NIGHT FEEDING BY GUPPIES UNDER PREDATOR RELEASE: EFFECTS ON GROWTH AND DAYTIME COURTSHIP

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Abstract. The nonlethal effects of predation threat can be pervasive but are also easily overlooked. We investigated effects of predation threat on feeding by guppies (*Poecilia reticulata*), and how threat-induced temporal shifts in feeding activity affect reproductive behavior and growth. Contrary to the view of the guppy as a ''diurnal'' species, our observations revealed that guppies free from severe predation threat expand their foraging into the nocturnal period. We found such nocturnal foraging to be as profitable as diurnal foraging, and guppies under threat incurred a substantial growth penalty when predators inhibited night feeding. Denial of night feeding also decreased daytime courtship by males, facultatively duplicating a classical observation comparing courtship intensity in contrasting predator regimes, but providing a novel mechanism for the effect. Our findings support the view that evaluations of predator effects on life histories should consider potential predator-caused alterations in size-specific energetic gain, along with the classical consideration of predator-altered mortality rates. The results of this study show that predation threat can induce a large, facultative shift in the temporal niche and vital rates of a prey species. We discuss some implications of the effect in the broader contexts of predator facilitation, evolution of life histories, and trait-dependent decisions to boost daily intake by expanded feeding times.

Key words: activity rhythms; courtship; Crenicichla alta; *diel migration; growth; guppy;* Hoplias malabaricus; *life history; nonlethal predation effect;* Poecilia reticulata; *predation; predator facilitation; Trinidad.*

INTRODUCTION

Animals have behavioral control of where and when to forage, and it has become axiomatic that predation threat plays a prominent role in shaping use of space and time by foraging animals (e.g., Kerfoot and Sih 1987, Houston and McNamara 1999, Kotler et al. 2002). However, while a substantial literature with experimental manipulations of predators documents predator-induced spatial shifts, evidence for predators' effects on the use of time (the temporal niche) has been somewhat more correlational and speculative (Lima and Bednekoff 1999, Reebs 2002). Here we explore a predator-induced, large shift in a prey species' temporal niche, asking whether it is facultative, whether it has implications for growth on a given resource base, and whether expansion of feeding into night hours has implications for a second behavioral trait, reproductive behavior observed during the day.

Our study species is the guppy, *Poecilia reticulata*, which has provided a model system for the study of the evolutionary and behavioral ecology of predation, yielding many studies that contrast fish from ''low predation'' vs. ''high predation'' sites in the rivers of Trinidad's Northern Range Mountains (see Plate 1) (Endler 1995, Houde 1997). In apparently all of these studies, the guppy has been viewed as a ''diurnal'' species regardless of the predation regime. Using the diurnal species paradigm, observations on daytime feeding, courtship, and other activities have been interpreted as different solutions to the trade-off among competing demands of feeding, courting, and avoiding predators within the daytime time budget (Houde 1997). Similarly, differences in growth rates have been interpreted as reflecting different resource availability among pools (Grether et al. 2001) and between predation regimes, with minor if any suppression of growth by the predator at a given resource level, as guppies feed vigorously in the daytime under both predation regimes (Reznick et al. 2001).

However, we report here that the diurnal paradigm is incomplete, as release from predation pressure can be accompanied by a pronounced expansion of feeding by the guppy into nocturnal periods. Specifically, we (1) explore the phenomenon of expanded feeding times under predator release in a natural stream; (2) evaluate

PLATE 1. Shallow edge habitat, typical of streams in the Northern Range Mountains of Trinidad, afford guppies and other taxa protection from piscivores inhabiting the main stream. Photograph by Douglas F. Fraser.

the relative efficacy of day and night feeding via an experiment in which guppies were denied night feeding, day feeding, neither, or both; (3) ask whether manipulation of a predator's presence facultatively alters growth of guppies taken from a common source; and (4) ask whether male guppies from a common source facultatively alter the time they allocate to daytime courtship in response to experimental denial of the opportunity for night feeding, simulating the energetic effect of predation threat without confounding that effect with the presence or absence of the predator in the daytime. We then discuss implications of these findings with regard to previous studies on evolution of behavior and life history under contrasting predation regimes.

