

RESOURCES AND OFFSPRING PROVISIONING: A TEST OF THE TREXLER-DEANGELIS MODEL FOR MATROTROPHY EVOLUTION

EDIE MARSH-MATTHEWS¹ AND RAELENN DEATON²

Sam Noble Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, 2401 Chautauqua Avenue, Norman, Oklahoma 73072 USA

Abstract. Theoretical models of the evolution of matrotrophy from a lecithotrophic ancestor suggest that resource availability plays a major role in selective scenarios favoring a change in offspring provisioning. We examined effects of feeding level on embryo provisioning in the livebearing fish *Gambusia geiseri*, a species with dual provisioning of embryos via both yolk sequestered in large eggs and post-fertilization mother-to-embryo nutrient transfer. Females were fed either once per day or once every three days for three months. Females fed daily had marginally larger brood size, significantly larger embryos, and a higher rate of nutrient transfer (assayed directly by injection of radiolabeled nutrients) than females fed every third day. There was no difference in the size of unfertilized eggs between the feeding treatments. Resource effects on matrotrophic provisioning in *G. geiseri* suggest that matrotrophy plays an important role in provisioning and allows females to adjust offspring size in response to resource availability.

Key words: lecithotrophy; matrotrophy; offspring number; offspring provisioning; offspring size; poeciliid; resource availability; viviparity.

INTRODUCTION

Offspring provisioning via mother-to-embryo transfer of nutrients (matrotrophy) is widespread in vertebrates and has evolved as the dominant mode of provisioning independently in all major clades (except birds), with multiple independent origins in squamates and fishes (Wourms et al. 1988, Blackburn 1992, Reznick et al. 2002). Blackburn (1992) used the term “substantial matrotrophy” to describe embryo-provisioning strategies in which most or all embryo nutrition is acquired from the mother following fertilization. Although less is known about nutrient transfer in species that provision developing offspring primarily through yolk sequestered in eggs, mother-to-embryo transfer of nutrients has been found to occur in almost every viviparous group that has been examined (Blackburn 1992), including species long thought to be strictly lecithotrophic (yolk-only provisioning; Marsh-Matthews et al. 2001, 2005). Blackburn (1992) called this dual provisioning strategy, in which embryo nutrition is derived from a combination of yolk and low levels of post-fertilization transfer “incipient matrotrophy,” and suggested that the evolution of incipient matrotrophy was coincident with the evolution of livebearing as a reproductive mode.

Proposed scenarios for the evolution of matrotrophy from a lecithotrophic livebearing ancestor typically

assume that matrotrophic females can produce larger broods than strictly lecithotrophic females, because the latter must pack all nutrients and energy needed for development into larger, and therefore presumably fewer, eggs (Thibault and Schultz 1978, Trexler and DeAngelis 2003). Several authors have suggested that the transition to matrotrophy is constrained by ecological conditions, primarily resource availability and predictability (Thibault and Schultz 1978, Reznick et al. 1996, Trexler 1997). Although Crespi and Semeniuk (2004) have recently suggested that substantial matrotrophy may result from parent-offspring conflict in which embryos appropriate maternal resources, they note that the retention of embryos and origin of nutrient transfer are “presumably driven by ecological selection pressures” (p. 637).

Ecological conditions favoring the evolution of matrotrophy from a lecithotrophic ancestor have recently been examined using analytic and simulation models by Trexler and DeAngelis (2003). Their models assume that matrotrophy increases the number of offspring produced, given that the final size (or quality) of offspring is equal for the two provisioning modes. The models also assume that matrotrophic females may produce more eggs than they can provision and bring to full term if resources available to the mother fall below some threshold.

The analytic model examined relative fitness of lecithotrophic and matrotrophic strategies under varying resource scenarios for a single reproductive bout. Outcome of this model suggests that matrotrophs have a fitness advantage under high resource conditions, but that advantage is limited by availability or predictability

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¹ E-mail: emarsh@ou.edu

² Present address: Department of Biological Sciences, Sam Houston State University, Huntsville, Texas 77341 USA.

