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## THE INFLUENCE OF FLUCTUATING RESOURCES ON LIFE HISTORY: PATTERNS OF ALLOCATION AND PLASTICITY IN FEMALE GUPPIES<sup>1</sup>

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**Abstract.** We investigated how resources are allocated to reproduction and how variations in resource availability influence reproductive allocation, offspring number, and offspring size in guppies (*Poecilia reticulata*). Our goal was to evaluate how plastic these variables are in response to environmental variation and to characterize the nature of this plasticity. Female guppies which had just given birth (litter 1) were assigned to either high or low levels of food availability until they gave birth to their next litter (litter 2, interval 1). They were then randomly reassigned to either high or low food with the constraint that there be equal numbers of individuals in each of four treatments: high–high, high–low, low–high, and low–low. They were maintained on this level of food availability until they produced their next litter (litter 3, interval 2). We analyzed variables that characterized the female after the birth of the third litter and the offspring in the third litter. These were two-way analyses, with intervals 1 and 2 as the main effects and high vs. low food as the levels of each effect.

The qualities of the third litter were influenced by both interbrood intervals, indicating that the resources used for producing the litter were derived from both intervals. Specifically, higher food availability during either interval resulted in a significant increase in the number of offspring in litter 3, independent of the size of the mother. This result indicates that the number of offspring produced in a litter will be a function of both the immediate and the past environment. Lower food during either interval resulted in an increase in the number of days between the second and third litters, indicating that, if resource availability is low, the female may delay the initiation of the next litter, allowing her to acquire more resources. Resource availability during both intervals also influenced how resources were allocated to individual offspring. Females responded to low food during the first interbrood interval by producing heavier offspring in litter 3. This increase in mass was almost entirely attributable to an increase in fat reserves. Such a result could represent adaptive plasticity, if it can be demonstrated that maternal fitness increases through the production of heavier offspring in a low-food environment.

**Key words:** *growth; offspring size; plasticity; Poecilia reticulata; reproduction.*

### INTRODUCTION

When an organism reproduces, where do the resources come from to support this investment? Are they derived from resources consumed as reproduction takes place, or are they instead derived from resources gleaned earlier and stored, or is there some combination of the two? For females, at what stage in reproduction are variables such as litter size and offspring size determined and how might these variables respond to changes in the environment such as temporal variation in resource availability? Is the nature of such environmental responses adaptive or is it instead an unavoidable consequence of how the litter is formed?

It is important to understand where the resources come from to support reproduction because the bal-

ance between stored reserves and current supplies will affect an organism's sensitivity to short-term environmental fluctuations. For example, if reproduction is supported entirely from reserves, then there may be little or no response to a short-term decline in resource availability. The ability to store resources for reproduction also represents a potential life history adaptation. It allows the parent to allocate resources to reproduction at a time when the potential fitness of the offspring is high but when resources are in short supply for the parent (Hahn and Tinkle 1965, Derickson 1976, Fitzpatrick 1976, Reznick and Braun 1987). Finally, adjustments in the patterns of allocation represent adaptive forms of phenotypic plasticity if such adjustments enhance the reproductive success of the individual.

Two examples illustrate the sort of variation seen in how organisms support reproductive activities. Meijer et al. (1989) found that female kestrels support reproduction largely by increasing food intake 14 d before egg-laying. Thus, there appears to be an immediate link

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between increased consumption by the female and the extra resources required for reproduction. This conclusion is supported by the earlier reproduction and increased clutch size seen in response to supplemental feeding (Meijer et al. 1988). In contrast, Fraser (1980) found that clutch size in the red-backed salamander (*Plethodon cinereus*) was not influenced by food availability during the 9-mo period before egg-laying. These animals reproduce every other year, so clutch size appears to be determined during the first 15 mo of the cycle. Contrary to clutch size, the rate of yolk deposition for individual eggs was influenced by food availability during the last 9 mo. Yolk deposition was also influenced by "condition," or the amount of stored reserves present at the beginning of the 9-mo experiment. Rate of yolk deposition may influence either the time of egg-laying and/or the size of individual eggs. The resources devoted to reproduction are therefore gathered over a long interval of time and are in part derived from the mother's somatic reserves. In general, there is a great deal of variation in how organisms support reproduction; describing and understanding this variation is likely to improve our understanding of the evolution of life histories.

