *Annals of the New York Academy of Sciences* 1360:75-100.

Furness, A. I., B. J. A. Pollux, R. W. Meredith, M. S. Springer, and D. N. Reznick. 2019. How conflict shapes the evolution in poeciliid fishes. *Nature Communications* 10:3335.

Ghalambor, C. K., D. N. Reznick, and J. A. Walker. 2004. Constraints on adaptive evolution: the functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *American Naturalist* 164:38-50.

- Gorini-Pacheco, B., E. Zandonà, and R. Mazzoni. 2017. Predation effects on matrotrophy, superfetation and other life history traits in *Phalloceros barpagos*. Ecology of Freshwater Fish 27:442-452.
- Greenfield, D. W. and J. E. Thomerson. 1997. Fishes of the continental waters of Belize. The University Press of Florida, Gainesville.
- Hagmayer, A., A. I. Furness, D. N. Reznick, M. L. Dekker, and B. J. A. Pollux. 2020. Predation risk shapes the degree of placentation in natural populations of live-bearing fish. Ecology Letters 23:831-840.
- Hagmayer, A., A. I. Furness, D. N. Reznick, and B. J. A. Pollux. 2018. Maternal size and body condition predict the amount of post-fertilization maternal provisioning in matrotrophic fish. Ecology and Evolution 8:12386-12396.
- Hart, M. W., M. Byrne, and M. J. Smith. 1997. Molecular phylogenetic analysis of life-history evolution in asterinid starfish. Evolution 51:1848-1861.
- Hart, S. P. and D. J. Marshall. 2013. Environmental stress, facilitation, competition, and coexistence. Ecology 94:2719-2731.
- Ho, A. F. L. C., C. L. Pruet, and J. Lin. 2016. Phylogeny and biogeography of *Poecilia* (Cypinodontiformes: Poeciliinae) across Central and South America based on mitochondrial and nuclear DNA markers. Molecular Phylogenetics and Evolution 101:32-45.
- Hrbek, T., J. Seckinger, and A. Meyer. 2007. A phylogenetic and biogeographic perspective on the evolution of poeciliid fishes. Molecular Phylogenetics and Evolution 43:986-998.
- Korneva, Z. V. 2005. Placental type interactions and evolutionary trends of development of uterus in cestodes. Journal of Evolutionary Biochemistry and Physiology 41:552-560.

- Korniushin, A. V. and M. Glaubrecht. 2003. Novel reproductive modes in freshwater clams: brooding and larval morphology in southeast Asian taxa of *Corbicula* (Mollusca, Bivalvia, Corbiculidae). *Acta Zoologica* 84:293-315.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends in Ecology and Evolution* 6:183-185.
- Marsh-Matthews, E. and R. Deaton. 2006. Resources and offspring provisioning: A test of the Trexler-DeAngelis model for matrotrophy evolution. *Ecology* 87:3014-3020.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101-127.
- Mateos, M., O. I. Sanjurjo, and R. C. Vrijenhoek. 2002. Historical biogeography of the livebearing fish genus *Poeciliopsis* (Poeciliidae: Cyprinodontiformes). *Evolution* 56:972-984.
- Meffe, G. K. and F. F. Snelson. 1989. An ecological overview of poeciliid fishes. Pp. 13-31 in G. K. Meffe, and F. F. Snelson, eds. *Ecology and evolution of livebearing fishes (Poeciliidae)*. Prentice Hall, New Jersey.
- Miles, D. B., B. Sinervo, and W. A. Frankino. 2000. Reproductive burden, locomotor performance, and the cost of reproduction in free ranging lizards. *Evolution* 54:1386-1395.
- Miller, R. R. 1975. Five new species of Mexican poeciliid fishes of the genera *Poecilia*, *Gambusia*, and *Poeciliopsis*. *Occasional Papers of the Museum of Zoology, University of Michigan* 672:1-44.
- Miller, R. R., W. Minckley, and S. Norris. 2005. *Freshwater fishes of Mexico*. University of Chicago Press, Chicago.
- Nychka, D., R. Furrer, J. Paige, and S. Sain. 2007. fields: tools for spatial data. R package version 9.6.
- Olivera-Tlahuel, C., A. G. Ossip-Klein, H. S. Espinosa-Pérez, and J. J. Zúñiga-Vega. 2015. Have superfetation and matrotrophy facilitated the evolution of larger offspring in poeciliid fishes? *Biological Journal of the Linnean Society* 116:787-804.

