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The trade-off between foraging and courting in male guppies

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Abstract. For animals to maximize their fitness, they must be efficient at foraging and prolific at reproduction. These activities are often considered as distinct and separate and are therefore studied in isolation of other behaviour patterns. However, many animal species must simultaneously choose between foraging and opportunities to reproduce. One such animal is the guppy, *Poecilia reticulata.* Four groups of male guppies were presented with the simultaneous choice of courting a female or feeding. As predicted by a state-dependent model, male guppies always fed prior to courting the female. Although the length of time male guppies spent feeding was inversely related to the rate at which food was provided, they consumed more when food was provided at a lower rate. Female size did not influence the length of time males spent feeding, but did affect the number of males that engaged in courtship, except for the very largest females. These females were from a domesticated strain and received the same courtship activity as wild females that were approximately one-eighth their size. These data suggest that male guppies make state-dependent decisions, choosing first to ensure they have sufficient energy reserves before investing time and energy in courtship.

Much of the research on animal behaviour has examined animals that live in temperate climates. These animals tend to have distinct breeding seasons, resulting in reproduction being temporally segregated from other activities. For this reason, field research on animal behaviour can be divided into two parts, research done within and outside the breeding season. There are also two major schools of thought for understanding animal behaviour: working within the paradigm of foraging theory (where rates of energy aquisition are used as a surrogate for fitness) and examining the processes necessary for successful reproduction (e.g. mate choice). For temperate species, it may be valid to apply both approaches to understand animal behaviour. But what of animals that must make reproductive and foraging decisions simultaneously? Some integration of these two approaches is necessary to understand how animals choose between these two activities.

Well-adapted animals are assumed to make decisions which maximize their fitness, and therefore must consider the fitness benefits and costs associated with each decision. When foraging, the costs involved will be both direct (i.e. the time and energy required to obtain food) and indirect (e.g. the risk of predation associated with obtaining food and lost opportunities to pursue other activities) and they will be primarily determined by features of the environment in which the animal forages. The benefits of foraging will be determined by the animal's ability to convert food energy into fitness and therefore will be largely an intrinsic characteristic of the animal (i.e. a part of its life-history strategy).

Sexual selection can produce dramatically different life-history strategies between males and females within a species. In many species, differences in conspicuousness to predators or in parental investment patterns might be expected to exert different selective pressures on the foraging behaviour of each sex. One such species is the guppy, *Poecilia reticulata.* This fish exhibits strong sexual dimorphism, with females attaining a larger size than males. Fertilization is internal and females give birth to litters of live young. After they mature (at approximately 2 months of age), they give birth year-round with a gestation period of 23–30 days. Males mature at approximately the same age as females, but their growth slows markedly at this time or stops altogether (Liley & Seghers 1975; Reznick 1983). The males are brightly coloured and compete for access to females. The species is highly promiscuous, with males neither defending territories nor providing parental care (Baerends et al. 1955).

The significance of energy intake to the fecundity of female guppies has been well documented (Hester