Our goal is to describe how resources are allocated to reproduction in female guppies and to determine whether different patterns of allocation represent plastic responses to fluctuating food availability. We have chosen to manipulate food availability because there is evidence that it varies over time in natural populations (Reznick 1989). In the laboratory, lower food rations cause lower fecundity and lower reproductive allotments (the percent of total weight that consists of developing embryos; Reznick 1983). We regularly see the same changes during the rainy season (a period of low food resources) in natural populations (Reznick 1989). Since the life-span of a guppy will frequently include both the rainy and dry seasons, many individuals will experience such a change in resource availability during their lives.

We also used changes in food availability to probe the questions regarding where the resources come from that comprise a litter and at what time offspring number and size are determined. It enabled us to assess changes in the pattern of allocation of resources to reproduction. Detecting such changes is the first step in determining if there is adaptive plasticity in how these resources are allocated.

#### MATERIALS AND METHODS

Guppies are viviparous and lecithotrophic (Wourms 1981). "Lecithotrophic" means that there is no placenta-like connection between the mother and young, so maternal investment ceases before the egg is fertilized. One litter is produced every 3–4 wk. There is evidence that *Poecilia latipinna* has facultative matrotrophy, or that a female can allocate resources to developing young under some circumstances (Trexler 1985);

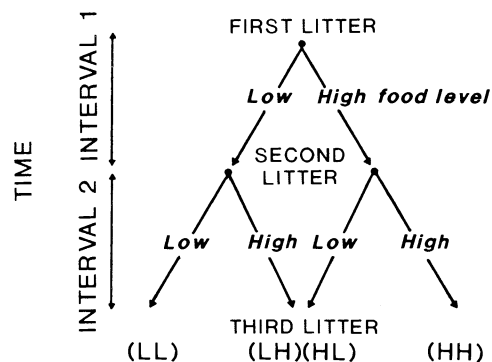


FIG. 1. The experimental design, following Hester (1964). The first litter corresponds to the litter born while the female was still being fed ad libitum. From this day on, females were assigned to either high or low food availability for interval 1. When they gave birth to litter 2, they were reassigned to either high or low food availability.

there is not yet any evidence for facultative matrotrophy in guppies.

Our experimental design was based on an earlier study by Hester (1964) (Fig. 1). Fish were maintained on a given level of food availability for the time required to produce one litter of young, then were randomly assigned to a new level of food availability. Hester was primarily concerned with the number of young produced, but also reported on interbrood interval and a crude measure of offspring size. Our study differed from his because it was more highly replicated and considered more dependent variables.

The experimental subjects were second and third generation laboratory-born fish derived from stocks collected in the El Cedro River in Trinidad. The females were reared with mature males in 38-L community tanks and were fed ad libitum on liver paste and brine shrimp nauplii. When they were large enough to have produced a few litters, they were isolated in 8-L aquaria and fed ad libitum until they produced their next litter (litter 1; Fig. 1). They were then randomly assigned to either a high or low level of food availability and were maintained on that ration until they produced their next brood (litter 2). The time interval between the first and second broods is referred to as "interval 1." After producing the second litter, they were again randomly assigned to a high or low level of food availability, with the constraint that there be equal numbers in each of four treatments: high-high (HH), high-low (HL), low-high (LH), low-low (LL). They were maintained in these conditions until they produced their third litter (interval 2). The HH treatment therefore received high food for interval 1 and again for interval 2. There were initially 10 females per treatment group. One female each was lost from the HH and LL treatments, so data are reported here for a total of 38 individuals.

We controlled food availability by giving the fish measured volumes of liver paste in the morning and

TABLE 1. Analyses of variance of dependent variables associated with the third litter of offspring.†

Source of variation	df	Female mass (mg)	Female % fat	Interbrood interval (d)	Reproductive allotment (%)	Number of offspring	Mean offspring mass (mg)	Lean mass of offspring (mg)
Covariate								
Female mass	1	...	...	...	...	6.93*	11.50**	...
Main effects								
Interval 1	1	7.20*	0.31 <sup>NS</sup>	6.07*	15.32**	7.11*	6.01*	1.59 <sup>NS</sup>
Interval 2	1	20.83**	18.55**	3.32†	0.01 <sup>NS</sup>	5.58*	0.13 <sup>NS</sup>	0.00 <sup>NS</sup>
I1 × I2	1	0.05 <sup>NS</sup>	0.41 <sup>NS</sup>	0.09 <sup>NS</sup>	2.33 <sup>NS</sup>	0.15 <sup>NS</sup>	4.02†	1.91 <sup>NS</sup>
Residual mean square	34	5544.6	0.0016	5.73	0.0024	16.98	0.0402	0.0274
R <sup>2</sup>		0.44	0.36	0.21	0.34	0.54	0.31	0.09

\* = .01 < *P* < .05; \*\* = *P* < .01; † = .05 < *P* < .10; <sup>NS</sup> = *P* > .10.