Ostrovsky, A. N., S. Lidgard, D. P. Gordon, T. Schwaha, G. Genikhovich, and A. V. Ereskovsky. 2016. Matrotrophy and placentation in invertebrates: a new paradigm. *Biological Reviews* 91:673-711.

Parenti, L. R., F. L. LoBostro, and H. Grier. 2010. Reproductive histology of *Tomeurus gracilis* Eigenmann, 1909 (Teleostei: Atherinomorpha: Poeciliidae) with comments on evolution of viviparity in atherinomorph fishes. *Journal of Morphology* 27:1399-1406.

Partridge, L. and P. H. Harvey. 1988. The ecological context of life history evolution. *Science* 241:1449-1455.

Pires, M. N., A. I. Banet, B. J. A. Pollux, and D. N. Reznick. 2011. Variation and evolution of reproductive strategies. Pp. 28-37 in J. P. Evans, A. Pilastro, and I. Schlupp, eds. *Ecology and Evolution of Poeciliid Fishes*. University of Chicago Press, Chicago, IL.

Plaut, I. 2002. Does pregnancy affect swimming performance in female mosquitofish, *Gambusia affinis*? *Functional Ecology* 16:290-295.

Pollux, B., M. Pires, A. Banet, and D. Reznick. 2009. Evolution of placentas in the fish family Poeciliidae: an empirical study of macroevolution. *Annual Review of Ecology Evolution and Systematics* 40:271-289.

Pollux, B. J. A., R. W. Meredith, M. S. Springer, T. Garland, and D. N. Reznick. 2014. The evolution of the placenta drives a shift in sexual selection in livebearing fish. *Nature* 513:233-236.

Pollux, B. J. A. and D. N. Reznick. 2011. Matrotrophy limits a female's ability to adaptively adjust offspring size and fecundity in fluctuating environments. *Functional Ecology* 25:747-756.

Quicazan-Rubio, E. M., C. L. van Leeuwen, K. van Manen, M. Fleuren, B. J. A. Pollux, and E. J. Stamhuis. 2019. Coasting in live-bearing fish: the drag penalty of being pregnant. *Journal of the Royal Society Interface* 16:20180714.

- Recknagel, H., N. A. Kamenos, and K. R. Elmer. 2018. Common lizards break Dollo's law of irreversibility: genome-wide phylogenomics support a single origin of viviparity and re-evolution of oviparity. *Molecular Phylogenetics and Evolution* 127:579-588.
- Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3:217-223.
- Reznick, D., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357-359.
- Reznick, D., M. Mateos, and M. Springer. 2002. Independent origins and rapid evolution of the placenta in the fish genus *Poeciliopsis*. *Science* 298:1018-1020.
- Reznick, D., R. Meredith, and B. B. Collette. 2007. Independent evolution of complex life history adaptation in two families of fishes, live-bearing halfbeaks (Zenarchopteridae, Beloniformes) and Poeciliidae (Cyprinodontiformes). *Evolution* 61:2570-2583.
- Reznick, D. N., A. I. Furness, R. W. Meredith, and M. S. Springer. 2017. The origin and biogeographic diversification of fishes in the family Poeciliidae. *PLoS ONE* 12:e0172546.
- Rodriguez, C. C. 2005. The ABC of model selection: AIC, BIC, and the new CIC. *AIP Conference Proceedings* 803:80-87.
- Santini, F., L. J. Harmon, G. Carnevale, and M. E. Alfaro. 2009. Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. *BMC Evolutionary Biology* 9:1.
- Schrader, M. and J. Travis. 2008. Testing the viviparity-driven-conflict hypothesis: parent-offspring conflict and the evolution of reproductive isolation in a poeciliid fish. *American Naturalist* 172:806-817.
- Shaffer, L. R. and D. R. Formanowicz. 1996. A cost of viviparity and parental care in scorpions: reduced sprint speed and behavioral compensation. *Animal Behavior* 51:1017-1024.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312-1313.

Stearns, S. C. 1976. Life-history tactics: a review of ideas. *Quarterly Review of Biology* 51:3-47.

Steward, J. R. and D. G. Blackburn. 1988. Reptilian placentation: structural diversity and terminology. *Copeia* 1988:839-852.

Thibault, R. E. and R. J. Schultz. 1978. Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). *Evolution* 32:320-333.