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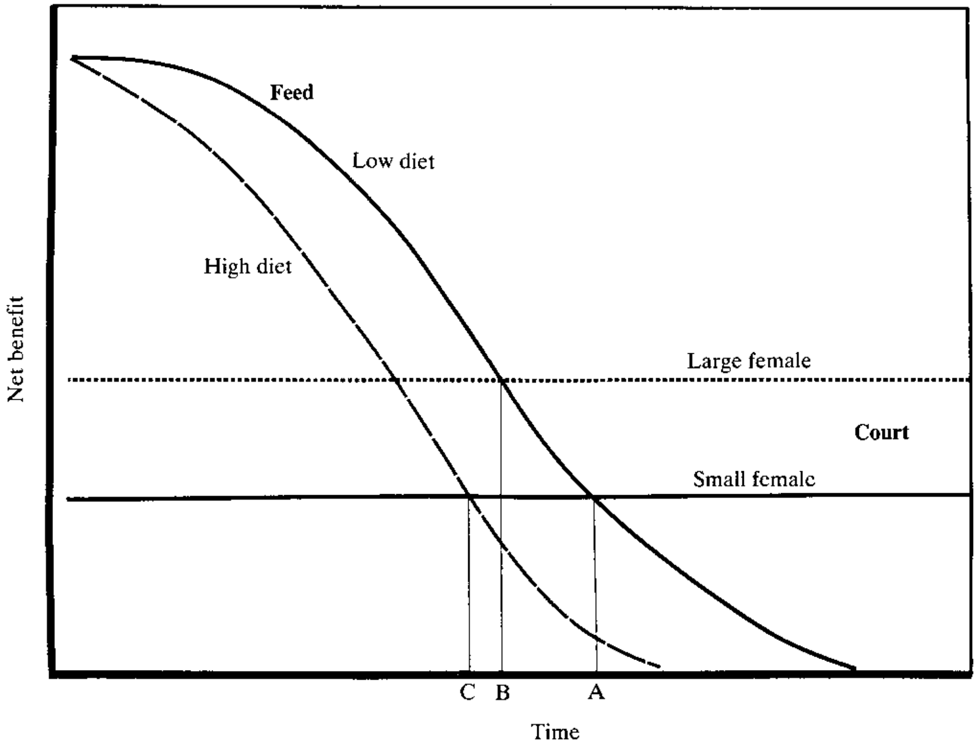

Figure 1. A model to describe how male guppies should trade off courtship and foraging opportunities. The ordinate represents the hypothetical net fitness benefits of either feeding or courting and the abscissa corresponds to time within an experiment. In this model the males on a low diet should switch from feeding to courting a small female at time A. Increasing the size of the female will reduce the switch time to B. Increasing the amount of available food will reduce the switch time to courting a small female to C. Both of these results were observed.

1964; Dahlgren 1980; Dussault & Kramer 1981; Reznick 1983). Because litter size is constrained by the size of the female (Reznick 1982, 1983), increased energy intake can increase fecundity by allowing the female to grow to a larger size. Furthermore, energy can also affect litter size directly: females on reduced diets may resorb oocytes to compensate for starvation stress (Hester 1964).

Although feeding by female guppies contributes directly to their fitness, the relationship is less direct for males. Feeding presumably increases male fitness by increasing life expectancy and possibly by increasing their probability of successfully courting a female. Note that these benefits from feeding will only contribute to future reproductive success. Consequently, the choice between feeding or courting a female may be considered analogous to a trade-off between current and future reproductive success. How should a male guppy make such a decision?

Courtship by male guppies is characterized by a series of sigmoid displays (Baerends et al. 1955) and therefore requires some fixed energetic cost (e.g. the energy associated with courtship and lost foraging opportunities). Although the male's ability to successfully court a female may be unaffected by his energetic state (above some threshold level), it will affect his ability to pay the costs of courtship (e.g. an energetically stressed male guppy may substantially increase its risk of starvation if it attempts to court a female). Similarly, the benefits derived from foraging will be inversely related to the male's energetic state. A model to explain this trade-off must therefore be state dependent (cf. Mangel & Clark 1988).

Figure 1 provides a simple state-dependent graphical model of this trade-off. The benefits derived from courtship are assumed to be dependent upon female size (because large females are capable of producing more offspring) and not related to the male's energetic state. However, the benefits derived from feeding are assumed to be inversely related to the males energetic state. When the male is at a low energetic state, the benefit from feeding should contribute to reducing its probability of starving to death. The higher the male's energetic state, the lower the probability of starving and thus the lower the associated benefits from feeding. When the male's energetic state is low and he is confronted with the simultaneous choice of courting a female or feeding, the relative benefits from feeding are highest. As the male's energetic state improves, the potential benefits from courtship will exceed those of feeding. At this time, male guppies should switch from feeding to courting. Increasing diet levels will increase the rate of improvement in the male's energetic state. This causes the benefits of feeding to decline more rapidly, resulting in an earlier switch from feeding to courting (compare points A and C in Fig. 1). The switch time from feeding to courting can also be reduced by increasing the benefits of courtship, for example, by courting a larger female (compare points A and B in Fig. 1). Diet level would not influence preference by males for particular females but would be determined solely by the characteristics of the female. This model makes specific, testable predictions for a guppy. First, male guppies that have previously been deprived of food should always feed before courting a female. Second, both female size and feeding rate will affect the length of time spent feeding. Increasing female size or increasing feeding rate should decrease the length of time spent feeding. Third, female size (but not diet level) will affect the willingness of male guppies to court a female. The following experiments test the predictions of this model.