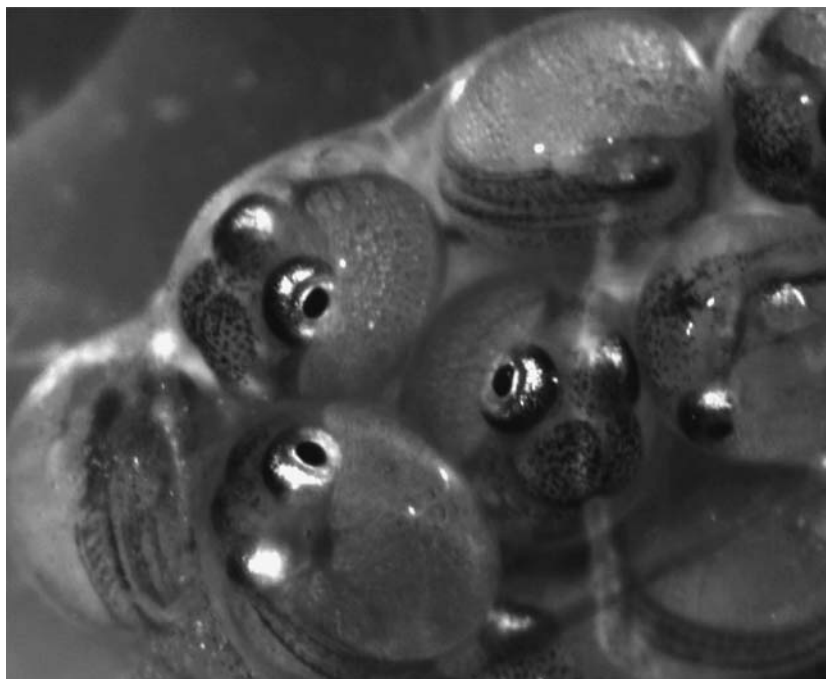


PLATE 1. Embryos of *Gambusia geiseri*, late Stage 5 to early Stage 6. Note the large amount of yolk remaining even at this late stage of development. Photo credit: E. Marsh-Matthews.

of food. In addition, the ability to reabsorb developing embryos and to recycle reclaimed nutrients favors the evolution of matrotrophy. Matrotrophic females were also predicted to have lower fat reserves than lecithotrophic females because resources are diverted to developing embryos rather than being stored.

The simulation model examined lifetime reproductive output for the two strategies under different levels of food availability and predictability, using data of Trexler (1997) on Sailfin Molly, *Poecilia latipinna*, to parameterize the models. The simulations predicted that matrotrophic females should have lower survival (and therefore shorter life spans) than lecithotrophic females, as a consequence of decreased fat reserves in matrotrophic females.

In species that exhibit “incipient matrotrophy,” yolk production and nutrient transfer together constitute a dual provisioning strategy. Such species provide excellent models with which to test the models of Trexler and DeAngelis (2003) because conditions that favor the addition of a matrotrophic component to a pure lecithotrophic strategy should also favor an increase in the matrotrophic component of a dual provisioning strategy. Species with dual provisioning also allow intraspecific comparison of responses to environmental manipulations that would not be possible if species with pure lecithotrophic provisioning were compared to those with post-fertilization transfer of nutrients.

In a dual provisioning strategy, the relative contribution of each nutrient source may vary under different environmental conditions. Trexler (1997) examined

maternal provisioning in Sailfin Mollies using an indirect assay for matrotrophy. He compared size of neonates with size of blastula-stage embryos in groups of females raised under different conditions (including resource variation). He found that females in high-feeding treatments had more embryos and were more matrotrophic than females in low-feeding treatments. Here we use experimental manipulation of resources (high and low-feeding treatments) combined with a direct assay of nutrient transfer to examine resource effects on offspring provisioning in another livebearing fish (*Gambusia geiseri*; see Plate 1) with a dual provisioning tactic.