‡ “Female mass” = the wet mass of the females after they gave birth to their third litter. “Female % fat” = the loss in the female’s somatic dry mass after extraction with anhydrous ether. “Interbrood interval” = the number of days between the birth of the second and third litters. “Reproductive allotment” = the dry mass of the third litter, divided by the total dry mass of the female, including the third litter. “Number of offspring” = the number of offspring in the third litter. “Mean offspring mass” = the mean dry mass of offspring in the third litter. “Lean mass of offspring” = the mean dry mass of offspring after extraction with anhydrous ether. Values reported for “female mass” (as a covariate), interval 1, interval 2, and I1 × I2 are *F* ratios with the residual mean square as the denominator. “R<sup>2</sup>” = the proportion of total variance attributable to main effects and the covariate.

newly hatched *Artemia* nauplii in the evening (following the methods of Reznick 1983). We quantified volume by packing the food into a Hamilton Micropipette, then administering 25  $\mu$ L per meal for high-food treatments and 5  $\mu$ L per meal for low-food treatments during both time intervals. Each fish was checked regularly to confirm that all available food was eaten. These rations were chosen to represent a food level just below ad libitum for the high-food treatment and just above the minimal maintenance ration for the low-food treatment, based on our experience in earlier investigations (e.g., Reznick 1983).

We measured length and mass of females after each litter, then preserved the females immediately after they produced their third litter. All offspring from litters 1–3 were also preserved immediately after birth. The female and all offspring were killed with an overdose of anesthetic and preserved in 5% formaldehyde. We dried the offspring overnight at 55°C, then measured dry mass. The females were dissected, as described in Reznick (1983). Reproductive tissues, which often included yolking ova for the next litter, were separated from somatic tissues. Any food remaining in the gut was removed. We then dried the tissues overnight at 55°C and measured the female’s somatic and reproductive dry mass. A female’s reproductive allotment was estimated as the dry mass of the third litter divided by the female’s somatic dry mass plus the mass of the third litter. We estimated the fat content of mothers and offspring by repeatedly extracting the dried tissues with anhydrous ether, then measuring the mass loss.

Dependent variables associated with the third litter were analyzed with a two-way analysis of variance, with the independent variables being the first and sec-

ond intervals. Dependent variables that characterize the mothers include growth during each interval, fat reserves after the third litter, the intervals between successive broods, and reproductive allotment in the third litter. Dependent variables that characterize the litters include the number of offspring, size of offspring (dry mass), and their fat content. Together, these variables make it possible to describe the pattern of resource allocation to the third litter. For example, the relative contributions of the two intervals to all of these dependent variables will gauge the degree to which each variable is determined during that time interval.

We evaluated the wet mass of the female after the second and the third litters as potential covariates for the analyses of the number and size of offspring in the third litter. The wet mass after the second litter accounted for a higher percent of the total variance than the third litter for these dependent variables, so it is included in the analyses. The assumptions of the analyses of covariance and variance were met for all of these analyses. All means reported in the text are least-squares means from the appropriate analysis of variance (GLM procedure; SAS 1985). All estimates of within-treatment variability are  $\pm 1$  SE, as estimated for these least squares means.

## RESULTS

### *Dependent variables that characterize the mothers*

*Female growth.*—There were no size differences, estimated as wet mass, between the high vs. low treatments at the beginning of the first interval ( $F_{1, 36} = 0.02$ , *P* = .88; mean “high” =  $276 \pm 17$  mg, mean “low” =  $272 \pm 17$  mg), so we have evaluated growth

