The effects of resource availability on alternative mating tactics in guppies (*Poecilia reticulata*)

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Food availability can influence the optimal allocation of time and energy among alternative behaviors such as foraging, courting, and competing for mates. If populations differ consistently in food availability, selection may cause geographic divergence in allocation strategies. At the opposite extreme, a norm of reaction may evolve such that food intake influences the allocation strategy of individuals in the same way in all populations. Between these two extremes, food intake reaction norms may diverge genetically among populations. For example, at sites where food is scarce, selection may strengthen the effect of food intake on behavior, whereas at sites with abundant food, selection may be weak or even oppose plasticity. We tested these ideas by raising male guppies from streams differing in food availability in a common laboratory environment on either low or high food levels, and then observing them in the presence of male competitors (from the same population and diet group) and receptive females. Males from low-food-availability streams spent more time foraging than males from high-food-availability streams, independent of food intake. Compared with males raised on the high food level, males raised on the low food level spent more time foraging and were less aggressive towards other males. Courtship display rate increased with food intake but only in males from low-food streams. In contrast, males from high-food streams showed greater plasticity with respect to male-male aggression. These results generally support the resource availability/behavioral tradeoff hypothesis while also revealing a surprising degree of ontogenetic complexity in a relatively simple system. *Key words:* aggression, alternative reproductive tactic, food availability, food intake, guppy, intrasexual competition. *[Behav Ecol]*

Sexually mature animals must distribute finite resources among activities such as foraging, aggressive competition, and courtship. Food intake may affect the optimal partitioning of resources to these behaviors by influencing overall physical condition (Belovsky et al., 1996; Blanckenhorn et al., 1995). Variation in food intake may lead to the evolution of condition-dependent strategies in which individuals exhibit different tactics depending on their energy reserves (Belovsky et al., 1996; Taborsky, 2001; reviewed by Gross, 1996). Aggressive mate-acquisition tactics are particularly risky in terms of energy loss, and also in terms of injury, predation, and missed foraging or courtship opportunities (Brick, 1998; Hack, 1997; Jakobsson et al., 1995; Kelly and Godin, 2001). Thus, the frequency and nature of aggressive interactions can be predicted to vary with the condition of the participants (Spohn and Moore, 1997; Stocker and Huber, 2001). For example, non-territorial male damselflies (*Calopteryx splendens xanthostoma*) either fight for access to territories or wait for a territory to become vacant (Plaistow and Siva-Jothy, 1996). Waiting is far less successful than fighting, but it is the only alternative for males who have insufficient fat reserves to engage in combat.

The study of life history variation along resource availability gradients has contributed to our understanding of how animals allocate finite resources to somatic growth versus reproduction (Bernardo and Agosta, 2003; Guillou and Lumingas, 1999; Reznick, 1983). Resource availability gradients may similarly be exploited to study behavioral tradeoffs (Carroll and Corneli, 1999). Sites with ample food supplies may favor aggressive mating tactics, whereas food-limited sites may instead favor alternative mating tactics. The optimal tactic for a given individual may depend on an interaction between its own food intake and the population average. Aggressive mating tactics should be less energetically costly in high-resource-availability environments because the overall energy budget of males is larger than in low-resource-availability environments. It follows that males should exhibit higher overall levels of aggression in high-resource environments and greater plasticity (i.e., responsiveness to changes in resource availability) in low-resource environments (Komers, 1997). Some attention has been given to the geographic relationship between resource availability and aggression in a foraging context (Dunbrack et al., 1996; Lahti et al., 2002), but very few if any studies have examined the relationship between resource availability and aggression in a mating context.

In this paper, we test predictions of the resource availability/behavioral tradeoff hypothesis in guppies (*Poecilia reticulata*), a species that occurs naturally along a replicated gradient in food availability and in which males exhibit a range of alternative mating tactics. We carried out a common garden experiment in which males from populations differing in food availability were raised from birth on two different food levels in the laboratory. This experimental design permitted us to measure, and distinguish between, three possible effects of food availability on male behavior: (1) evolved (genetic) responses to food availability at the population level, (2) effects of food intake on the behavior development of individual males (phenotypic plasticity), and (3) evolved differences between populations in the plastic response to food intake (genotype by environment interaction). Before presenting specific predictions, we briefly review pertinent information on the study system.