Based on the Trexler and DeAngelis (2003) model, we predicted that female *G. geiseri* in the high-feeding treatment would produce more and smaller eggs (in accordance with the assumptions of the model), exhibit higher levels of nutrient transfer to developing embryos, and to be leaner than females in the low-feeding treatment. Given that the matrotrophic assay used in this study requires euthanizing females, we were unable to compare survivorship of females in different feeding treatments.

METHODS

Females used in this study were from laboratory stock originally collected from the South Concho River, Tom Green County, Texas, USA on 24–25 July 2003, and held in the greenhouse laboratory at the Aquatic Research Facility at the University of Oklahoma. Fish were housed in a trough (340 L) with flow-through well

water (approximately 20°C) and fed every 1–2 days until 22 October 2003 when assigned to experimental containers. Fish were assigned at random in groups of 10 to plastic boxes (51 × 36 × 6.5 cm; approximately 12 L volume) with flow-through water. From 22 October 2003 to 9 February 2004 (111 d), all fish were fed commercial flake food every two days to standardize pre-experimental conditions. At each feeding, food was liberally distributed across the surface of the box so that each fish in the box had access to food. Excess food was flushed from the box by the flow through of water. During this period, boxes were examined periodically and if fish had died or escaped from a box, fish were redistributed to maintain the density of 10 fish per box as nearly as possible.

During inspection of boxes, females were also examined for the presence of an anal spot (Farr and Travis 1986) that indicates presence of mature eggs or embryos. At the outset of the experiment, all females assigned to boxes appeared gravid and exhibited an anal spot, so we knew that all were mature. By December, females no longer appeared gravid. The lack of an anal spot at this time gave us confidence that broods assayed in the experiment were produced during the period of experimental manipulation.

On 9 February 2004, boxes were assigned at random to one of two feeding schedules: fish were fed either daily (high) or every three days (low). Fish were exposed to these feeding treatments from 9 February 2004 to 6–9 May 2004, a period of approximately three months. We have unpublished data that show that short-term exposure to these feeding levels results in variation in soluble fat content of females in *Gambusia geiseri*. In a previous study conducted over a 30-day period under similar laboratory conditions, there was a highly significant difference in mass of soluble somatic fat (SSF), corrected for total eviscerated body mass (EBM) between females on high- and low-feeding treatments (ANCOVA, $F_{1,77} = 52.4$, $P < 0.001$; EBM, $F_{2,77} = 61.87$, $P < 0.001$; feeding treatment, $F_{1,77} = 22.76$, $P < 0.001$). Females fed every day had almost twice as much soluble somatic fat as those fed every three days. Estimated marginal means (± 1 SE) at EBM = 146.05 mg were 21.54 ± 1.29 mg of soluble somatic fat for the high treatment and 12.73 ± 1.29 mg for the low treatment.

By 7 March 2004, females were again gravid and expressed an anal spot. Beginning on 23 March 2004, females were placed with males that had been collected from the South Concho River on 20 March 2004. Although, in the original design of the experiment, males were to be added to each box containing females, there were too few males available for that design. Instead, two groups of males (eight in one group, seven in the other) were established in holding tanks. Females from a given box were introduced into a holding tank with males for 2–3 days. At any time, one box each from the high- and low-feeding treatments was chosen at random

for exposure to males, and high and low treatments were alternated between the two groups of males.