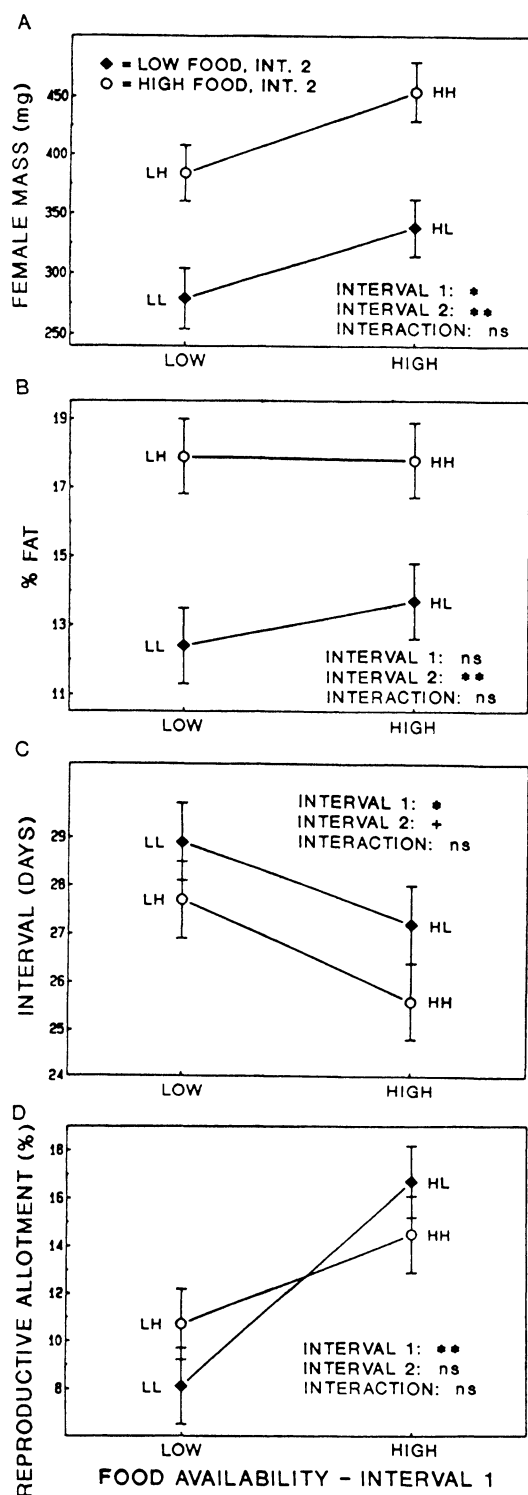


FIG. 2. Variables that characterize the mother. Each panel includes a summary of the significance of the illustrated main effects. \*\* =  $P < .01$ , \* =  $P < .05$ , † =  $.05 < P < .10$ , ns = not significant. (A) Female wet mass after giving birth to the third litter. See text for interpretation of the effects of each time interval. (B) Female fat content after the birth of the third litter. The dependent variable equals the percent of mass lost after extraction with anhydrous ether. (C) The effect of

simply as size of the females after giving birth to the second and third litters. Females grew more if they received high food during either the first or second time intervals (Table 1, Fig. 2A). The x axis in Fig. 2A represents food availability during the first interval. An effect of the first interval is manifested as either a positive or negative slope between the average of the two points at each level of food availability on the x axis. In this case there is a positive slope, implying that females which received high food during the first interval were larger at the end of the study than females that received low food during the first interval. The two different lines represent high vs. low food availability during the second interval. If there is an effect of the second interval, then one of these lines will have a different elevation along the y axis. In this case, females that received high food during the second interval were larger, and thus grew faster, than those that received low food, so the high-food line has a higher intercept.

**Female fat content.**—The quantity of stored fat in females following the birth of litter 3 was significantly influenced by the second time interval, but not by the first (Table 1, Fig. 2B). The significant effect of the second interval can be seen as the difference in the y intercepts of the two lines in Fig. 2B. This difference indicates that females that received high food during the second interval had greater fat reserves after they produced their third litter than females that received low food. The near-zero slope of each of these profiles indicates that there is no carryover effect of food availability during the first time interval on a female's fat reserves after the second time interval.

**Interval between the second and third broods.**—The time interval between the second and third broods was shorter if the female received high food rations during either the first or second intervals (Table 1, Fig. 2C). The average negative slope of the two lines (Fig. 2C) indicates that high food during the first interval results in the more rapid production of the third brood (mean "high" =  $26.4 \pm 0.5$  d, mean "low" =  $28.3 \pm 0.5$  d). Food availability during the second interval has the same effect, although the magnitude of the effect was smaller (mean "high" =  $26.7 \pm 0.5$  d, mean "low" =  $28.0 \pm 0.5$  d) and not significant ( $P = .0773$ ).