The mating tactics of male guppies, in increasing order of presumed energetic investment, include sneaking copulations without courtship, displaying to females prior to copulation (courtship), and aggressively inhibiting rival males (Farr, 1989; Houde, 1997; Jirotkul, 2000; Kelly and Godin, 2001; Rodd and Sokolowski, 1995). Aggressive tactics range from

jockeying for position next to females, to displaying to, chasing, and biting rivals (Brooks and Caithness, 1999; Houde, 1988). That energetic tradeoffs influence male behavior in the short term has been suggested by food deprivation studies. Abrahams (1993) showed that males switch from foraging to courting in a predictable fashion depending on hunger levels, and Griffiths (1996) found that hungry males spent less time foraging in the presence of females than in their absence. Males raised on chronically low food levels are known to mature later and at a smaller size than males raised on high food levels (Reznick, 1990), but the long-term effects of food availability on male behavior remain unstudied. The objective of our study was to examine the evolutionary and developmental effects of variation in food availability on the full suite of male mating tactics in this species.

Adaptive phenotypic plasticity can reduce or eliminate selection along environmental gradients (reviewed in Price et al., 2003; West-Eberhard, 2003). In the present context, if male mating tactics have evolved to respond plastically to food intake, this could eliminate selection for divergence in mating tactics along the food availability gradient. Conversely, adaptive divergence between populations in response to an environmental factor could eliminate the need for a plastic response to that factor (especially if the environmental gradient is steep). The implication is that we cannot, a priori, make robust predictions about how food availability will affect both the development of and population divergence in mating tactics. Nevertheless, we can make predictions about the direction of these effects, if present. Furthermore, we can predict that if populations have not diverged genetically along the food availability gradient, then food intake should have the predicted plastic effects on mating tactics, and vice versa. With these qualifications, our predictions were as follows:

(1) Genetic divergence predictions. Compared to males from high-resource-availability streams, males from low-resource-availability streams should (a) allocate more time to foraging, (b) sneak copulations more frequently, (c) court less frequently, and (d) engage in less intense male-male aggression.
(2) Plasticity predictions. Compared to males raised on the high food level, males raised on the low food level should (a) allocate more time to foraging, (b) sneak copulations more frequently, (c) court less frequently, and (d) engage in less intense male-male aggression.
(3) Genotype by environment interaction predictions. Compared to males from high-resource-availability streams, males from low-resource-availability streams should be more plastic in their response to food intake in the ways listed above.

METHODS

Study populations

The main source of food for guppies in nature is unicellular algae (Dussault and Kramer, 1981), the abundance of which is largely a function of forest canopy cover. Streams that receive more light have larger standing crops of algae, but not correspondingly higher densities of guppies, than streams that receive less light (Grether et al., 2001). In the high-light, high-resource-availability streams, female and juvenile guppies grow faster, and males mature at larger sizes, than their counterparts in the low-resource-availability streams (Grether et al., 2001; unpublished data).

The fish used in this study were first-generation (G_1) laboratory descendants of fish collected from 8 to 10 pools in each of four streams in the Northern Range of Trinidad in June 2000. The streams were chosen during a survey of several river drainages conducted in the spring of 2000, based on criteria outlined in Grether et al. (2001): (1) intact primary or old secondary growth rainforest; (2) relatively homogeneous forest canopy cover; (3) separated from streams differing in canopy cover or predator assemblage by multiple barriers to guppy dispersal, including two or more waterfalls; and (4) no predatory fish, except *Rivulus hartii*. Among streams meeting these criteria, we chose two streams representing the available extremes in forest canopy cover in each of two stream drainages (Aqui River [high resource] and a small tributary of the Madamas River [low resource] in the upper Madamas drainage [Universal Transverse Mercator Grid coordinates, Zone 20: PS 939.2 886.6, PS 950.1 880.0]; Small Crayfish River [high resource] and Large Crayfish River [low resource] in the upper Quare drainage (PS 970.7 835.2, PS 696.5 832.2]). As in Grether et al. (2001), our goal was to compare guppy populations exposed to different levels of canopy cover, and thus resource availability, without the potentially confounding effects of phylogenetic divergence between drainages and differential predation.