Matrotrophy assays were conducted May 6–9 2004, approximately 40 days after exposure to males. At 20°C, the gestation period in *G. geiseri* is approximately 50 days (E. Marsh-Matthews, unpublished data). Nutrient transfer was quantified using the method described by Marsh-Matthews et al. (2005), which employs injection of a radiolabeled nutrient followed by scintillation assay of embryo radioactivity. Similar techniques have been used to quantify nutrient transfer in other species (e.g., garter snake [Hoffman 1970], butterflies [Boggs and Gilbert 1979, Boggs 1997], rockfish [MacFarlane and Bowers 1995], skink [Swain and Jones 1997]). In this study, females were injected in the caudal peduncle with 5 μ L tritiated leucine (all females were injected with Lot 445-020-120; 120 Ci/mmol; Moravek Biochemicals, Brea, California, USA), euthanized in MS-222 two hours post-injection, and preserved in 5% formalin until dissection. Females were dissected to remove a liver sample and to remove embryos from the ovary. Tissues removed for dissection were rinsed twice in distilled water prior to drying. Two rinses are sufficient to ensure that radioactivity detected in tissues represents leucine incorporated into that tissue and not contamination from blood or other maternal fluids (Marsh-Matthews et al. 2001, 2005). Individual embryos removed from the ovary were staged according to Meffe (1987), dried for 10 days at 40°C, weighed to the nearest 0.001 mg, and prepared for scintillation assay following Marsh-Matthews et al. (2005). Radioactivity detected in embryos (measured as disintegrations per minute, dpm) was used to quantify nutrient transfer.

The sample of female liver was also dried, weighed, and assayed for radioactivity. Swain and Jones (1997) found that uptake of tritiated leucine occurred rapidly in the both blood and liver of the viviparous lizard, *Niveoscincus metallicus*. Liver radioactivity therefore serves as an indicator of uptake of the amino acid by the female and availability of the labeled nutrient for transfer to, or uptake by, embryos. Liver uptake of tritiated leucine by the mother in this study was quantified as $LIV = \log_{10}(\text{liver dpm}/\text{liver sample mass})$.

In addition to developing embryos, 30 females had unfertilized, but large and translucent (therefore presumably mature) eggs in the ovary. Partially fertilized broods are occasionally observed in females captured gravid in the field (E. Marsh-Matthews, personal observation), but the large number of females with partially fertilized broods in this study likely resulted from limited access to males. In his studies on matrotrophy of Sailfin Molly, Trexler (1997) used early embryos (blastodisc stage) rather than unfertilized eggs as a measure of lecithotrophic investment by females to assure that yolk-loading was complete. In this study, unfertilized eggs were used as a measure of lecithotrophic investment by females only if they occurred in broods that also had developing embryos. Although *G.*

geiseri broods may exhibit a developmental gradient (Marsh-Matthews et al. 2005), true superfetation (embryos in non-contiguous stages of development) has not been documented for this species.

To assess female condition, eviscerated female carcasses were weighed to the nearest 0.001 g, rinsed six times overnight (or longer) in petroleum ether to extract soluble nonstructural fats (Trexler 1997), dried overnight at 40°C, and reweighed. Female condition was quantified as the residual from least-squares linear regression of mass of somatic fat (calculated as pre-extraction mass minus post-extraction mass) on pre-extraction mass.

For each brood examined in this study, we calculated summary statistics of both maternal and brood characteristics. Total brood size (TBS) included all developing embryos plus any unfertilized eggs and any aborted embryos. Calculations of mean embryo mass (MEM) and mean embryo radioactivity (MER) included only developing embryos. Mean embryo radioactivity was based on \log_{10} -transformed dpm for each developing embryo in the brood. Each brood was assigned a developmental stage based on the predominant stage present in the brood; if several stages were present in nearly equal numbers, an intermediate value was assigned.

Mean embryo radioactivity in this study was a linear function of liver uptake by the mother: $MER = 0.58LIV + 0.59$; $R^2 = 0.57$, $P < 0.0001$). In a previous study, Marsh-Matthews et al. (2001) found that very low levels of maternal liver radioactivity resulted in detectable radioactivity in only a fraction of embryos in a brood (i.e., there was a threshold). In this study, all females showed liver activity above threshold and all embryos assayed from each brood had detectable radioactivity. Effects of maternal uptake in this study were removed by using the residual of the linear regression of MER on LIV in subsequent analyses.

