

Effects of temporal patterning of predation threat on movement of a stream fish: evaluating an intermediate threat hypothesis

Douglas F. Fraser · James F. Gilliam ·
Brett W. Albanese · Sunny B. Snider

Received: 4 August 2005 / Accepted: 17 February 2006 / Published online: 6 June 2006
© Springer Science + Business Media B.V. 2006

Abstract The addition of nocturnal, *Hoplias malabaricus*, and diurnal, *Crenicichla alta*, predatory fishes downstream of barrier waterfalls increases predation threat for a killifish, *Rivulus hartii*, in Trinidadian streams. We hypothesized that the diel patterning of predation risk would affect prey movement rates, and tested this hypothesis by comparing movement in river sites/zones containing both the nocturnal and diurnal predator with movement in river sites/zones containing only the nocturnal taxon. We evaluated this prediction in the framework of an intermediate threat hypothesis (ITH) that holds that movement will be highest at some intermediate level of threat. We marked prey fish in study sites in two watersheds of a river, each with waterfalls that divided the river into three zones: a predator absent zone (P0), a zone with one nocturnal predator (P1), and a zone with one nocturnal and one diurnal predator (P2), and tested the ITH prediction that movement will be ordered as

$P0 < P1 > P2$. The single predator promoted longitudinal movement by *Rivulus* ($P0 < P1$), while zones with the two predators retarded movement for small *Rivulus* ($P1 > P2$) as predicted by the ITH. However, movement by larger, less vulnerable *Rivulus* remained elevated ($P1 = P2$ or $P2 > P1$). A displacement experiment in each zone found that threat tended to reduce the probability of a displaced fish reaching home, but the two predator zones did not differ from one another in their effect on this probability. Hence, the prediction that predator activity over the full 24 h diel cycle would retard movement, $P2 < P1$, was not supported with respect to homing. Because habitat and predator communities change predictably from headwater streams to larger rivers in many lotic ecosystems, we present a conceptual model for predicting fish movement behavior along this continuum. The model posits an important role for predation threat, and the size and spacing of refuge patches, suggesting that human alterations of these factors will affect the natural movement of fish in streams.

D. F. Fraser (✉)
Department of Biology, Siena College, Loudonville,
NY 12211, USA
e-mail: fraser@siena.edu

J. F. Gilliam · S. B. Snider
Department of Zoology, North Carolina State University,
Raleigh, NC 27695-7617, USA

B. W. Albanese
Georgia Department of Natural Resources, Social Circle,
GA 30025-4714, USA

Keywords Stream corridor · Population spread ·
Dispersal · Homing · Predation threat · Habitat
matrix

Introduction

The movement of individual organisms in both aquatic and terrestrial environments is important to

ecological processes such as population spread (Rahel 2002), metapopulation dynamics (Doncaster et al. 1997), and local species richness (Angermeier and Winston 1998) and to applications such as reserve design (Schultz 1998). Except perhaps at the smallest spatial scales, movement in spatially heterogeneous environments will often involve movement through hostile gaps, i.e., locations that contain an elevated hazard of predation and in which conspecifics are rare or absent. Hostile gaps that create spatial fragmentation of a population might also create dynamic fragmentation, or decreased movement among fragments (Culp and Scrimgeour 1993; Harvey et al. 2004). However, movement or the lack of movement across such gaps, which has consequences for the dynamics of fragments, e.g. subpopulations, remains unexplored for most ecosystems (e.g. Schultz 2001; Vandermeer and Carvajal 2001). Issues involving hostile gaps are especially germane to riverine systems, in which fish or other watercourse-restricted organisms move along an essentially linear path, with moving individuals obligatorily crossing a variety of habitats that can differ in danger, or perceived danger. Pools and/or riffles in riverine ecosystems can harbor predators that create hostile gaps if those predators substantially raise the cost of movement across those gaps, e.g., pools. Thus, it is reasonable to hypothesize that occupancy of pools by a predator, whether due to long-standing biogeographic patterns or recent invasions, will lower movement, and hence gene flow and recolonization, through hostile gaps. Using a combination of experimental manipulations and a large-scale field study, we compare movement by a stream fish through habitats containing gaps that vary in degree of hazard owing to the presence of one or more predators. In this study we find partial support for an intermediate threat hypothesis (ITH), which holds that movement will be highest at some intermediate level of threat.