To maximize the genetic diversity of fish used in the experiment, we obtained offspring for the G_1 generation from approximately 120 (25 to 35 per population) wild females. This represents a potentially much larger number of sires, because females mate multiply in the wild and can store sperm for up to 8 months (Winge, 1937).

Food level manipulation

The laboratory populations were housed at the University of California, Los Angeles campus in a temperature-controlled (24.0 ± 1.5°C water temperature) room at 12 : 12 h photoperiod (mixed daylight spectrum fluorescent and incandescent light). To prevent the guppies from eating algae, we treated the water in their housing aquaria and in the observation aquaria with 2-chloro-4, 6-bis-(ethylamino)-s-triazine (Algae Destroyer, Aquarium Pharmaceuticals, Chalfont, Pennsylvania, USA) and removed any visible algae regularly. Wild-caught females were individually housed in 8-l tanks, fed a standard diet of commercial flake food (Tetramin or Tetra Spirulina, depending on the day of the week; Tetra, Blacksburg, Virginia, USA) twice per day (once per day on weekends) and allowed to give birth. Newborn G_1 fish were housed in 8-l plastic tanks in mixed-sex broods at densities of 1–6 fish per tank. Each tank potentially contained offspring from multiple females, but offspring did not vary in age by more than 14 days.

Newborn fish were randomly assigned to either the low-food or the high-food treatment. Within each treatment, food amounts were adjusted to the age and density of fish in the tank and were increased as the fish aged, as described below. The high food level was approximately as much as guppies of a given age are willing to eat on a twice-daily feeding schedule, and the low food level was one-third that amount. As the fish aged, we increased food levels every 2–3 weeks. On average, the low food levels were increased by 12.6% per week over the first 20 weeks, by 4.7% per week over weeks 21–40, by 3.2% over weeks 41–60, and by 1.5% after week 61 until their use in observations. The comparable numbers for the high food level are 10.8%, 5.5%, 3.2%, and 1.5%. Because male guppies essentially stop growing after reaching sexual maturity (Snelson, 1989), we did not increase male food levels after 20 weeks of age. The diets met the standards of all high-quality commercial fish feeds for tropical fish and consisted of a mixture of spray-dried white fishmeal (41.8%), wheat-flour (47%), vegetable oil (2.0%), vitamin premix (1.0%), and gelatin (8.1%). The estimated protein content was 40% and the fat content was 10% (Lamon M, personal communication,

2001). The food level treatment resulted in significant differences in male size in males from all four populations (ANOVA for standard length [SL]; population, $F_{3,337} = 1.73$, $p = .16$; food level, $F_{1,337} = 223.3$, $p < .0001$; population × food level, $F_{3,337} = 0.88$, $p = .45$; Figure 1).

Fish were sexed under a dissecting microscope well before sexual maturity, at either 13–15 weeks of age (low food) or 10–12 weeks of age (high food). We anesthetized fish using MS222 and looked for black pigment spots near the gonopore (females) and skin iridescence or the beginnings of gonopodial development in the anal fin (males). After sexing, males were housed in 8-l tanks at densities of 1–4 males per tank, and females were housed in 38-l tanks at initial densities of 20 fish per tank (densities of females gradually decreased as they were used in the observations). To allow males to have courtship experience, we housed one mature stock female with each male group for at least 7 days prior to focal observations. Females used in the experiment remained virgins until they were used in focal observations.

Focal male observations

We used an open-aquarium design (Grether, 2000; Houde, 1997) in which males and females could interact with each other during the observations. This design allowed us to simultaneously examine male aggressive, courtship, and foraging behavior. Observations were conducted in 180-l aquaria with natural, multicolored gravel bottoms and plastic bubblers connected to undergravel filters. Three such observation aquaria were in operation at once; when possible males from different populations in the same drainage were tested simultaneously. We conducted the tests in a windowless room maintained on the same light : dark schedule as the lab. The observation aquaria were covered with brown paper on three sides, and observations were made from the fourth side. Each aquarium was illuminated from the top with one daylight-spectrum fluorescent tube. Otherwise, the room was dark, to maximize the visibility of the fish to the observer and to minimize the visibility of the observer to the fish.