Response variables examined in this study (TBS, MEM, MER) are known to be interrelated or correlated with other life history variables (Trexler 1997, Marsh-Matthews et al. 2005). To screen for these possible interrelationships, we performed least-squares multiple regressions for each response variable (as the dependent variable) using all variables suspected to be related as independent variables in the analyses. For TBS, we examined female standard length and MEM: only female size explained significant ($P < 0.001$) variation in TBS. For dependent variable MEM, we used female size, developmental stage, and TBS as independent variables: only developmental stage explained significant variation in MEM ($P = 0.007$). For dependent variable MER, TBS, MEM, and developmental stage were included as independent variables: only TBS explained significant variation in MEM ($P = 0.004$). Those variables found to be significantly related to a response variable were used as covariates in subsequent analyses.

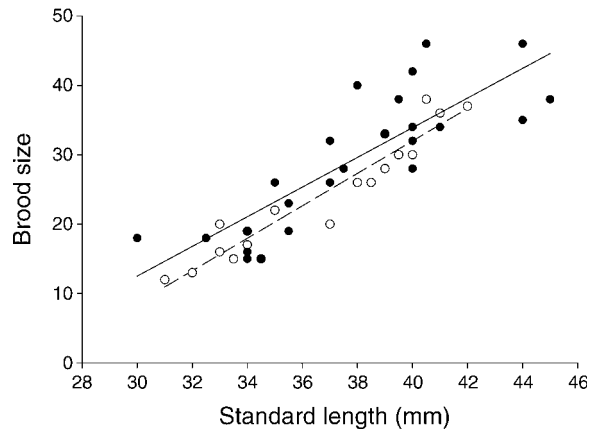


FIG. 1. Brood size (total number of developing embryos plus unfertilized eggs) as a function of female standard length. The low-feeding treatment is indicated by open symbols and the dashed line; the high-feeding treatment is indicated by solid symbols and the solid line.

We screened data for box effects and effects of exposure to different groups of males within each treatment. Each response variable was first adjusted for any relevant covariates by residual analysis, then boxes within a treatment were compared using Kruskal-Wallis tests. Nonparametric tests were necessary given the differences in numbers of females with developing embryos in different boxes (range, 1–5). No difference in any response variable was found among boxes, so females within a feeding treatment were pooled for further analyses. Adjusted response variables for females exposed to different male groups were also compared using a Kruskal-Wallis test, and no difference between groups was found for any response variable. Statistical analyses were performed using SPSS 12.0 for Windows (SPSS, Chicago, Illinois, USA).

RESULTS

Forty-five females had developing embryos (at mid stage 6 or earlier) and showed uptake of leucine in the liver. Three additional females had embryos in late stage 6. In a previous study, Marsh-Matthews et al. (2005) found that nutrient transfer to embryos drops precipitously near parturition; we therefore omitted these late stage 6 broods from further analyses. Twenty-one females from the low-feeding treatment and 24 from the high treatment were included in matrotrophy analyses.

Total brood size increased with female size in both treatments (Fig. 1), and was marginally larger in females from the high-feeding treatment (ANCOVA, $F_{2,42} = 81.292$, $P < 0.001$; SL $F_{1,42} = 142.016$, $P < 0.001$; feeding treatment $F_{1,42} = 3.522$, $P = 0.068$). Estimated marginal means (\pm SE) (at female standard length = 37.09 mm) were 25.07 ± 0.97 embryos per brood for the low treatment and 27.60 ± 0.91 embryos per brood for the high treatment.