Promotion by threat and an intermediate threat hypothesis

The distribution of the study species, the killifish, *Rivulus hartii*, extends from the lowlands into the highest headwaters of Trinidad's Northern Range Mountains. Above the lowlands, rivers typically have three zones that differ in predation hazard

experienced by *Rivulus*. The upstream limit of each zone corresponds with one of the many waterfalls in the rivers, apparently reflecting historical events in breaching waterfalls by predators: (a) "P0," an upper zone in which *Rivulus* exists with no strongly piscivorous fish, (b) "P1," a middle zone where *Rivulus* occurs with a strong piscivore *Hoplias malabaricus*, and (c) "P2," a lower zone where *Rivulus* occurs with both *Hoplias* and a second piscivorous fish, the pike cichlid, *Crenicichla alta*. Our observations indicate that *Hoplias* forages most actively during twilight and at night (Fraser and Gilliam 1992; Gilliam and Fraser 2001), and *Crenicichla* is most active during the day (Endler 1987). Consequently, a *Rivulus* moving through gaps in the P2 Zone is subject to daytime threat by *Crenicichla*, and crepuscular/nocturnal threat by *Hoplias*.

Previous work has shown that *Hoplias* severely reduces *Rivulus* density in the river, and causes spatial fragmentation of the remaining individuals (Fraser et al. 1995; 1999). In the P0 Zone, *Rivulus* is abundant throughout the main river: in pools, riffles, and in isolated flood pools which flank the main river. However, in the P1 and P2 Zones, *Rivulus* is generally restricted to shallow, cobbly riffles and isolated pools. This near absence of *Rivulus* in river pools in the P1 and P2 zones creates strong spatial fragmentation of the prey population in those zones. We hypothesized that such spatial fragmentation would be accompanied by dynamic fragmentation, or reduced movement along the river. Thus, we expect to observe less movement in the presence of hostile gaps (P1 and P2 Zones) if (a) the predator's presence decreases the probability that a given fish will attempt movements, especially across pools and other predator-occupied gaps, and (b) the predator kills some of the fish that attempt movement, reducing the movement actually accomplished and observed. On the other hand, we might expect to observe more movement if (c) fish that attempt to move, if not killed, travel further to find safe habitat, (d) fish in local refugia are forced to "scatter" in the event of spates that expose them to predators or drying that eliminates the refuge, versus those in areas lacking hostile gaps (P0 Zone), which can find safe habitat anywhere nearby, (e) density in refuge patches promotes emigration, and (f) areas lacking hostile gaps (P0 Zone) have few vacant patches to reward movers with high resources, versus the

fragmented P1 and P2 Zones where local extinctions in the fragmented landscape provide such opportunities.

In both a preliminary experimental stream experiment (Fraser et al. 1995) and a full field study comparing P0 and P1 Zones in the Guanapo River of Trinidad (Gilliam and Fraser 2001), we found that predators were net promoters of movement. Here, using a second watershed that contains a two-predator zone (P2), we replicate and expand the previous work. In doing so, we pose an intermediate threat hypothesis (ITH) that holds that movement is highest at some intermediate level of threat. For the specific case of comparing the P1 and P2 Zones, our rationale is that the two reasons above for less observed movement (a–b) will become stronger in the P2 Zone, but the above arguments for more movement (c–f) will not become stronger, because the population is fragmented about equally in the P1 and P2 Zones. Hence, the predicted ordering of movement is $P0 < P1$, as found previously, plus hypothetically $P1 > P2$, resulting in the ITH, $P0 < P1 > P2$.

Alternatives to the ITH include contradiction of the previous finding of $P0 < P1$, no difference between P1 and P2 (i.e. the effect of threat is a plateau effect), and that increasing threat further enhances movement, i.e., $P1 < P2$. In addition to directly testing predictions of the ITH for longitudinal movement in the river using a field mark-recapture study, we also used a displacement experiment in each of the three river zones to test for homing success under increasing predation threat.