To minimize the effects of competition for food on aggressive interactions (Dunbrack et al., 1996; Magurran and Seghers, 1991), we regularly removed visible algae from the observation aquaria. In addition, we fed the fish ad libitum twice per observation day (15 min prior to the first focal observation and immediately after the second focal observation; we conducted three focal observations per male; see below). This allowed us to examine the effects of lifetime food intake without the potentially confounding effects of short-term hunger levels. We filtered the water in the aquaria using a high-flow-rate charcoal canister filter (Marineland Magnum 350 convertible canister filter, Moorpark, California, USA) after each set of observations, to minimize chemical effects (Crow and Liley, 1979) on the behavior of fish in subsequent observations. To minimize laboratory effects on aggressive behavior, we used first generation descendants of wild-caught fish, an even sex ratio (3:3), very low densities of fish per observation tank (Houde, 1997; Magurran and Seghers, 1991), and males that had not been housed together (Grether, 2000; Houde, 1997). We also attempted to minimize body size disparities within male and female groups. Male groups consisted of three individuals from the same population raised on either low or high food, whose relatedness to each other was unknown but who were no more than 14 days apart in age. Female groups consisted of three mature virgins from the same population as the males. The females were housed out of sight of mature males until they were used in the observations, so that their behavior could not be influenced by prior experience with mature males (Grether, 2000).
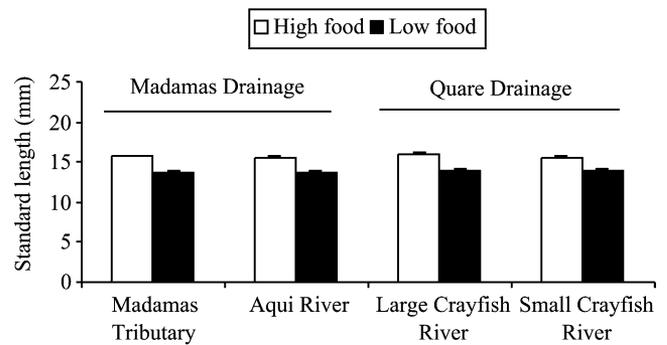

Figure 1
Standard lengths of male guppies from four Trinidad populations reared in the lab on the two food levels. In the Madamas drainage, Madamas Tributary ($n = 78$) is the low-resource-availability stream and Aqui River ($n = 90$) is the high-resource-availability stream. In the Quare drainage, Large Crayfish River ($n = 90$) is the low-resource-availability stream and Small Crayfish River ($n = 87$) is the high-resource-availability stream. Means +1 SE are shown (except where the SE is too small to be shown).

A trial was initiated by releasing the three males chosen for testing into the observation aquarium between 0930 and 1100 h, after their color patterns were studied and sketched. Males were chosen based on body size similarities and not based on color patterns. Male guppies (even full siblings) usually differ in the location or presence of color spots, and we therefore had no trouble differentiating males based on their color patterns. Females were released into the observation aquarium shortly after the males. The fish were then fed. On the following morning, the fish were fed again and the first observation session began at least 15 min after the feeding, between 0930 and 1100 h. We performed at least three replicate focal observations of 5 min per male, alternating between males in a predetermined, random order. A minimum of 20 min elapsed between consecutive focal observations on a given male. Behavioral observations were recorded on a Macintosh PowerBook 1400cs computer using an event recorder program written in TrueBASIC Silver Edition (code available from G. F. Grether upon request). We conducted observations on a total of 345 males (Quare drainage: 177 males, Madamas drainage: 168 males) and an equal number of females. Immediately following their use in observations, males were weighed to the nearest 0.1 mg and their SL (the length from the anterior-most portion of the jaw to the caudal peduncle) was measured using digital calipers (± 0.01 mm readout).

We recorded the time spent foraging, following females, and engaging in interference competition (two or more males simultaneously displaying to or following the same female). We also recorded the rates of sigmoid courtship displays, sneak copulations (forced copulation attempts not preceded by display, in which gonopodial contact with the female's ventral surface was visible), dominance interactions (supplanting, displaying, chasing, or biting directed from one male to another while neither was following or courting a female), and escalation of interference competition and dominance interactions to displays, chases, or bites between males. Dominance interactions were usually distinctly one-sided and thus one male could be classified as dominant and the other as subordinate.