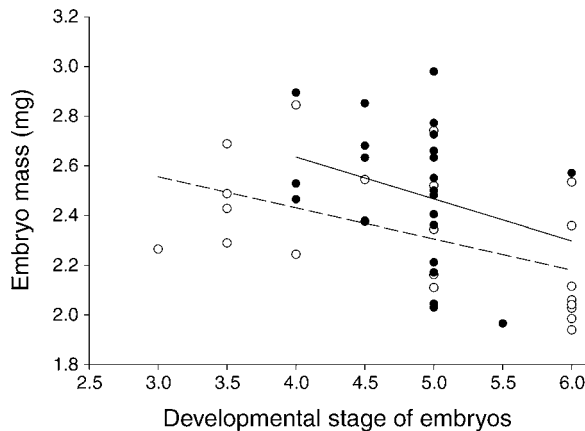


FIG. 2. Mean embryo mass as a function of embryonic stage of development. The low-feeding treatment is indicated by open symbols and the dashed line; the high-feeding treatment is indicated by solid symbols and the solid line. Development stages of embryos (modified from Meffe [1987]) are as follows: stage 2, blastodisc; stage 3, primitive streak; stage 4, eye pigmentation evident, little dorsal pigmentation; stage 5, eyes formed, dorsal pigmentation well developed, large to moderate amount of yolk remaining; stage 6, amount of yolk reduced.

Mean embryo mass decreased significantly with developmental stage (STG) in both treatments (Fig. 2) and was significantly higher in females from the high-feeding treatment (ANCOVA, $F_{2,42} = 6.710$, $P = 0.003$; STG $F_{1,42} = 7.918$, $P = 0.007$; feeding treatment $F_{1,42} = 5.1068$, $P = 0.029$). Estimated marginal means (at developmental stage = 4.85) were: 2.32 ± 0.05 mg per embryo for the low treatment and 2.49 ± 0.05 mg per embryo for the high treatment.

Nutrient transfer (measured as mean embryo radioactivity corrected for radioactivity of the maternal liver by residual analysis) increased significantly with total brood size in both treatments (Fig. 3), and was significantly higher in females from the high-feeding treatment (ANCOVA, $F_{2,42} = 6.477$, $P = 0.004$; TBS, $F_{1,42} = 4.443$, $P = 0.041$; feeding treatment, $F_{1,42} = 4.328$, $P = 0.044$). Estimated marginal means of the residual of embryo radioactivity on maternal liver activity (at total brood size = 26.42 embryos) were -0.051 ± 0.03 mg per embryo for the low treatment and 0.045 ± 0.03 for the high treatment.

For the 30 females (15 in each treatment) that had unfertilized eggs in addition to developing embryos, there was no significant difference in size of unfertilized eggs between treatments ($t = 0.51$, $df = 28$, $P = 0.61$).

The number of females with aborted embryos was similar in both treatments. In the low treatment, four of 21 females (19%) had one or more aborted embryos; in the high treatment, six of 24 females (25%) had aborted embryos.

Female condition, as assayed by extraction of soluble fats, did not vary between feeding treatments ($t = 0.151$, $df = 42$, $P = 0.88$).

DISCUSSION

Results of our resource manipulation experiment supported some, but not all, of our predictions based on the model by Trexler and DeAngelis (2003). As predicted, females on higher resource levels produced (marginally) larger broods and exhibited higher levels of nutrient transfer. Increased matrotrophy was not accompanied, however, by a decrease in size of eggs (an assumption of the Trexler and DeAngelis model). Furthermore, the Trexler and DeAngelis (2003) model assumes no difference in final offspring size or quality for the two reproductive strategies, but we found that better-fed, more matrotrophic females produced larger embryos at each stage of development. Although our findings did not match the specific assumptions of the Trexler and DeAngelis (2003) model, our findings do support the general prediction that higher resource levels favor a more matrotrophic strategy. This suggests that the model may be applicable over a more general set of fitness-related responses.