**Reproductive allotment.**—Reproductive allotment was significantly higher if the female received high food during the first time interval, but was not influenced by the second time interval (Table 1, Fig. 2D). The influence of the first time interval is evident in the average positive slope of the two lines in Fig. 2D. This result indicates that the first interval alone influences

←

ration level on the interval between the second and third broods. (D) Reproductive allotment (litter dry mass/total dry mass) for the third litter.

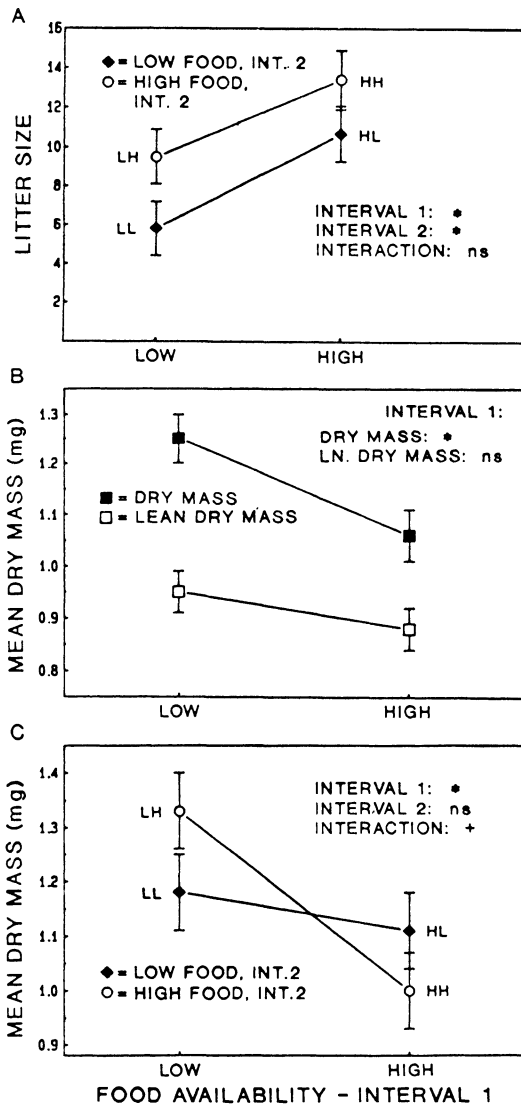


FIG. 3. Variables that characterize the offspring. Symbols and format as in Fig. 2. (A) Number of young in the third litter. This analysis included, as a covariate, the mother's postpartum wet mass after giving birth to the second litter. (B) Dry mass of offspring in the third litter. The upper line (■—■) represents the mean dry mass, an estimate of offspring size. The lower line (□—□) represents the lean dry mass of the same offspring. Only the effects of food availability during the first time interval (the x axis) are depicted here. (C) Dry mass of offspring in the third litter. This figure represents the effects of both time intervals on the mean dry mass of the offspring.

the total mass of the third litter, probably because most of the investment in the litter is determined by the time the previous litter was born, or shortly thereafter.

#### *Dependent variables that characterize the offspring*

**Litter size (with female size as a covariate).**—High food levels during both time intervals were associated

with more offspring in the third litter (Table 1, Fig. 3A). The magnitude of the influence of the first time interval (mean "high" =  $12.1 \pm 1.1$  young, mean "low" =  $7.7 \pm 1.1$  young) was greater than that of the second time interval (mean "high" =  $11.4 \pm 0.9$  young, mean "low" =  $8.3 \pm 0.9$  young). Recall that reproductive allotment, which estimates the size of the reproductive "package" relative to the females size, was not affected by the second interval. If the second time interval does not influence the relative size of the package but does influence the number of offspring, it must also influence offspring size. Also, litter size is positively correlated with female size, and higher food results in increased growth and larger body size. Including female size as a covariate thus tends to reduce the apparent differences in litter size between the high- and low-food treatments; when female size was not included as a covariate, the magnitude of the differences between treatments was greater for the first time interval (without covariate, "high" = 13.3 young, "low" = 6.5 young) but barely changed for the second interval ("high" = 11.2 young, "low" = 8.5 young).

**Offspring size.**—We first illustrate the results for just interval 1 (Fig. 3B). The upper line in Fig. 3B is the value for all individuals that received either high or low food during the first interval alone. This means that we averaged across the second time interval (i.e., the "low" value is the average of the LL and LH treatments). Females that received low food during the first interval produced heavier babies than those that received high food (Fig. 3B, Table 1). The lower line represents the average lean dry mass of the same offspring; with fat reserves removed, most of these mass differences disappeared. The low-food fish still tended to be heavier, but the difference was no longer significant. The size differences between the two treatments are therefore mostly attributable to the differences in fat reserves. Females that received less food and had lower fat reserves of their own packed more fat reserves into each embryo.