Data analysis

We constructed separate ANOVA models to examine the proportion of time males spent foraging, following females,
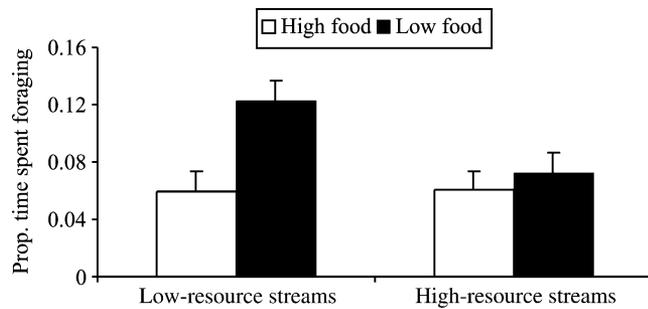
Figure 2
Proportion of time spent foraging during focal male observations by males raised on the two food levels, from low- and high-resource-availability streams ($n = 345$). Means +1 SE are shown. See Table 1 for the results of statistical analysis of these data.

Table 1

Analysis of variation in male guppy foraging behavior as a function of male food level, stream resource availability, and male group

	Time spent foraging
Food	$4.75_{1,337}$; .03
Resource availability	$4.82_{1,337}$; .03
Food × resource availability	$1.72_{1,337}$; .19
Male group (food, resource availability)	$0.20_{4,337}$; .94

Means are shown in Figure 2. Values are F_{df}; p. Degrees of freedom (df) were calculated using the Satterthwaite method and rounded to the nearest integer.

and competing, and the frequency of sigmoid courtship displays, sneak copulations, and dominance interactions. We also examined the proportion of competition and dominance interactions that escalated to chases and/or bites between males. For all of the analyses, food level (in the laboratory) and stream resource availability (in the field) were treated as fixed-effect terms, and male group (the group of three males observed together) was included as a random effects term nested within stream resource availability and male food level.

Although we used a constant density of fish and minimized size differences between males during the behavior tests, the behavior of the males could have been influenced by the size distribution or density of fish in the housing tanks. To determine whether it was important to take these variables into account, we constructed two ANCOVA models for each dependent variable, one including the SL and standard deviation (SD) of standard-length of males within an observation group as covariates, and the other including housing density as a covariate. None of the covariates in these models was significant (male SL: all $p > .052$; SD in male SL: all $p > .19$; housing density: all $p > .22$ with the exception of the sneak copulation rate model, $p = .050$ prior to correction for multiple tests). Therefore, we present the results of analyses excluding male size and housing density.

We also considered the age of males during the behavior tests as a covariate and included age in the final models if warranted (males ranged in age from 19 to 113 weeks). In the initial models, we included age (i.e., the mean age of males in a group) as a covariate if it correlated significantly with the dependent variable. The following variables were not correlated with age: time spent foraging, time spent following females, and the proportion of competition interactions and dominance interactions that escalated to chases and bites (all $r < .10$, all $p > .07$). The following variables were correlated with age: courtship display rate ($r = -.17$, $p = .0023$), time spent in interference competition ($r = -.22$, $p = .0001$), sneak copulation rate ($r = .19$, $p = .0004$), and dominance interaction rate ($r = .18$, $p = .0008$), and we therefore included age as a covariate in the initial models for these variables. Because of chance differences in the males available for use in the observations, males from low-resource streams were older than males from high-resource streams (ANOVA; resource availability: $F_{1,329} = 5.11$, $p = .02$; food level: $F_{1,329} = 0.18$, $p = .67$). Therefore, for the dependent variables that were correlated with age, we used a truncated data set of males ranging in age from 37 to 77 weeks in the analyses. For sneak copulation rate and dominance interaction rate, the assumptions of ANCOVA were met (Tabachnick and Fidell, 2001), and we constructed models including age as a covariate. These analyses revealed no significant age effect (sneak

copulation rate: $F_{1,299} = 0.20$, $p = .66$; dominance interaction rate: $F_{1,299} = 1.38$, $p = .24$). Therefore, we present analyses excluding the age covariate. For courtship display rate and time spent in interference competition, the data violated the assumption of homogeneity of regression slopes, and we instead employed a model with age as a categorical variable (Tabachnick and Fidell, 2001) with three levels, young (37–48 weeks), medium (49–56 weeks), and old (57–77 weeks). This analysis for courtship display rate revealed no significant age category term ($F_{2,276} = 1.81$, $p = .17$). Therefore, we present the analysis for this model excluding an age term.