The relationship between maternal resource levels and offspring provisioning is complex, and studies on other species have reported variable results. Trexler (1997) reported smaller size of blastodisc embryos in Sailfin Molly, *Poecilia latipinna*, raised under high salinity, high food conditions relative to those raised under low salinity, low food. Reznick and Yang (1993) examined effects of maternal resource level across two interbrood intervals in the guppy (*Poecilia reticulata*). They found that guppies maintained on high rations produced more and smaller offspring in the third brood than those maintained under low resource conditions, but found that guppies switched from low to high resource levels in

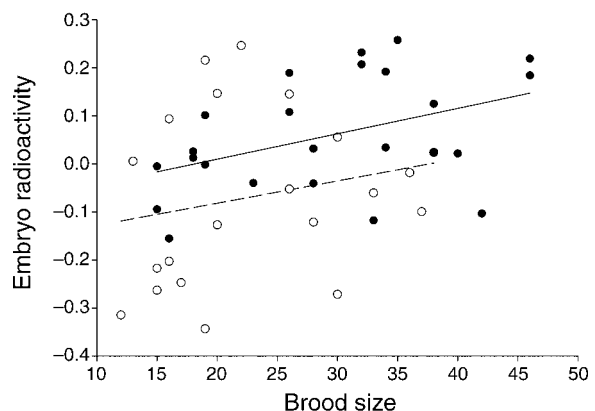


FIG. 3. Mean embryo radioactivity (corrected for maternal liver activity by residual analysis) as a function of brood size. Mean embryo radioactivity (MER) was calculated as the mean of \log_{10} -transformed disintegrations per minute of all developing embryos in a given brood. Because MER was found to be a function of maternal liver radioactivity (LIV), MER was corrected using residuals from the linear regression of MER on LIV ($MER = 0.58LIV + 0.59$). The low-feeding treatment is indicated by open symbols and the dashed line; the high-feeding treatment is indicated by solid symbols and the solid line.

intervals between broods produced larger offspring in the third brood than those maintained on low rations (and those switched from high to low ratio produce larger offspring than those maintained on high rations). They noted that, among other mechanisms, “such an increase in offspring size could be accomplished with maternal investment during development” (p. 2016). Both *P. latipinna* and *P. reticulata* have large, yolky eggs, and therefore a presumably large lecithotropic component to offspring provisioning. Studies on substantial matrotrophs (sensu Blackburn 1992) have reported increased embryo or neonate size for females in high resource conditions as in the poeciliid *Heterandria formosa* (Reznick et al. 1996) and the placental lizard *Pseudemoia pagenstecheri* (Shine and Downes 1999).

Our finding that high resource levels resulted in no reduction in egg size, but did result in increased embryo provisioning in *G. geiseri* may reflect relative fitness consequences of increased offspring size versus increased brood size in this species. *Gambusia geiseri* exhibits high rates of predation on neonates (Hubbs 1996), which may act as an important factor selecting for large offspring (as in *Poeciliopsis*, Weeks and Gaggiotti 1993). We do not have data from this experiment to confirm that larger, better-provisioned embryos result in larger neonates in *G. geiseri* (because of the destructive nature of our matrotrophy assay). Unpublished data for *G. affinis*, however, show that females fed daily produce larger neonates over a shorter gestation period than females fed every three days for broods developed entirely under experimental conditions similar to those in this study (M. Brooks, unpublished data). Overall, our data suggest that the response to increased resources in this species is a (slight) increase in brood size without compromising some minimum offspring size (based on initial egg size), and increased provisioning to individual embryos given that resource levels remain high during gestation. Furthermore, matrotrophy may allow females to “supersize” embryos when resource levels are high, by reducing loss of mass during development. Although there was some evidence of embryo abortion in females in this experiment, the phenomenon was not related to resource level, suggesting that resource levels in the low treatment were not sufficiently low to initiate embryo abortion and possible nutrient recycling.

We also predicted that females exhibiting higher levels of matrotrophy would be in poorer condition. We found no difference in condition (measured as soluble somatic fats) at the end of the experiment, despite differences in feeding levels that are known to result in condition differences in *G. geiseri* in the short term (30 days). Our results therefore suggest that better-fed females divert excess energy to embryos rather than store additional fat, and hence are leaner than would be expected based on feeding level.