METHODS

I used guppies collected from a lowland section of the Quaré River in Trinidad. For these experiments, groups of 10 male guppies were observed choosing between feeding and courtship opportunities, and their spatial distribution through time was used to indicate their relative preference for each option. These experiments used four different groups of similar-sized male guppies with average wet weights of 0·175, 0·182, 0·169 and 0·176 g, respectively. The males were housed in 90-litre experimental aquaria throughout the experimental period so that no daily acclimation periods were required. They were maintained on a 12:12 h light: dark cycle and fed NutraFin (TM) and brine shrimp (*Artemia* sp.) ad libitum daily between experiments. During experiments the fish were maintained exclusively on onion fly, *Delia antigua*, eggs and provided a weekly supplement of NutraFin flakes for essential nutrients.

I presented each group of 10 males with a choice of either courting a female or feeding at the opposite end of the aquarium (Fig. 2). Onion fly eggs were provided by a feeder which presented them at a constant rate over a wide area throughout the experiment, ensuring that all males had equal access to the food (Abrahams 1989). Diet level was manipulated by providing food at four different rates (6, 12, 24 and 48 mg of food per 25 min, only two groups were tested at the 6 mg diet level). The females were isolated from males 4 weeks prior to the beginning of these experiments and were presented to the males in round 4-litre glass jars. Females were maintained in separate 20-litre aquaria and were fed NutraFin and brine shrimp ad libitum daily.

For these experiments, females were divided into five different size classes based on their wet weight (g) as follows: (1) 0·07–0·10 g, (2) 0·15–0·20 g, (3) 0·35–0·40 g, (4) 0·83–0·92 g and (5) 1·40–1·80 g. Females for size class 5 were larger than those from the wild population and were obtained from a domesticated stock maintained by the University of Manitoba Zoology Department. To ensure that females remained within these size classes, they were anaesthetized (with 2-phenoxyethanol) and weighed every 2 weeks. Females approaching the upper limits of the size range were replaced.

When the jar containing a female was added to the aquarium, the lid was removed and the jar filled with water from the aquarium. The top of the jar was covered by a fine mesh screen, providing both visual and chemical contact between the males and the female. The jar was placed in the aquarium 5 cm from the end opposite the feeder.

Experiments were conducted in a stratified random order. A diet level was randomly selected. Within each diet level, female size and end of tank for presentation were chosen randomly. The selected combination was presented to the males three times in one day, with each trial being separated by at least 3 h to prevent satiation. Each combination of diet level, female size, and female position was tested in this way.