All data were square-root transformed prior to analysis to meet parametric assumptions. We corrected for multiple tests within distinct categories of variables (courtship behavior, interference competition, and dominance interactions) using Bonferroni corrections. All analyses were conducted using JMP 3.2.2 (SAS Institute, Inc., Cary, North Carolina, USA).

RESULTS

Male age and behavior

After truncating the age distribution to eliminate age differences between treatment groups (as described above), two variables were negatively correlated with age: courtship display rate ($r = -.24$, $p < .00001$) and time spent in interference competition ($r = -.29$, $p < .00001$). For time spent in interference competition, there was a significant effect of age category ($F_{1,276} = 4.27$, $p < .00001$) and a significant age category × food interaction term ($F_{2,276} = 8.02$, $p = .0004$) that resulted because time spent in competition decreased with age for high food males but was relatively unaffected by age for low food males.

Genetic divergence in behavior

Males from the low-resource streams foraged more than males from the high-resource streams (Figure 2; Table 1). There was no significant effect of population resource availability on the other behaviors (Tables 2 and 3).

Plasticity in behavior

Males from the low-food treatment allocated significantly more time to foraging than males from the high-food treatment (Table 1; Figure 2). There was no significant effect of the food treatment on sneak copulation rate, courtship display rate (Figure 3A), or time spent following females (Figure 3B; Table 2). Low-food males from the high-resource streams spent more time in interference competition than high-food males (Table 3; Figure 4A); however, high-food males escalated to chasing and biting significantly more frequently than low-food males (Figure 4B). High food males also engaged in dominance interactions significantly more

frequently than low food males (Table 3; Figure 5). However, the proportion of dominance interactions that escalated to chasing and biting did not differ significantly between food treatment groups.

Genotype by environment interactions

There was a significant food × resource availability interaction for courtship display rate, caused by the greater effect of the food treatment on males from the low-resource streams than on males from the high-resource streams (Figure 3A). There was also a significant food × resource availability interaction for time spent competing and dominance interaction rate (Table 3; Figures 4 and 5), because males from the high-resource streams responded to the food treatment more than males from the low-resource streams.

DISCUSSION

Food intake strongly influenced the foraging and reproductive behavior of male guppies from the streams we examined. Males raised from birth on the low food level spent more time foraging, and were less aggressive in a mating context, than their high food counterparts. This suggests that males with reduced access to food plastically alter their behavior to facilitate future reproduction (by foraging) at the expense of current reproduction (Abrahams, 1993; Siems and Sikes, 1998). We found some evidence for genetic divergence among populations: males from low-resource streams spent more time foraging than males from high-resource streams. In addition, we observed differences in the degree to which males from different streams altered their behavior in response to food intake (i.e., genotype by environment interactions). The change in courtship display rate in response to food intake was greater for males from the low-resource streams than for males from the high-resource streams, suggesting that males from low-resource streams are better able to adjust their mating effort in response to food intake. For time spent competing and dominance interaction rate, the pattern was reversed, and males from high-resource streams were more plastic in their response to food intake.

Our results support other studies showing a direct impact of male food intake on the frequency and nature of male mating behavior (Engqvist and Sauer, 2003; Plaistow and Siva-Jothy, 1996). Male guppies raised on the low food level engaged in less frequent escalated interference competition and dominance behavior than males raised on the high food level, suggesting either that males facultatively adopted aggressive mating tactics based on their body condition, or that aggressive mating tactics entailed energetic costs that low-food males were unable to bear. Interestingly, the food treatment did not directly influence other aspects of reproductive behavior (time spent following females, sneak copulation rate, courtship

Table 2

Analysis of variation in male guppy mating behavior as a function of male food level, stream resource availability, and male group

	Sneak copulation rate	Sigmoid courtship display rate	Time spent following females
Food	$0.004_{1,304}$; .95	$0.29_{1,292}$; .59	$2.05_{1,337}$; .15
Resource availability	$0.68_{1,304}$; .41	$0.11_{1,292}$; .74	$0.17_{1,337}$; .68
Food × resource availability	$0.08_{1,304}$; .77	$7.58_{1,292}$; .006	$0.29_{1,337}$; .59
Male group (food, resource availability)	$4.17_{4,304}$; .003	$1.75_{4,292}$; .14	$1.25_{4,337}$; .29