METHODS

Sites, taxa, and field methods

We observed guppy foraging and courtship behavior in two river drainages in the Northern Range Mountains of Trinidad, West Indies. Study sites in Ramdeen Stream, a small, forested tributary of the Arima River fully described in Fraser and Gilliam (1992) and Dugatkin and Godin (1992), consisted of pools in an upstream, predator-released and a downstream, predator-threatened, section of the stream. The principle piscivore in the predator-threatened, lower reaches of Ramdeen Stream is *Hoplias malabaricus*. Weaker predators, the killifish *Rivulus hartii*, freshwater eel *Synbranchus marmoratus*, and the catfish *Rhamdia sebae*, are also present. Study sites in the Guanapo River (Gilliam and Fraser 2001), contain *Hoplias* below but not above a barrier waterfall, while the weak predators occur throughout both study areas.

Day–night observations

To facilitate observations in the two predator zones of Ramdeen Stream, we used enclosures made of window screen (0.1 m deep × 0.4 m wide × 0.4 m long) established along a shore of each observation pool. We

stocked three guppies of each sex, collected from the observation pool, into each enclosure. Day and night observations were both made by lying quietly on a bank <0.5 m above the observation enclosure. We observed focal females, recording the number of feeding bites during 5-min observation intervals. For night observations we used a hand-held night vision scope (Litton Electro-Optical Systems, Tempe, Arizona, USA). At the Guanapo River sites, we used the same procedure as at Ramdeen Stream except that guppies were unenclosed and observed only at night. For the Guanapo guppies we compared untransformed bites per minute, taken by different individuals, in the two predator treatments (no predator zone vs. predator zone), by an independent *t* test with unequal variances. At Ramdeen Stream, guppies were restocked daily at the end of the evening observation period. Hence, the same individuals were observed in both day and night the following day. For these we used the *t* test to compare only night feeding rates in the two predator treatments. Because multiple observations were made on each individual, we used only the first night observation for each of the three females. Data were taken for three days/nights in Ramdeen Stream and two nights in the Guanapo River.

Efficacy of day–night feeding

Night feeding, while present under predator release, might nonetheless be ineffective relative to daytime feeding. To isolate the efficacy of night and day feeding, we measured growth of guppies from Ramdeen Stream in a 2 × 2 factorial design: day + night feeding (14 h, 10 h), day only (14 h, 0 h), night only (0 h, 10 h), and fasted (0 h, 0 h), in flow-through, independent compartments (0.75 m long × 0.30 m wide × 0.1 m deep) of six experimental streams located on a bank of Ramdeen Stream (Fraser et al. 1995). Water was delivered to the units from a nearby first-order stream by pipes, and each unit received its own independent water supply. Each unit contained natural gravel/mud substrates.

To fully isolate night feeding, we confined and released guppies before sunrise and after sunset, 0500 hours and 1900 hours, respectively, hence including crepuscular periods in the day treatment. We stocked three mature female guppies, taken from a nearby stream, into each experimental unit and manipulated feeding time by confining guppies in 3.8-L plastic bags; e.g., fish allowed only day feeding were held in bags every night (10 h) for 8 d, while fish allowed only night feeding were held in bags every day (14 h). Fish allowed 24 h of feeding were netted and bagged each day, but then immediately released. Prior to weighing at the beginning and end of 8 d fish were held in individual containers for 6 h to empty guts. The experiment was simultaneously replicated four times. Growth was analyzed as the instantaneous change in mass ([ln(final mass) − ln(initial mass)]/8 d) in a two-way ANOVA.

Growth under predation threat

The hypothesis that guppies increase their daily intake in the absence of predation threat predicts that manipulation of predator abundance should produce changes in guppy growth rate. We evaluated this prediction directly by measuring growth of guppies from a common genetic source, the *Hoplias*-occupied section of Ramdeen Stream. Using guppies from one source to measure growth under contrasting predator treatments avoids the issues of evolved genetic differences that would apply to measuring growth in established field populations without the experimental manipulation. We created six pairs (blocks) of stream pools, 1.0 m wide × 1.5 m long, in the experimental stream facility, with each block consisting of a predator free pool paired with a pool containing *Hoplias* (total lengths 149–170 mm). Stream pools were flanked by shallow cobbled edges affording refuge for guppies. Each stream pool received its own independent water supply piped from a first-order tributary. We used female guppies, 11.8–16.8 mm standard length, and stocked each pool with 10 individuals at a density of 6.7 guppies per m², which is equivalent to natural densities reported for low predation localities (Reznick et al. 2001). Guppies were weighed and standard lengths measured at the beginning and end of 19 d. Individuals were uniquely marked by injection with a dot of elastomer (Gilliam and Fraser 2001). Instantaneous growth rates were analyzed by a general linear model (GLM) with one fixed factor (predator present or absent), one random factor (block), and one covariate (initial mass).