Materials and methods

The mark-recapture study was conducted in the P0, P1 and P2 Zones of the Turure River, located in lower montane rainforest of the Matura Forest Reserve. Each treatment (P0, P1, P2) was replicated twice. The two P0 and P1 study areas were located in separate branches of the river, each with a dendritic drainage of similar area. The P2 study areas were both located in the main stem of the river, and separated by 500 m; this separation proved adequate as we documented no movements between sites during the study. All study areas were located between 75 and 175 m elevation, where the stream bed is predominantly cobble and gravel with alternating pools and riffles within the thalweg (Table 1). These streams exhibit excellent water clarity under base flow conditions during both the dry and wet seasons. Each study zone was divided into three areas: a central area in which *Rivulus* were marked, and a search area up- and downstream of the marking area in which *Rivulus* were caught and examined for marks but not marked; employing such “extralimital” zones lessens biasing of data toward individuals that move only short distances within the marking zone (Albanese et al. 2003). Owing to differences in density of fish between zones, we attempted to equalize sample sizes by adjusting river lengths of the marking zones, which varied from 70 m (P0) to 300 m (P2). The up- and downstream extralimital areas were nominally 100 m but varied from 80 to 100 m. The predator *Hoplias* was observed in all parts of P1 and P2, but due to barrier falls, the predator *Crenicichla* was

Table 1 Characteristics of streams at six study sites on the Turure River, 2002–2003. All measurements expressed in meters

River Branch	Predator Zone	Stream order	Mean (SD) width of thalweg <i>N</i>	Mean (SD) length of riffles (refugia) <i>N</i>	Mean (SD) pool length (gaps betw. refugia) <i>N</i>
West (main stem)	P0	2	4.2 (0.06) 3	10.5 (5.1) 6	18.6 (3.7) 2
	P1	3	6.1 (0.87) 3	16.4 (17.1) 8	21.7 (11.2) 3
	P2	3	8.7 (1.56) 3	13.5 (13.5) 11	19.7 (5.2) 6
East	P0	2	2.5 (0.45) 3	13.8 (11.6) 10	7.1 (2.8) 4
	P1	3	2.7 (0.65) 3	28.0 (12.3) 12	11.1 (2.1) 5
	P2	3	7.7 (2.10) 3	20.7 (18.3) 10	7.7 (0.3) 3

found in all parts of P2 only. *Hoplias* were encountered during night searches for *Rivulus*. *Crenicichla* were rarely visible at night, but their presence was readily confirmed by snorkeling in daytime. Neither predator was ever found above the barrier waterfalls separating P0 from P1, nor was *Crenicichla* found above the barrier separating P1 from P2.

The movement study: evaluating the intermediate threat hypothesis

To assess movement, we marked and recaptured fish at approximately 2-month intervals between January 2002 and January 2003. We marked a total of 3577 *Rivulus* (P0 Zones = 1359, P1 Zones = 1205, P2 Zones = 1013), which were collected from all habitats within the river banks. We searched for *Rivulus* after dark when they can be located visually and dip netted. Each *Rivulus* was placed in a reclosable plastic bag at its point of capture. Its location was marked with a labeled flag permitting return of the fish to its exact microhabitat after processing. *Rivulus* were anesthetized, total length measured to the nearest mm, sexed and marked by injection with an elastic polymer (Northwest Marine Technology, Inc., Shaw Island, Washington, USA). We marked each fish uniquely using 7 body positions and 5 colors to generate triplet codes; each fish received three dots of elastomer. We marked fish >25 mm total length (TL) using a tuberculin syringe with 29 1/2 gauge needles, and we weighed each fish to the nearest 0.001 g on a digital balance. We ran measuring tapes along the river from permanent starting points to record each fish's location. The study period included one dry (January through May), and one wet season (June through December). We note that *Rivulus* exhibits continuous reproduction across both seasons making any movement that might be related to mating the same throughout the year.