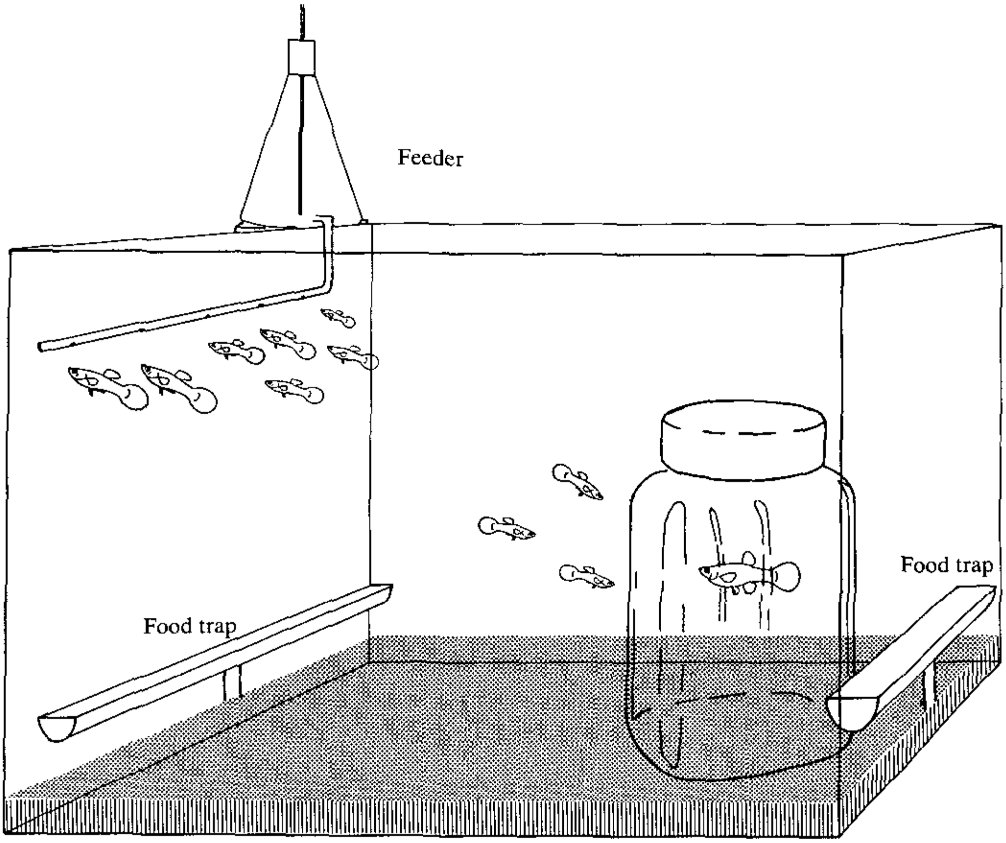

Figure 2. Apparatus used for the experiments. Note that the positions of the feeder and the female can be reversed in this apparatus. Food is provided by the feeder and removed from the apparatus by the food traps.

Experiments were performed by first placing the feeder at one end of the aquarium and then placing the female at the opposite end. As soon as the female was in the aquarium, I started the flow of food from the feeder. I recorded the number of males feeding or actively courting the female every 30 s for 25 min using a metronome sampling technique.

To quantify the influence of time I divided each experiment into five successive time periods (10 sequential observations per time period). If there was no temporal component to these experiments, then no significant differences should exist between male activities in these five successive time periods. From these data, temporal changes in male activity within an experiment could be detected.

To quantify the absolute amount of time devoted to foraging and courtship, I defined the time spent foraging as the time from the beginning of the experiment to the point at which more than 50% of the males had switched to courting the female for at least three successive observations (see example in Fig. 3). If no switch point was observed, it was designated to occur at 25 min (the end of the experimental period). Note that since the feeders provided food at a constant rate (Abrahams 1989), the time spent foraging should be linearly related to the absolute amount of food consumed. For statistical analysis, groups of males were considered at the level of independent observation.

RESULTS

If, as assumed by this model, male guppies make state-dependent decisions they should prefer to feed before courting a female when they have been deprived of food. During these experiments, a significant change in behaviour through time was observed. Both the proportion of males feeding

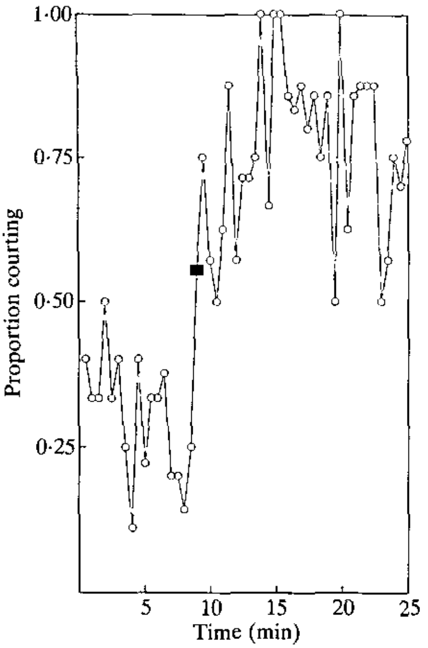

Figure 3. The results of a single experiment at the 24-mg diet level illustrating the change in male behaviour with time. Initially the males fed, but then switched (■) to courting the female (as defined in the text).

and those courting the female were significantly influenced by the time period during which these experiments took place (Table I). Male behaviour was also significantly influenced by diet level and the particular group of males studied (see below and Table I).