Means are shown in Figure 3. Values are F_{df}; p. df were calculated using the Satterthwaite method and rounded to the nearest integer. With Bonferroni correction for three tests, $\propto$ corrected = 0.017.

display rate), so that the investment into reproductive strategies depended on the behavior involved. Similarly, increased risk of predation reduces aggression, but not courtship or copulation activity, in male guppies (Kelly and Godin, 2001). Presumably, aggressive mating tactics are the most labile because they are less implicitly connected with reproductive success than courtship and copulation.

Aggressive mating tactics are also thought to be more costly than other reproductive behaviors (Hack, 1997; Jakobsson et al., 1995). Males exhibit aggressive mating tactics more frequently when competition for females is intense, such as when densities are high (Jirotkul, 1999b) or when operational sex ratios are more male-biased (Jirotkul, 1999a; Souroukis and Cade, 1993). We found that older males and males with restricted food intake were less likely to be aggressive, consistent with the idea that fighting to gain access to females is only profitable for some males under some conditions. Empirical studies of guppies have been equivocal about the relationship between aggression and reproductive success (Brooks and Caithness, 1999; Gandolfi, 1971; Gorlick, 1976; Houde, 1988; Kodric-Brown, 1993), possibly because different researchers have studied different populations. Controlled studies of multiple, non-domesticated guppy populations are needed to determine the benefits associated with aggressively competing for females in this species.

One of the goals of the present study was to generate predictions for field differences in behavior between males in low-resource versus high-resource streams. Field observations would also address whether aggressive behavior is an artifact of lab settings (e.g., Bruce and White, 1995; Gorlick, 1976; Houde, 1997). Unlike territorial fish species (Forsgren et al., 1996; Giles and Huntingford, 1984), guppies do not usually

Table 3

Analysis of variation in male guppy aggressive behavior as a function of male food level, stream resource availability, and male group

	Time spent competing	Proportion of competitions that escalated to chases/bites	Dominance interaction rate	Proportion of dominance interactions that escalated to chases/bites
Food	$7.37_{1,276}$; .007	$5.21_{1,328}$; .02	$15.75_{1,304}$; < .001	$1.68_{1,80}$; .20
Resource availability	$0.32_{1,276}$; .57	$1.18_{1,328}$; .28	$3.15_{1,304}$; .08	$1.53_{1,80}$; .22
Food × resource availability	$11.39_{1,276}$; .0008	$0.29_{1,328}$; .59	$7.41_{1,304}$; .007	$0.45_{1,80}$; .50
Male group (food, resource availability)	$1.93_{12,276}$; .032	$1.71_{4,328}$; .15	$12.08_{4,304}$; < .0001	$2.75_{4,80}$; .034

Means are shown in Figures 4 and 5. Values are F_{df}; p. With Bonferroni correction for four tests, $\propto$ corrected = 0.0125. The analysis for time spent competing included an age term. df were calculated using the Satterthwaite method and rounded to the nearest integer.
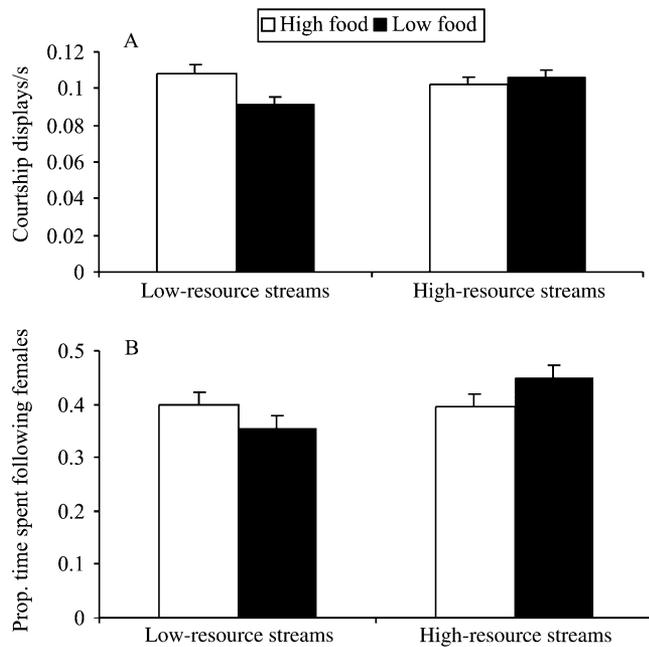
Figure 3
Courtship display rate (panel A; $n = 300$) and proportion of time spent following females (panel B; $n = 345$) during focal observations of male guppies from low- and high-resource-availability streams raised on the low and high food levels. Means +1 SE are shown. See Table 2 for the results of statistical analysis of these data.