Effect of night feeding on diurnal courtship and feeding by males

Previous studies have contrasted courtship by males in or from low predation and high predation sites, and the emphasis on interpretation of differences has been on daytime predation threat (Houde 1997). We asked whether restricted night feeding would facultatively al-

ter male behavior in the daytime, an important phenomenon for interpretation of field patterns and perhaps laboratory feeding protocols, if true. We tested for this effect in Ramdeen Stream by establishing 8 observation enclosures made of window screen (0.1 m deep × 0.4 m wide × 0.4 m long) along both shores of a stream pool, with two treatments, 12-vs. 24-h feeding, alternating between enclosures. We stocked three adult females and two adult males into each enclosure. Guppies were collected from a nearby tributary lacking *Hoplias*. Guppies in four enclosures were night-fasted (12-h feeding) by confining them in clear plastic bags from 1830 to 0630 hours. At 1830 hours all guppies were captured, but only those in the 12-h feeding treatment were retained in bags overnight. We observed feeding and courtship from the stream bank, recording the amount of time each male tended a female, i.e., orientation toward a female and usually within one female body length, and the number of bites taken by each during a 3-min observation period. We made these observations during three time periods, early morning (0630–0830 hours), midday (0900–1500 hours), and late day (1600–1800 hours). We repeated the observations on the same fish over the next five days. We analyzed the time males spent tending females and the number of bites taken in 3-min intervals by repeated-measures ANOVA.

RESULTS

Fig. 1A and B illustrates the phenomenon of predator-restricted feeding by the guppy. Previously we found that guppies shifted to extreme pool edges at dusk if the predator *Hoplias* was present, but not otherwise (Fraser and Gilliam 1992). Our new finding, using night vision scopes in Ramdeen Stream and the Guanapo River, is that such shifts are accompanied by complete or near cessation of feeding in localities containing *Hoplias*. In contrast, guppies in low predation localities did not hide at the margins, but continued to feed (Ramdeen Stream, $t = 3.99$, df $= 8$, $P = 0.004$; Guanapo River, $t = 2.43$, df $= 11$, $P = 0.033$). If night feeding is energetically rewarding, the removal of night feeding in the predator's presence may significantly alter resource acquisition.