The model predicted that time spent feeding (i.e. the switch point) should decline with both increasing female size and increasing rates of food availability. As illustrated in Fig. 4, diet level significantly influenced the time at which each switch point occurred (ANOVA, $F_{3,47} = 24{\cdot}5$, $P = 0{\cdot}0001$) but female size did not ($F_{4,47} = 0{\cdot}31$, NS). At the 6-mg diet level, male guppies tended to feed for the duration of the experiment. Increasing diet levels resulted in a more dramatic shift in activities, with a steep decline in the proportion of males feeding over time and an increasing proportion of males courting.

Female size, diet level and male group had a significant influence on the average number of male guppies courting the female (Table II). However, when this analysis was restricted to include only that time period following each switch point, only female size had a significant influence on the number of males courting a female (Fig. 5). No effect of diet level persisted after the switch point (Table II). The greatest number of males courted females from size classes three and four (Student–Neuman–Keuls comparison of means test, $\alpha = 0{\cdot}05$), the largest females from their population (size class 5 females were from a domesticated strain).

It may be possible that male guppies only initiate courtship after consuming some finite quantity of food. As the feeders provided food at a constant rate (Abrahams 1989), the time males spent feeding should have been proportional to the amount of food they consumed. Therefore, if guppies always consume the same amount of food prior to switching, the time males spent feeding should be inversely proportional to diet level. Figure 6 illustrates the observed switch points and those that would be expected if guppies consumed the same absolute amount of food at every diet level (the amount consumed at the 48-mg diet level was used to generate the expected switch points at the other diet levels). The average switch point occurred significantly later than predicted at both the 24-mg ($t_{119} = 6{\cdot}66$, $P < 0{\cdot}001$) and the 12-mg ($t_{119} = 4{\cdot}84$, $P < 0{\cdot}001$) diet levels. At the 6-mg diet level, the predicted switch point would occur approximately 3·5 min after the experiment ended. At this diet level, 58 of 60 experiments resulted in no observed switch from feeding to courting.

The number of males that were classified as neither using the feeder nor courting the female increased significantly after the switch point (paired t-test, $t_{419} = 13{\cdot}66$, $P < 0{\cdot}0001$). Prior to the switch point, an average of 2·3 males were observed neither feeding nor courting, compared with 5·6 males after the switch point.

DISCUSSION

For an animal to maximize its fitness, it can neither exclusively feed nor exclusively pursue opportunities to reproduce. Some compromise between these activities must exist. I developed a model based on the prediction that animals should make state-dependent decisions between these two activities. As predicted, male guppies tended to structure their behaviour, feeding before courting a female. Furthermore, these data demonstrated that manipulated levels of food availability profoundly altered both feeding and courtship decisions. As

Table I. ANOVA to determine the influence of female size, diet level, male group and time period within an experiment on the proportion of male guppies courting a female or feeding

		Feeding		Courtship	
Source	*df*	*F*	*P*	*F*	*P*
Group	3	100·81	0·0001	146·53	0·0001
Time	4	6·49	0·0001	5·40	0·0003
Diet	3	164·14	0·0001	154·33	0·0001
Female	4	2·73	0·0292	6·26	0·0001
Diet × female	12	0·79	0·6602	1·31	0·2110

Data were arcsin square-root transformed prior to analysis. Error degrees of freedom for these analyses were 323 (see text for details).