defend areas of a stream and do not form distinct dominance hierarchies in the wild, leading to the argument that overt aggression may be uncommon and unimportant for reproductive success in nature (Brooks and Caithness, 1999; Farr, 1975,
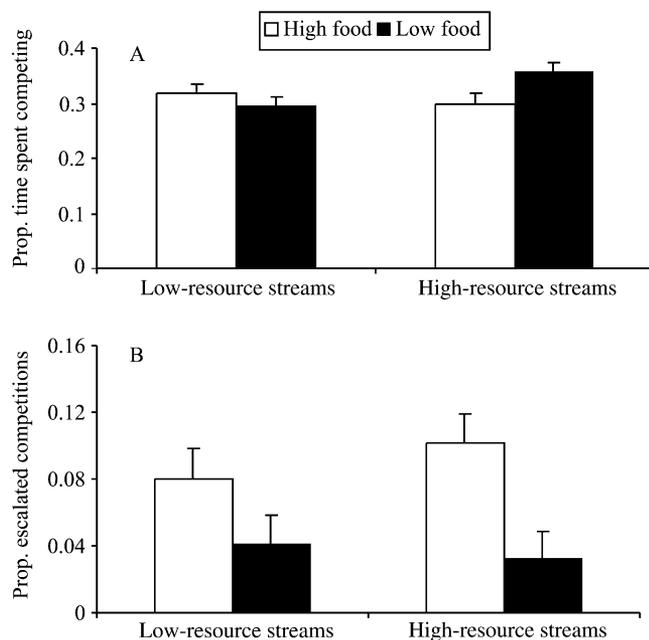

Figure 4
Proportion of time spent in interference competition interactions (panel A; $n = 300$) and proportion of competitive interactions that escalated to chases/bites (panel B; $n = 336$) as a function of food level for male guppies from low- versus high-resource-availability streams. Means +1 SE are shown. See Table 3 for the results of statistical analysis of these data.
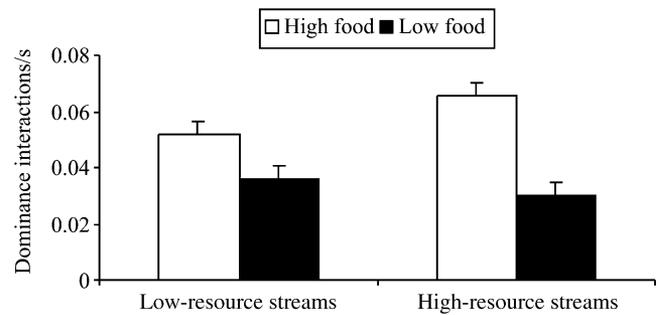

Figure 5
The rate of dominance interactions observed in focal observations, in relation to male food level and resource availability ($n = 312$). Means +1 SE are shown. See Table 3 for the results of statistical analysis of these data.

1989; Houde, 1988). However, female guppies are only receptive for a few days of each reproductive cycle, and they indicate their receptivity chemically (Crow and Liley, 1979). Therefore, the operational sex ratio within a pool is often male-biased (Houde, 1997), and several males may attempt to court the same female, leading to aggressive interference (Brown and Godin, 1999; Farr, 1989; Jirotkul, 1999a). In addition, the frequency and significance of aggression may vary with environmental conditions (Brooks and Caithness, 1999; Rodd and Sokolowski, 1995), and studies of low-predation populations suggest that aggression may be important (Ballin, 1973; Kodric-Brown, 1992, 1993; but see Houde, 1988). Based on the results of our lab study, we predict that males in low-resource guppy streams will allocate more time to foraging and engage less frequently in escalated interference competition and dominance interactions than males in high-resource streams.

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