Analysis of the ITH

We used Statistica software (version 6.1, Statsoft Inc., Tulsa, Oklahoma, USA) for all analyses in this study. We divided the fish into 2 size classes, which reflect differences in vulnerability to the predators. *Hoplias malabaricus* is a strong piscivore capable of consuming prey fish measuring over a third of its own body length (Winemiller 1989; Fraser and Gilliam

unpublished observations), leaving virtually all *Rivulus* marked in the P1 and P2 areas vulnerable to *Hoplias* over the range of *Hoplias* sizes that we typically observe in the predator zones, 80–350 mm TL. However, vulnerability to *Crenicichla* likely falls on the smaller size class. The data for the size range of prey taken by *Crenicichla* are almost exclusively based on guppies, *Poecilia reticulata*, and are conflicting. Johansson et al. (2004) reviewed these studies and also found empirically that capture success of *Crenicichla saxatilis* declined significantly between 30 mm and 40 mm TL. In splitting the recapture data into size classes in this study, we assume that *Rivulus* >41 mm TL would face reduced predation threat from *Crenicichla*. Although we have imperfect knowledge of how vulnerability to *Crenicichla* changes with *Rivulus* body size, this limit allowed us to maintain adequate sample sizes in each size group. We assume that all P1 zone *Rivulus* will be under a strong crepuscular-nocturnal threat by *Hoplias*, with threat relaxed during the day. *Rivulus* in the P2 zone will experience the same crepuscular-nocturnal threat, but small fish will also experience threat from *Crenicichla* during the day.

For each recapture we arbitrarily assigned positive values to upstream moves and negative values to downstream moves, and calculated net movement per day as $([\text{position at recapture}] - [\text{previous position}]) / [\text{days since last captured}]$. Because our sampling interval was about two months, we present data as net movement per 60 days. We compared the rate of population spread, operationally defined as the standard deviation of the frequency distribution of signed (downstream = negative) distances moved per 60 d for P0 vs. P1 and P1 vs. P2 for each of the two size classes. We tested for differences via *F*-tests with *df* based on total counts of individuals.

We used the generalized linear model (GLZ) to test for the effect of the two factors, predators (P0, P1, P2), and replication (East, West Branch) on distance moved per 60 d. The GLZ was employed, because our general movement study produced highly skewed distributions of absolute distances moved (many “zero” nonmovers). For these nonnormal distributions generalized linear models provide flexibility in model (distribution) choice (McCullagh and Nelder 1989). Chi-square tests of our distributions against standard alternatives showed that the data approximated an exponential function (two of six

movement distributions fit an exponential function). We therefore based the GLZ analyses on the gamma distribution, which is equivalent to an exponential function when the rate parameter (p) is close to one (Winer 1991). We transformed absolute distances moved as distance +1.0 to enable use of the LOG link function (McCullagh and Nelder 1989). We separately tested each of the two size classes for the effect of two factors, predators (P0, P1, P2) and replication (East, West Branch), on the absolute distance moved per 60 d (distances unsigned). The GLZ uses maximum likelihood methods, which are tested by the Wald Statistic.

Displacement experiment

The ITH is based partly on the idea that fish perceive movement as more hazardous in the P1 and P2 zones than in the P0 zone, with threat in P2 being sufficiently high as to discourage movement relative to P1. We tested this prediction for the perception of risk, $P0 < P1 < P2$, by displacing fish in the three predator levels and testing for propensity to home. In the mark-recapture study we observed some long-distance moves by fish that were later recaptured at their initial mark site, suggesting that displaced *Rivulus* might attempt to home. In the displacement experiment all captured *Rivulus* were relocated to a new site within their respective study area ($n=6$ study areas in the Turure River). We also chose three additional study areas, one in each predator zone, in the nearby Guanapo River. We used a randomization procedure to assign each *Rivulus* to its new displacement site. Each displacement site was one previously occupied by a *Rivulus*, thereby avoiding displacements into unsuitable microhabitats. As with the marking study, we resampled after two months, and measured the distance moved by each fish.