Fig. 2 shows that night feeding was rewarding to the guppies, as guppies allowed to feed at night grew significantly faster than those denied night feeding (ANOVA: $F_{1,12} = 7.407$, $P = 0.019$). Day feeding was also effective ($P = 0.002$), and the contributions of day and night feeding were additive (no significant interaction term, $P = 0.64$). Further, an hour of day feeding and an hour of night feeding were about equally beneficial, e.g., compare day vs. night only in Fig. 2. Feeding within the 10-h night period increased the instantaneous growth rate by an increment of ~0.0057 per day, i.e., ~0.57% of body mass per day (instantaneous growth units are [gram per gram]/day, i.e., one per day), while the 14-h day feeding period increased growth by
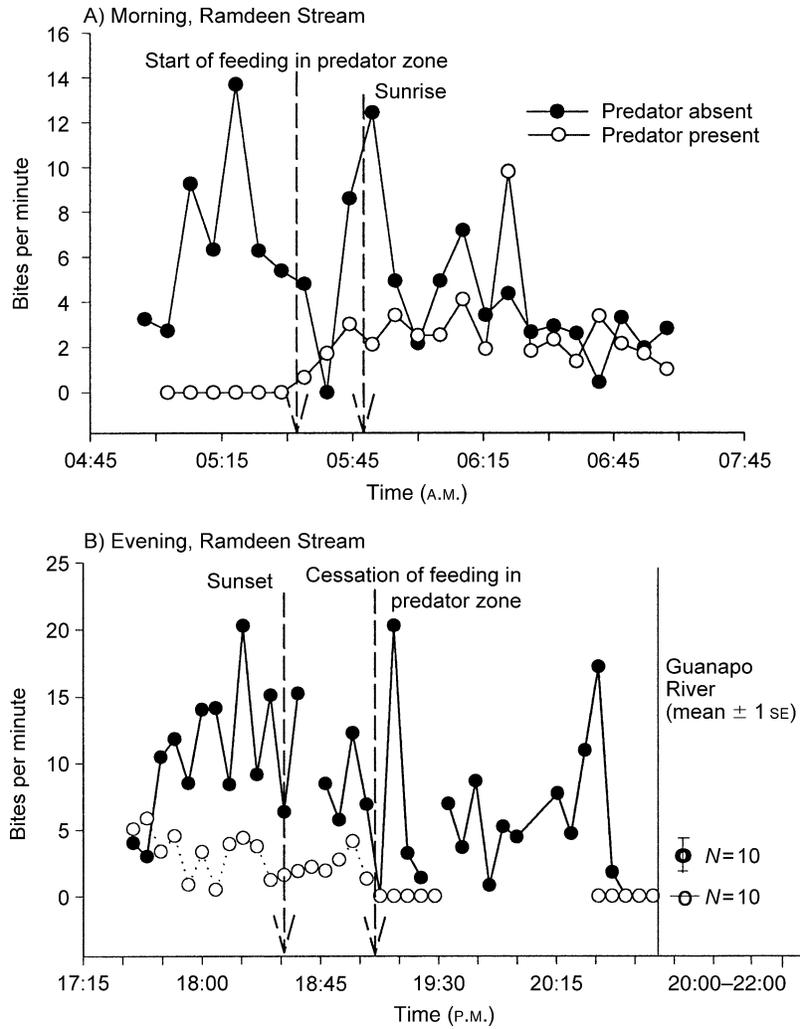
FIG. 1. (A) Morning feeding time budgets of female guppies in Ramdeen Stream in the presence and absence of the predator *Hoplias*. (B) Evening feeding in Ramdeen Stream and, at far right, the Guanapo River. The start and cessation of feeding by guppies in the predator zones (dashed arrows) occur, respectively, shortly before sunrise and shortly after sunset.
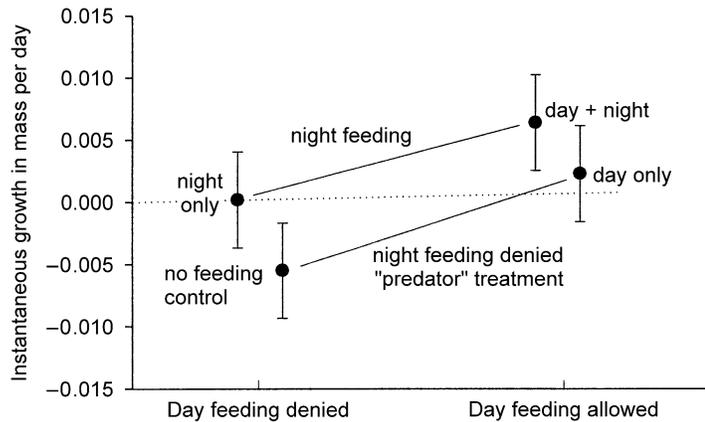
FIG. 2. The effect of night feeding on the growth rate of guppies. Vertical bars are 95% confidence intervals. Night feeding was efficacious, as the growth of guppies in night-only and day-only treatments were almost identical.
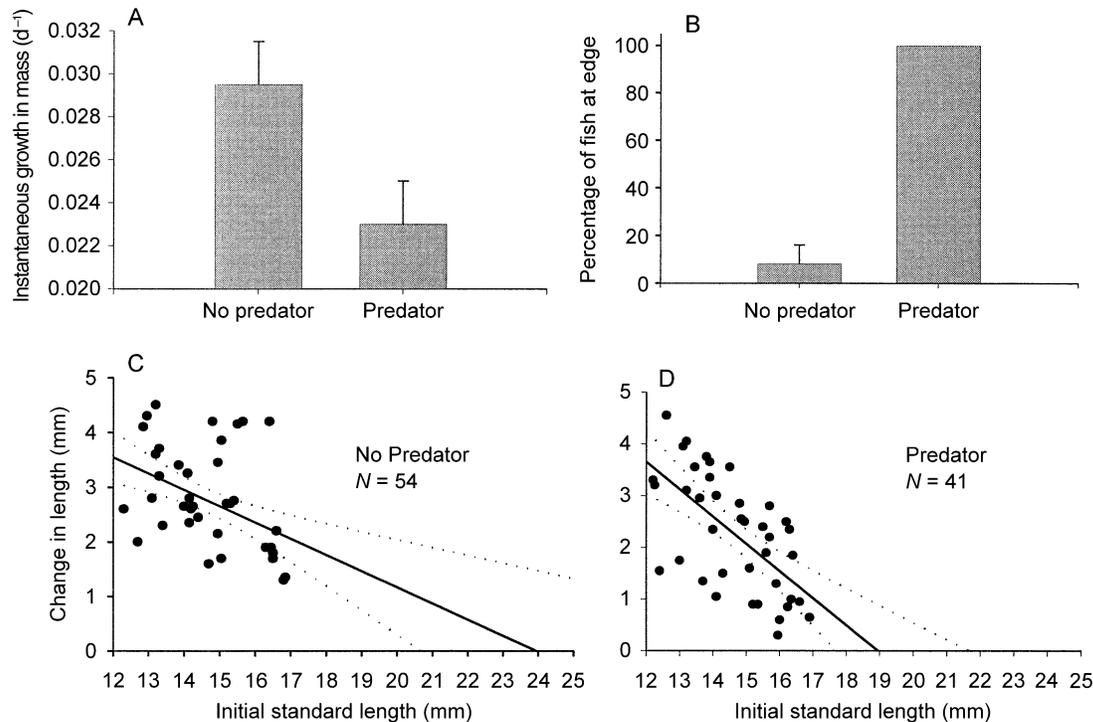
FIG. 3. The experimental effect of the predator *Hoplias* on (A) growth rate of guppies and (B) distribution of guppies in experimental pools at night. Vertical bars are 95% confidence intervals. (C, D) The depressive effects of *Hoplias* on growth were size-specific, impacting larger guppies disproportionately.