The Trexler and DeAngelis (2003) model also predicts that more matrotrophic females should have shorter life

spans if there are condition-dependent mortality risks in the environment. We were unable to assess survivorship in this experiment because the matrotrophy assay requires euthanizing the female. Brooks (2005), however, did assess survivorship in *G. affinis* between females maintained on different feeding treatments (identical to those used in this study). She found that females in the high-feeding treatment had shorter life spans in the laboratory than those on a low-feeding treatment. Although Brooks (2005) did not assay matrotrophy in her study, *G. affinis* also exhibits a dual provisioning strategy (Marsh-Matthews et al. 2005), and those females fed higher rations may have also been more matrotrophic.

Regardless of feeding level, female *G. geiseri* with larger broods were more matrotrophic in our experiment. This result is consistent with findings in a wide variety of organisms (see Sakai and Harada 2001 for examples) that older/larger females produce larger eggs/offspring. The “typical” explanation for this phenomenon is that larger females may be better able to acquire and/or store resources that are then available for offspring provisioning. Sakai and Harada (2001) have suggested, however, that increased size of offspring in females with higher resource levels is only expected if transfer of resources from mother to offspring is limited at their interface (e.g., the ovarian follicle in *Gambusia*), and the maximum rate of transport increases with maternal size (or resource condition). The assumption is that larger females have absolutely more resources available for transport to, or extraction by, the offspring at the mother-embryo interface. The model (called the “terminal-stream-limitation” model) assumes that resource extraction by each offspring is independent of that by other offspring, and is therefore not a direct function of the number of offspring in the brood.

Increased provisioning with increased brood size in *G. geiseri* (as observed in this experiment) is consistent with the predictions of the “terminal-stream-limitation” model because brood size increased as a function of female size for females in both feeding treatments, and the significant positive relationship between brood size and provisioning found in this study likely reflects that relationship. A previous study on matrotrophic provisioning in *Gambusia* (Marsh-Matthews et al. 2005) showed within-brood variation in nutrient transfer, as would be expected if transport/extraction for a given embryo is independent of that of others in the brood.

Based on results of this study, matrotrophy in *G. geiseri* appears to play a somewhat different role in the overall embryo provisioning strategy than that assumed by the Trexler and DeAngelis (2003) model, but it nonetheless potentially increases maternal fitness in high-resource environments. In addition, matrotrophy may diversify the overall provisioning strategy, particularly if the matrotrophic and lecithotropic components respond to different thresholds of resource variation. In our study, which examined only the first brood

following resource manipulation, only the matrotrophic component of provisioning responded. Longer term studies, however, over multiple broods, or with resource shifts, might reveal different thresholds of response for matrotrophic and lecithotrophic components, which would allow maternal manipulation of offspring size over a wide range of resource conditions. The role of “incipient” matrotrophy in *Gambusia* and other species is largely unstudied, but our findings suggest that embryo provisioning in these species should be reexamined in the context of a dual provisioning strategy.

The Trexler and DeAngelis (2003) model proposes an ecological context for the evolution of matrotrophy from a lecithotrophic ancestor. In a recent paper, however, Crespi and Semeniuk (2004) suggest that, once evolved, the matrotrophic component of provisioning may be co-opted by embryos to appropriate maternal resources at a higher rate than is adaptive for the female. If that is the case, the evolution of substantial matrotrophy is largely the result of selection for traits that affect the outcome of parent-offspring conflict. Species such as *G. geiseri* (in which the matrotrophic component is, at least in part, related to female characteristics) may provide the best opportunity to understand the origin and evolution of matrotrophy as a reproductive strategy. And, given that production of the egg is under maternal control, species with dual provisioning may also provide insight into the factors that “tip the balance” in favor of parent or offspring in matrotrophic species.

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