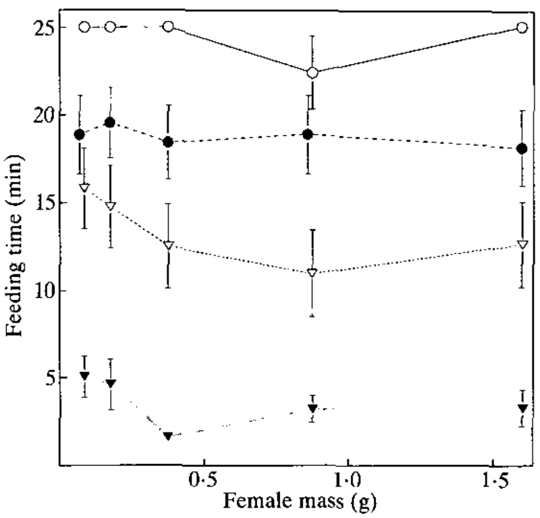

Figure 4. The effect of female size on the length of time spent feeding for the 6 (○), 12 (●), 24 (▽) and 48 (▼) mg diet levels.

illustrated in Fig. 6, increasing levels of food availability resulted in an overall reduction in the absolute amount of food consumed by male guppies.

Variation in courtship opportunities had little impact on foraging decisions. Contrary to the model, males did not alter their foraging time in response to female size. This result was partially due to strong inter-group variation in male response to the females. Separate ANOVAs for each group indicated that the length of time spent foraging by males was significantly affected by female size for three of the four groups studied. Nevertheless, courtship opportunities appeared to exert less influence on foraging behaviour than vice versa. This may be a result of the value of a courtship opportunity being discounted by the probability of success. If courtship success was determined by the males energetic state, this would alter the model presented in Fig. 1. The lines describing the benefits of courtship should increase with energetic state rather than remaining flat. This would result in a diminished effect of female size on the time spent feeding (i.e. reduce the distance between points A and B in Fig. 1).

Male guppies exhibited distinct preferences for females of different size classes. This is consistent with other studies of male preference for females in fish (Sargent et al. 1986; Coté & Hunte 1989), amphibians (Berven 1981; Verrell 1982), and insects (Gwynne 1981; Johnson 1982). However, this size preference existed only for females from their own population. The very largest females (size class 5) were from a domesticated strain, yet the males appeared to make no distinction between them and size class 2 females, even though these females differed in size by approximately eight-fold. There are two possible explanations for this result. Very large females within a population may be senile and therefore have limited reproductive potential. Courtship decisions by males may reflect this phenomenon. Alternatively, males may not be as attracted to females from different populations. This result has been observed with competitive mating experiments and is attributed to female mate choice (Houde 1988; Luyten & Liley 1991). It is possible that variation in the behaviour of male guppies may contribute to this observation.

Courtship increased with increasing food levels, also in accordance with the model. This might be

Table II. The influence of diet level and female size on the number of males courting a female for the entire experiment and after the switch point

Source	Full experiment			After switch		
	df	*F*	*P*	*df*	*F*	*P*
Group	3	31·06	0·0001	1	0·90	0·3515
Diet	3	13·03	0·0001	3	0·66	0·5851
Female	4	6·71	0·0002	4	4·69	0·0061
Diet × female	12	0·89	0·5597	8	0·31	0·9546

Error degrees of freedom were 47 for the entire experiment and 24 after the switch point (switch points were not observed in all experiments).

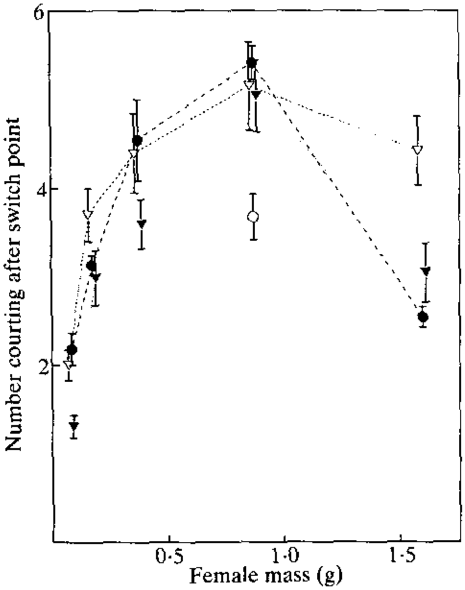

Figure 5. The number of males courting the different sized female after the switch point for the 6, 12, 24 and 48-mg diet levels (symbols as in Fig. 4). Note that at the 6-mg diet level, males were only observed to switch between feeding and courting when provided with females from size class 4.