~0.0078 per day, a remarkably similar contribution of growth per hour of feeding. Observations made with a night vision scope confirmed that guppies were feeding in all parts of the experimental units at night, as in the daytime.

These findings of predator-influenced night feeding and the efficacy of night feeding suggest that a manipulation of predator abundance should produce changes in guppy growth rates. The presence of *Hoplias* in stream pools resulted in a significant reduction of growth in mass of guppies as compared with guppies in *Hoplias*-free pools ($F_{1,5} = 12.97$, $P = 0.015$). Fig. 3A shows that growth rate was reduced by 22% when evaluated at the mean value of the covariate (initial mass), and the reduction in growth was accompanied by a strong shift to edge areas at night (Fig. 3B). In the day, guppies used all pool areas in both treatments. Analysis of growth in length gave the same result with $P = 0.020$. Mean survival was 0.93 in each treatment (± 1 SE = 0.05 and 0.08 for the no predator and the predator treatments, respectively).

Rather than falling uniformly across all size classes, the predator-related growth reduction fell more strongly on the larger fish (Fig. 3C, D). Analyzing the data by mass rather than length gave the identical result as in Fig. 3C, D and regressions of body mass on body length were the same for fish in the two treatments (slope and intercept, $P > 0.95$ for each). Thus, the predator-induced restructuring of the growth pattern

strongly appears to be due to changes in net intake rather than redirected allocation to reproductive vs. somatic tissue.

As shown in Fig. 4A, allowing night feeding facultatively and substantially increased daytime tending of females by males (repeated-measures ANOVA, $P = 0.046$), with the effect clear in the morning and midday, but becoming statistically insignificant later in the day. This finding shows the same contrast in courtship intensity between high and low predation localities seen in a previous observational study (Luyten and Liley 1985), but provides a completely new explanation for the difference. Fig. 4B suggests that overall daytime feeding activity was elevated by about one-half in males that were denied night feeding, but the treatment effect was not statistically significant (repeated-measures ANOVA, $P = 0.233$ for the night feeding effect).