We next consider the results for offspring dry mass with the first and second intervals treated separately (Table 1, Fig. 3C). The negative slope of the lines once again demonstrates that high food during the first interval is associated with smaller offspring in the third litter. The more prominent feature of the figure is the difference in the slopes of the lines which represent the influence of the second interval. There is no overall effect of the second interval, but the difference in slopes, the interaction, is just short of significance (Table 1;  $P = .053$ ). This result indicates that there is an effect of switching food availability, independent of the level of food itself (E. Schultz, *personal communication*). Fish that switch from low to high food produce larger babies than those that receive low–low food. Similarly, fish that switch from high to low food produce larger babies than those that receive high–high levels of food.

## DISCUSSION

*Model of allocation*

The first application of these results (summarized in Table 2) is to describe the source of the resources used to produce a litter. The mode of reproduction in guppies creates an expectation for the results. Guppies appear to make a rapid investment in eggs prior to fertilization, then retain them during development without investing further energy in embryonic growth (Wourms 1981, Reznick and Endler 1982). We therefore expected that the characteristics of the third litter would be determined largely by the first interval, since most of the second interval corresponds to a time when the embryos are developing but no further investment is being made by the mother. This expectation is upheld in terms of reproductive allotment and fat storage. The reproductive allotment (dry mass of offspring/total female dry mass, including offspring) for the third litter is determined entirely during the first time interval, or by the time the second litter is born.

The mother's fat reserves appear to play some role in determining this allotment. There was a significant contribution of food consumed during the second interval to a female's fat reserves after the third litter, but no contribution of consumption during the first interval to fat reserves after the third litter. This suggests that reserves present after the production of a litter are used immediately for the next litter. If we assume that food availability during the first time interval similarly influenced the female's fat reserves after the birth of litter 1, then these reserves must have been used for the production of litter 2 and no reserves were carried over from interval 1 to litter 3.

Contrary to our expectations, three aspects of reproduction were influenced by both time intervals. First, the number of days between the second and third broods was significantly influenced by food availability during the first and second intervals. Low food during either interval caused an increase in the amount of time between the second and third litters. This suggests that a female is provisioning the next brood with a combination of reserves present when the previous brood was born plus food consumed immediately after the birth of the previous brood. If she does not have sufficient reserves or if food availability is low after the birth of the previous litter, then she will defer initiation of the subsequent brood for a few days to increase the amount of resource devoted to the next litter.

Hester (1964) reported that food availability did not influence interbrood interval. He did not report any details of his results, so it is not possible to examine the trends in his data. This difference in our results may be due simply to the size of the experiment; our study involved three times as many subjects per treatment and hence is more likely to detect a significant response in any dependent variable. Our result also duplicates one from an earlier study (Reznick 1983).

TABLE 2. Summary of the response to low food availability, compared with that for high food availability. We also indicate which interval influenced the dependent variable.

Response	Interval influencing variable
a. Lower growth rates of the mothers	both
b. Less fat storage by the mothers	2
c. Longer interbrood interval	both
d. Lower reproductive allotment	1
e. Fewer offspring	both
f. Larger, fatter offspring	1, interaction

The number of offspring is also influenced by food availability during both time intervals. High food availability during both intervals causes an increase in litter size. The pattern is thus the same as for interbrood interval. Both Hester (1964) and we found that a female has a pool of yolking ova present by the time a litter is born. The number of ova recruited from this pool into the subsequent litter therefore appears to be influenced by both food availability up until the birth of the previous litter and availability after that litter is born.

Hester also reported that there were distinct size classes of ova which could predict the size of subsequent litters. This appears to contradict our result; however, his observations were qualitative and were not supported by a documentation of discrete size modes of ova. We did not observe discrete size classes and instead saw what appeared to be a continuum of different-sized ova.

Finally, there was also a complicated influence of the two time intervals on the size of individual offspring. Low food during the first time interval resulted in an increase in offspring mass, primarily as fat reserves. The contribution of the second interval was manifested as an interaction between the two periods, rather than a direct effect. This suggests that a female will increase the amount of resources devoted to each offspring in response to a change in food availability, regardless of the direction of the change (see Fig. 3C). Hester reports no influence of food availability on offspring size. He estimated offspring size by length, rather than mass. Since the difference was primarily in the amount of fat reserves, we may also have failed to see length differences, had we measured our offspring in this fashion.