Analysis of displacement experiment

Our objective was to test for the ability of the two levels of predation threat to retard movement, and we analyzed the data in two ways. First, we calculated the distance from home for each individual, in each study area, arbitrarily choosing 3 m as our operational definition of “homed” fish. Second, because we might expect homing success to depend on the distance displaced, we examined the probability of

reaching home by each fish as a function of distance displaced. Owing to the size of the P0 study areas, fish in those zones could not be displaced >175 m. Therefore, we restricted the analysis to those fish that were displaced ≤ 175 m in any of the three river zones. Further, in a preliminary analysis we found no effect of size class on the distance from home upon recapture ($F_{1,227} = 0.38$, $p=0.539$), and therefore combined the two size classes for this analysis. We used the GLZ analysis to test distance from home (\log_{10}), as the dependent variable in the two predator zones (0, 1 + 2 combined). We then tested for differences in the relationship between distance from home (\log_{10}) versus distance displaced (\log_{10}) with a GLZ analysis based on the normal distribution.

Results

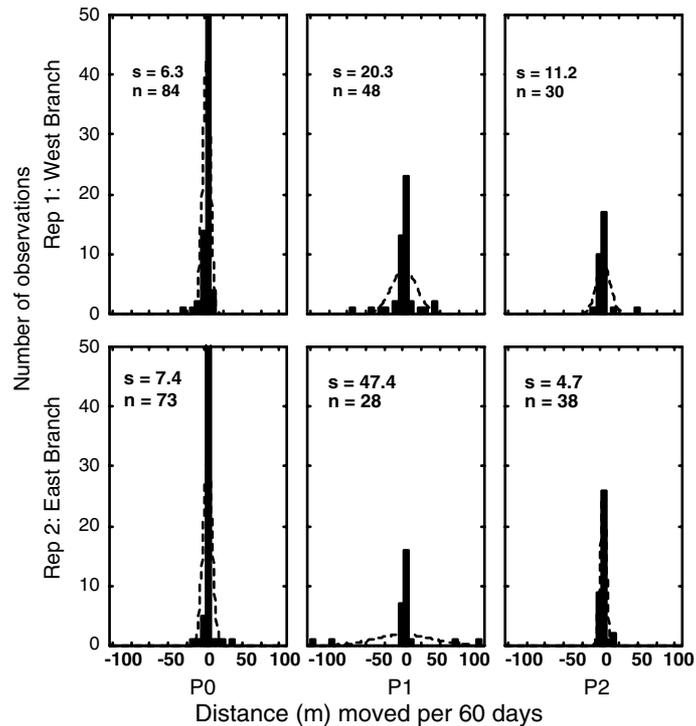
Mark-recapture study

Consistent with findings for the P0 and P1 zones of our previous study (Fraser et al. 1995) the density (number per 100 m of river) of *Rivulus* in each river zone, was always $P0 > P1 > P2$; mean density (\pm SD), $N = 6$: East Branch $P0=133.8$ (28.2), $P1=53.5$ (15.8), $P2=32.7$ (9.3); West Branch $P0=161.2$ (30.2), $P1=36.4$ (10.1), $P2=22.9$ (5.7).

In addition to the 3577 *Rivulus* we marked, we caught another 3079 *Rivulus* in the extralimital zones above and below the six study areas combined. Only 55 of these fish were marked. Further, only 3 of the 55 recaptures were within 20 m of the limit of the extralimital zone, suggesting that few moved beyond. We detected no up- or downstream bias in movement direction.

The population spread of *Rivulus* <41 mm TL, in each of the three predator zones, of each replicate, supports the predicted ITH pattern of $P0 < P1 > P2$ (variance ratio test West Branch: P0 vs. P1: $F_{48,84}=10.51$, $p<0.001$; P1 vs. P2: $F_{48,30}=3.31$, $p<0.001$; East Branch: P0 vs. P1: $F_{28,73}=40.57$, $p<0.001$; P1 vs. P2: $F_{28,38}=101.86$, $p<0.001$; Fig. 1). None of the distributions show a directional bias in movement (West Br. P0 [mean \pm SE]: $-1.0 \pm .68$, t -test vs. zero, $p=0.15$; P1: -1.3 ± 2.93 , $p=0.67$; P2: 1.3 ± 2.93 , $p=0.52$; East Br. P0: $0.8 \pm .87$, $p=0.38$, P1: -2.11 ± 8.95 , $p=0.81$, P2 = $1.11 \pm .76$, $p=0.16$). However, in contrast to the ITH result for small