DISCUSSION

The findings reported here appear unique in demonstrating a predator-induced alteration of nocturnal feeding that is accompanied by changes in growth and reproductive behavior. Many species of fish exhibit plasticity in activity patterns, and Reebs (2002) reviews the causal factors for facultative shifts to being more or less nocturnal, diurnal, or crepuscular. However, he points out that avoidance of predators is often invoked as a cause for these shifts, but notes that these assertions are usually made in the absence of experimental
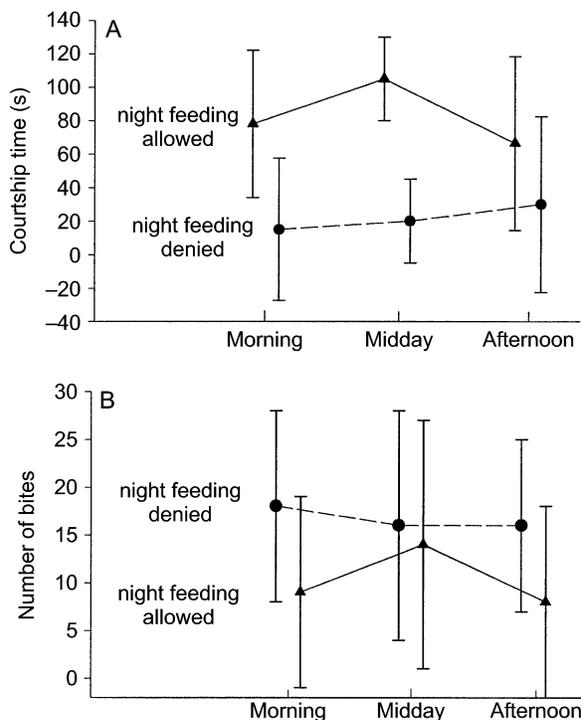
FIG. 4. Experiment in Ramdeen Stream to test for the effect of preventing night feeding on (A) time that males spend tending females and (B) male feeding activity. Means per 3-min samples and 95% confidence intervals are shown. Prevention of night feeding facultatively shifted daytime courtship to a lower level. Definitions: morning, 0630–0830 hours; midday, 0900–1500 hours; afternoon, 1600–1800 hours.

studies. Our finding of predator-responsive night feeding, with its diel shifts in habitat and foraging activity, is analogous to predator-implicated diel movement and activity patterns observed in some other taxa, e.g., vertical migrations of zooplankton in stratified lakes (Dini and Carpenter 1991, Lampert 1993, Liebold and Tessier 1997), horizontal migrations of zooplankton in shallow lakes (Burks et al. 2002), foraging activity in minnows (Culp 1989) and mayfly larvae (Culp and Scrimgeour 1993), and foraging activity and movements in desert rodents (Brown 1999, Kotler et al. 2002).

Our findings call for some reassessment of classical interpretations of predator-influenced differences in courtship observed in nature. In particular, interpretations of spatial variation in guppy courtship (Houde 1997) will need to consider not only arguments based on diurnal costs and benefits of courtship behaviors, but also the effects of nocturnal feeding on daytime behavior. In a classical field study, Luyten and Liley (1985) reported a greater time allocation to courtship by males under predator release, and interpreted that result as reflecting an adaptive adjustment to reduced mortality cost of courtship in such environments. However, our results offer the completely new interpretation that the energy subsidy generated from nocturnal feed-

ing energetically frees the guppies to increase reproductive activity during the day. Further, laboratory and field studies have not always shown the same result as found by Luyten and Liley (Farr 1975, Magurran and Seghers 1994), and consideration of field and laboratory feeding conditions might help to resolve some of these discrepancies.