A second possible interpretation of this interaction between intervals is that it is caused by facultative matrotrophy (Trexler 1985). The switch in food availability was associated with both increased offspring size (interaction in Fig. 3C) and increased reproductive allotment (Fig. 2D) without a parallel change in interbrood interval (Fig. 2C). Although the interactions are not significant, they suggest that such an increase in offspring size could be accomplished with maternal investment during development.

In summary, the characteristics of a litter are determined by both interbrood intervals that precede it. The total mass of a litter relative to the size of the female (reproductive allotment) is determined at the time that the previous litter is born. The yolking ova and fat reserves present at that time appear to influence strongly the investment in the next litter. However, the number of offspring and the quantity of resources devoted to each offspring is influenced in part by conditions after the birth of the previous litter. The time required for the influence of the second interval can be seen in the extended interbrood interval associated with lower levels of food availability. This extra time may be required to obtain extra resources and to devote more resources to each yolking ova.

#### *Plasticity of allocation to individual offspring*

We define plasticity as changes in the phenotype in response to changes in some aspect of the environment (Bradshaw 1965). The most common forms of plasticity studied as adaptations are polyphenisms, or plasticity that is expressed as discrete alternative morphologies. Examples of these were reviewed by Stearns (1989) and include phenomena such as the "conic" vs. "bent" forms of the acorn barnacle (*Chthamalus anisopoma*) (Lively 1986a, b). Conic forms are more resistant to predation by gastropods; however, the predator resistance is attained at the cost of slower growth and reduced fecundity. Because of the costs and benefits associated with the bent morphology, it only enhances fitness in the presence of predators. In the absence of predators, reduced growth and lower fecundity results in a reduction in fitness relative to conic forms. Such trade-offs are an essential part of adaptive plasticity. Without them, a single morphology can represent the best solution to a varying environment (Lively 1986b).

In general, such discrete forms of plasticity are relatively easy to investigate. They tend to be induced by key factors in the environment, such as the presence of predators. The mechanisms in turn yield clues about the possible adaptive significance of the trait. However, most forms of plasticity are not so discrete in their expression. The examples illustrated here are the variables that characterize the life history, particularly offspring size. It is easy to induce environmental changes in such variables, but it is more difficult to determine whether or not these changes are adaptive.

In an earlier investigation of phenotypic plasticity in guppies, Reznick (1990) considered the influence of food availability on age and size at maturity in males. Lower food caused maturity at a later age and smaller size. This change could be the consequence of the same pattern of development being expressed in different environments, but it might also represent a specific response to a change in the environment which enhances the individual's fitness. Distinguishing between these alternatives is critical to the argument that the plasticity represents an adaptation. In the case of male

guppies, the pattern of development changed in response to growth rate; faster growing individuals initiated the process of maturation at a larger size than the more slowly growing individuals. This delay allowed faster growers to attain a larger size than would otherwise have been possible. Initiating maturation at a smaller size allowed the slow growers to attain maturity at an earlier age than would otherwise have been possible. This plasticity in the pattern of development therefore allows a trade-off between the age and size at maturity. Subsequent studies could consider the adaptive significance of this trade-off.

A second way of identifying adaptive plasticity is to first consider how patterns of allocation change in response to changes in the environment, then to consider the consequences of these changes. For example, it is well known that if a fish receives more food it will grow faster and produce more young (e.g., Scott 1962, Reznick 1983). While this general trend is not surprising, it is of interest to know if there are regular changes in the pattern of allocation of resources, such as to the number vs. size of young. If there are such changes, then it is possible to evaluate the costs and benefits associated with them and hence to evaluate their adaptive significance.

The production of fewer, larger offspring by the low-food females or by females which experience a change in resource availability represents such a change in allocation. Consider it first as a response to low food. In this context, one must first evaluate the correlation between a female's environment and the environment that her offspring will experience. Rainy vs. dry seasons in their natural habitat appear to influence resource availability (Reznick 1989) and are sufficiently long for an offspring to experience the same conditions as the parent when the eggs were formed, so we expect the correlation to be positive.