counter-intuitive if changes in the males' energetic state were not considered: one might expect the value of foraging to be high when more food was available and therefore increase its value relative to courtship. However, as animals become satiated, the cost of not foraging (e.g. the probability of starvation) should decrease, causing an earlier switch to alternative activities, such as courtship. This is analogous to the prediction by McNamara et al. (1987) that male birds should sing more often and earlier in the day as foraging success increases (i.e. more rapid satiation).

Mate choice by guppies has attracted considerable attention in the literature (for recent examples see Kodric-Brown 1985, 1989; Houde 1987, 1988; Houde & Endler 1990; Long & Houde 1989). All of these studies have examined mate choice from the female's perspective and indicate that females prefer males with more yellow, orange and red coloration. The males obtain these colours from carotenoid pigments in their diets (Endler 1983) and are hypothesized to be honest signals of the male's foraging ability and thus his genetic quality. What is more contentious is whether courtship intensity, which may reflect the male's energetic state, affects his ability to successfully court a female (see Farr 1980; Houde 1988). Although this experiment provided no possibility for successful courtship, males were far less willing to engage in courtship at low diet levels than they were at higher diet levels. Furthermore, the onion fly eggs provided to these guppies contained no carotene (Richards & Davies 1977) so that only energetic benefits were provided while feeding. This result is consistent with the explanation that courtship by male guppies is energetically expensive and therefore avoided at low foraging rates.

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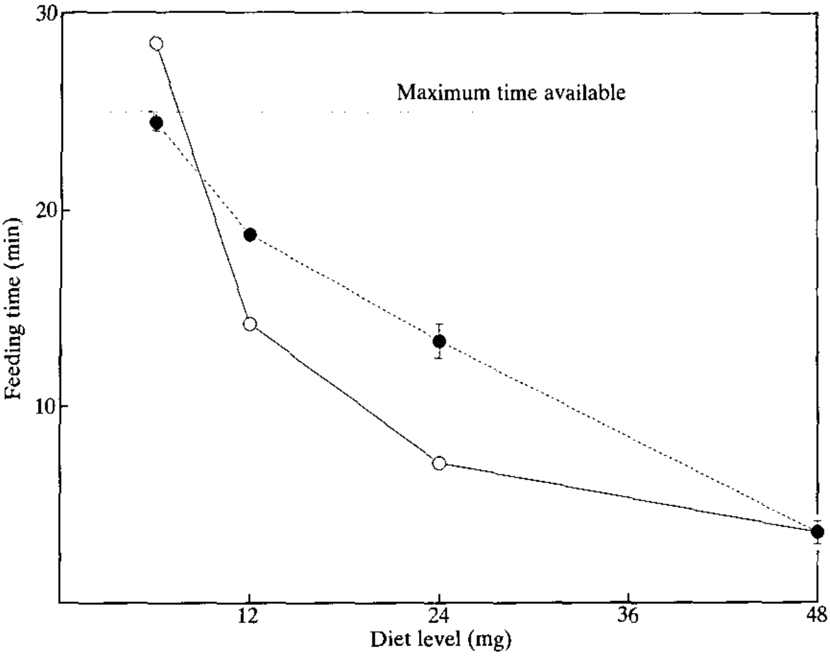

Figure 6. The mean (±SE) observed (●) and predicted (○) length of time that male guppies spent feeding for each diet level. Predicted time spent feeding assumes male guppies consume the same absolute amount of food at every diet level.

experiments. I thank E. Goldberg for her assistance in completing these experiments. L. Dill, M. West and two anonymous referees provided helpful comments on the original manuscript. Financial support was provided by an NSERC operating grant.

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