While we experimentally manipulated only *Hoplias*, the guppy system may serve as a useful example of facilitation, one of the effects of multiple predators on the behavior of prey (e.g., Kotler et al. 1992, Soluk 1993, Sih et al. 1998). Although *Hoplias* was sufficient to induce diel shifts, guppies usually face more than one predator. In many streams the diurnal fish *Crenicichla alta* shapes daytime activity patterns (Seghers 1974, Endler 1987, Magurran and Seghers 1990), and the nearly ubiquitous killifish *Rivulus hartii* sometimes preys on young guppies (Liley and Seghers 1975), although the extent of its effect on guppy behavior remains unknown. How guppies allocate these multiple sources of hazard remains largely speculative, but some beginning investigations are intriguing. In addition to river edges with clear land/water boundaries, rivers like the Guanapo also have patches with flat, complex, cobble edges and riffles at which the river edges are less starkly defined. *Rivulus hartii* often occupies such microhabitats, and we have noticed that when guppies shift horizontally to edges at night, many do not deeply infiltrate the shallow riffles where they presumably could continue foraging nearly free from threat by *Hoplias*. Instead, guppies position themselves in a narrow band along the outer edges of patches (D. F. Fraser and J. F. Gilliam, *unpublished data*), as if adopting a compromise position, partially avoiding both *Hoplias* and *Rivulus* but avoiding neither completely. Diurnally, their relative abundance in different parts of the water column, main current, backwaters, and so on may best be modeled as an ideal free distribution with consideration of the costs associated with foraging in the current (Tyler and Gilliam 1995) plus habitat-specific mortality threat (Gilliam and Fraser 1987, Gilliam and Fraser 1988, Grand and Dill 1999), while the inclusion of crepuscular and nocturnal shifts in foraging effort and habitat may best be modeled as a problem in allocation of risk (Houston and McNamara 1999, Lima and Bednekoff 1999). Additional studies are needed to clarify how guppies allocate risk over the entire diel time cycle.

Reznick et al. (2001) and Grether et al. (2001) have argued for including resource intake as a factor affecting evolution of guppy life histories across environmental gradients, and our finding of predator-altered growth supports this view. For example, models by Kozlowski (1992) and Abrams and Rowe (1996) predict maturation at smaller sizes if juvenile growth rates are reduced, all else held equal. However, while we agree with Reznick et al. (2001) and Grether et al. (2001) that resource levels and, more specifically, re-

source intake should be considered along with predator-induced mortality in interpreting guppy life histories, there is no comprehensive theory tailored to this particular system to guide interpretations of how size-specific intake and size-specific mortality should act jointly to structure the five classical traits often considered in the literature on guppy life histories: maturation age, maturation size, clutch size, offspring size, and reproductive effort (Reznick and Travis 2002). The idea of such an integration has appeal; e.g., size-specific growth and size-specific mortality can carry equal weight in determining survival to a given size, because size-specific mortality rate represents the instantaneous probability of death per time spent at a given size, while growth rate determines the instantaneous amount of time exposed to mortality at that size (Werner and Gilliam 1984, Reznick et al. 1996). A comprehensive theory integrating mortality and intake as influences on the five life history traits could guide empirical work on unanswered questions of whether and how patterns of size-specific resource intake, as influenced by predators, competitors, and physical variables, act in concert or in opposition to patterns of size-specific mortality in structuring life histories of guppies in the field. Empirically, there is no published information that assesses whether severe predators such as *Hoplias* and *Crenicichla* cause a net increase or a net decrease in size-specific growth rate in field populations, after density dependence, facultative behavioral adjustments, and evolution occur; a remaining challenge is to disentangle predator effects from other, confounded environmental effects, because high predation sites also tend to be in wider, more downstream areas with more open canopy (Reznick et al. 2001, Reznick and Travis 2002). Also, concurrent with depressed night feeding, facultative or evolutionary responses to increased predation threat could result in guppies increasing their daytime intake, e.g., by schooling (Liley and Seghers 1975) or increasing their boldness in feeding (Fraser and Gilliam 1987).

Although we have documented the existence and efficacy of night feeding under predator release, we do not assert that guppies will always feed at night in the absence of *Hoplias*, nor that guppies will never feed at night in the presence of the predator. We have not quantified factors, other than the predator effect, that affect night feeding. Qualitatively, we have noticed that night feeding under predator release may be more vigorous under bright moonlight than under low light due to moon phase or cloud cover. The potential to feed at night represents a latent ''burst of power'' available to guppies in the high predation zones of rivers, and an increase of food level or waning predation threat could be predicted to induce night feeding in otherwise high predation locales, if the expected gain in reproductive value due to intake outweighs the expected loss of existing reproductive value due to death (Skalski and Gilliam 2002), quantities that will depend on phenotypic traits such as sex, size, condition, coloration for males, and brood stage for females.

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