If the mother's environment is a good predictor of the offspring's environment, then it is worth considering what the relative fitness is of low-food vs. high-food offspring in both types of environments. One result which would support an adaptive interpretation of these data would be little or no difference in the fitness of the two types of offspring when compared in a high-food environment, but higher fitness for the low-food offspring when the two are compared in a low-food environment (Fig. 4). This result incorporates the same sort of trade-off as in the barnacle example cited above. If there is little or no difference in offspring fitness in a high-food environment, then producing larger offspring could reduce maternal fitness because it also means producing fewer offspring or devoting more resources to reproduction, without any payoff. On the other hand, if there is an advantage to producing larger offspring in a low-food environment, then there is a direct payoff for the mother which can compensate for producing fewer offspring with higher fat reserves.

Such interactions between egg size and fitness in dif-



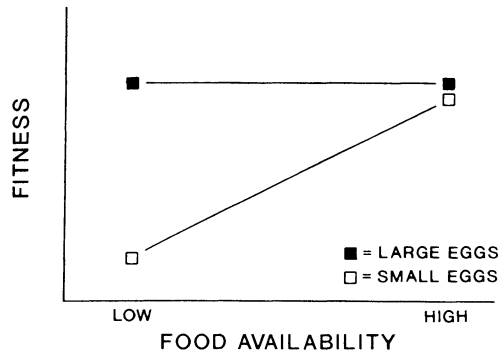


FIG. 4. Hypothetical interaction between offspring size (fat content) and fitness in high- vs. low-food environments. Such an interaction would support the argument that this plasticity in offspring size and fat content is an adaptation to changes in food availability.

ferent environments have been seen in fish (Hutchings 1991), amphibians (Berven and Chadra 1988, Kaplan 1992, Parichy and Kaplan 1992), and microcrustacea (Tessier and Consolatti 1989). Kaplan (1992) and Parichy and Kaplan (1992) emphasize that the relative fitness of offspring derived from large vs. small eggs may depend on the environment in which they were compared, rather than there being a uniform advantage associated with a given egg size.

Consider next the response in offspring size to a change in food availability. Here, the response is similar to "bet-hedging" (Seger and Brockman 1987) because fewer, possibly higher quality offspring are produced in response to what appears as an uncertain environment. The net effect in a variable environment could be a reduction in both the mean and variance in the number of successful offspring that are produced.

In either case, this investigation has revealed a change in the pattern of resource allocation in response to a change in the environment. Females that have access to less food have far lower fat reserves, but devote more resources to each offspring. This change in the pattern of allocation of resources can in turn lend itself to specific experiments which evaluate the possible adaptive significance of the plasticity, and hence enable us to consider whether or not this plasticity is an adaptation, as opposed to simply being a consequence of growing up in a different environment.

#### ACKNOWLEDGMENTS

We thank Mike Hirshfield, who originally suggested that it would be worthwhile to repeat Hester's study, but consider a more complete range of dependent variables. We thank Heather Bryga for her help in the laboratory and Ms. Bryga, Helen Rodd, and two anonymous reviewers for their helpful comments on earlier versions of the manuscript, many of which were incorporated in the final version. Finally, we are very grateful to Eric Schultz for his interpretation of the interaction between food availability and time interval for offspring size. This research was supported by NSF grants BSR8818071 and DEB-9119432.

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## ERRATA

In an article by R. Given Harper, Steven A. Juliano, and Charles F. Thompson (“Avian hatching asynchrony: brood classification based on discriminant function analysis of nestling masses,” *Ecology* **74**(4): 1191–1196), two column headings were switched in Table 2 (p. 1194). In the columns for “Asynchronous = 32” under “True group frequency” the labels of the two “Classified as” columns were reversed: “Synch.” should read “Asynch.” and “Asynch.” should read “Synch.”

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In an article by Roger Arditi and Henni Saïah (“Empirical evidence of the role of heterogeneity in ratio-dependent consumption,” *Ecology* **73**(5):1544–1551), two errors occurred. In *Methods* the final two sentences of the first paragraph on p. 1547 should read:

Two different concentrations were used for the algal food supply:  $22.4 \cdot 10^3$  cells/mL and  $146.8 \cdot 10^3$  cells/mL. The “low food” cascades received therefore  $1222 \cdot 10^3$  cells/h and the “high food” ones  $7993 \cdot 10^3$  cells/h.

On the same page, in the third paragraph, the next-to-last sentence should read:

The modified environment for *Daphnia* was not run at low food conditions.

The rest of the paper remains unchanged. We thank William Murdoch for pointing out these errors to us.