Torres-Dowdall, J., F. Dargent, C. A. Handelsman, I. W. Ramnarine, and C. K. Ghalambor. 2013. Ecological correlated of the distribution limites of two poeciliid species along a salinity gradient. *Biological Journal of the Linnean Society* 108:790-805.

Trexler, J. C. 1997. Resource availability and plasticity in offspring provisioning: Embryo nourishment in sailfin mollies. *Ecology* 78:1370-1381.

Trexler, J. C. and D. L. DeAngelis. 2003. Resource allocation in offspring provisioning: An evaluation of the conditions favoring the evolution of matrotrophy. *American Naturalist* 162:574-585.

van der Bijl, W. 2018. phylopath: easy phylogenetic path analysis in R. *PeerJ* 6:e4718.

van der Sleen, P. and J. S. Albert, eds. 2017. Field guide to the fishes of the Amazon, Orinoco, and Guianas. Princeton University Press, Princeton.

van Egmond, E. M., P. M. van Bodegom, J. R. van Hal, P. S. P. van Logtestijn, M. P. Berg, and R. Aerts. 2018. Nonadditive effects of consumption in an intertidal macroinvertebrate community are independent of food availability but driven by complementarity effects. *Ecology and Evolution* 8:3086-3097.

van Proosdij, A. S., M. S. Sosef, J. J. Wieringa, and N. Raes. 2015. Minimum required number of specimen records to develop accurate species distribution models. *Ecography*.

- Wake, M. H. and R. Dickie. 1998. Oviduct structure and function and reproductive modes in amphibians. *Journal of Experimental Zoology* 282:477-506.
- Weber, M. G., L. Mitko, T. Eltz, and S. R. Ramírez. 2016. Macroevolution of perfume signalling in orchid bees. *Ecology Letters* 19:1314-1323.
- Wildman, D. E., C. Chen, O. Erez, L. I. Grossman, M. Goodman, and R. Romero. 2006. Evolution of the mammalian placenta revealed by phylogenetic analysis. *Proceedings of the National Academy of Sciences USA* 103:3203-3208.
- Wilson, A. J. 2014. Competition as a source of constraint on life history evolution in natural populations. *Heredity* 112:70-78.
- Wooding, P. and G. Burton. 2008. Comparative placentation: structures, functions and evolution. Springer-Verlag, Berlin.
- Wourms, J. P. 1981. Viviparity: the maternal-fetal relationship in fishes. *American Zoologist* 21:473-515.
- Wourms, J. P., B. D. Grove, and J. L. Lombardi. 1988. The maternal-fetal relationship in viviparous fishes. Pp. 2-134 *in* W. S. Hoar, ed. *Fish Physiology*. Academic Press, London.
- Zeh, D. W. and J. A. Zeh. 2000. Reproductive mode and speciation: the viviparity-driven conflict hypothesis. *Bioessays* 22:938-946.
- Zeh, J. A. and D. W. Zeh. 2008. Viviparity-driven conflict. *Annals of the New York Academy of Sciences* 1133:126-148.

Figure 1. A. Best-scoring maximum likelihood tree of 94 species in the family Poeciliidae. The ancestral state reconstruction of matrotrophy is mapped onto the phylogeny, with blue colors depicting lecithotrophy and orange colors matrotrophy (as indicated by the color scale of ln-transformed matrotrophy index values). B. Frequency histogram of the distribution of matrotrophy index values in extant poeciliid species. The solid red line represents the average ancestral state reconstruction for the matrotrophy index across 250 random trees with dotted lines indicating the 95% confidence interval for the estimate. C. Frequency histogram depicting the relative change in matrotrophy index between all nodes and their descendants.

Figure 2. A. Representation of the full model used for phylogenetic path analysis (see Figure S2 for a comprehensive depiction of alternative models). Highlighted in red are variables and paths associated with the top models exhibiting $\Delta\text{CIC}_c < 2$. Numbers represent correlation coefficients (r) associated with the top model (top number) and the secondary model (bottom number). Note that the factor predation was absent from the secondary model. B. Landscape of matrotrophy variation as a function of net primary productivity and competition. Colors correspond to variation in matrotrophy, with blue colors depicting maternal provisioning strategies toward the lecithotrophy end of the spectrum and orange colors strategies toward the matrotrophy end (as indicated by the color scale of ln-transformed matrotrophy index values).