Fig. 1 Movement distributions of *Rivulus*, ≤ 41 m TL in each of the three predator zones (P0, P1, P2). The two branches of the Turure River (reps) are shown separately. Population spread (standard deviation) of the small size class in each of the three predator zones conforms to the predictions of the ITH, $P0 < P1 > P0$, in each replicate

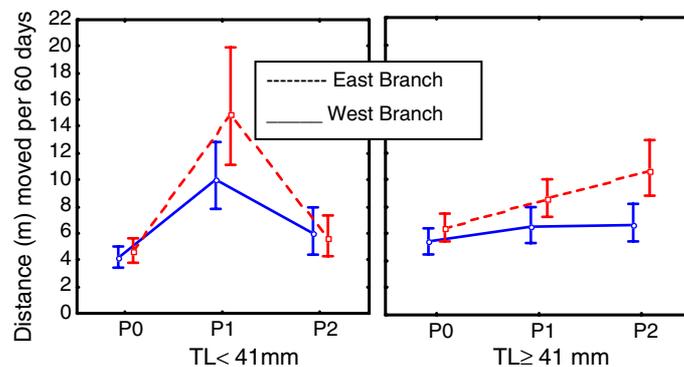


Rivulus, variance of movement distances for fish ≥ 41 mm TL, does not conform to the ITH pattern, but rather suggests a plateau effect of predation where $P0 < P1 = P2$ (West Branch: $P0$ vs. $P1$: $F_{123,172}=1.92$, $p < 0.001$; $P1$ vs. $P2$: $F_{123,120}=1.21$, $p > 0.05$; East Branch: $P0$ vs. $P1$: $F_{195,204}=1.90$, $p < 0.001$; $P1$ vs. $P2$: $F_{150,195}=1.34$, $p > 0.05$).

Interestingly, the ITH pattern is present if we relax the restriction on vulnerable fish size altogether, and consider all sizes simultaneously (West Branch: $P0$ vs. $P1$: $F_{170,253}=3.48$, $p < 0.001$; $P1$ vs. $P2$: $F_{170,147}=1.67$, $p < 0.01$; East Branch: $P0$ vs. $P1$: $F_{221,274}=48.83$, $p < 0.001$; $P1$ vs. $P2$: $F_{221,182}=1.37$, $p < 0.05$).

Figure 2 clearly shows the effect of the three factors, predators, *Rivulus* size class, and replicate location. The left panel shows that the ITH pattern for the small *Rivulus* in the three predator treatments was consistent between replicates (East vs. West Branch, Wald Statistic = 2.19, $p = 0.14$), and $P2 < P1$, as predicted by the ITH (Wald statistic = 59.5, $p < 0.001$). The $P0$ vs. $P1$ comparison was not tested owing to a limitation on the number of post-hoc tests permitted in the GLZ design, but Fig. 2 shows the established $P1 > P0$ pattern. The replication \times predator treatment interaction was not significant (Wald Statistic = 2.39, $p = 0.12$). The right panel shows that movement by

Fig. 2 Relationship between distance moved, standardized to 60 d, and predator zone for the two size classes of *Rivulus* in the Turure River. The small size class follows the predicted patterns of the ITH, $P0 < P1 > P2$, while larger fish show either a plateau, $P1 = P2$ (West Branch) or an additive, $P2 > P1$, effect (East Branch)



the large *Rivulus* was neither diminished in the P2 locations (P1 vs. P2; Wald Statistic = 0.46, $p = 0.50$), nor consistent between replicates (East vs. West Branch, Wald Statistic = 15.6, $p < 0.001$), and the replication \times predator treatment interaction was not significant (Wald Statistic = 0.098, $p=0.75$). Rather, movement by the large fish showed a plateau (P1=P2) effect in the West Branch and a somewhat augmented predator effect (P2>P1) in the East Branch.

Lastly, the distributions of movement distances shown in Fig. 1 exhibit the same strongly leptokurtic pattern that was evident in the Guanapo River mark-recapture study (Gilliam and Fraser 2001). Most *Rivulus* are non-movers, remaining in the same general location over long periods of time.

Displacement experiment

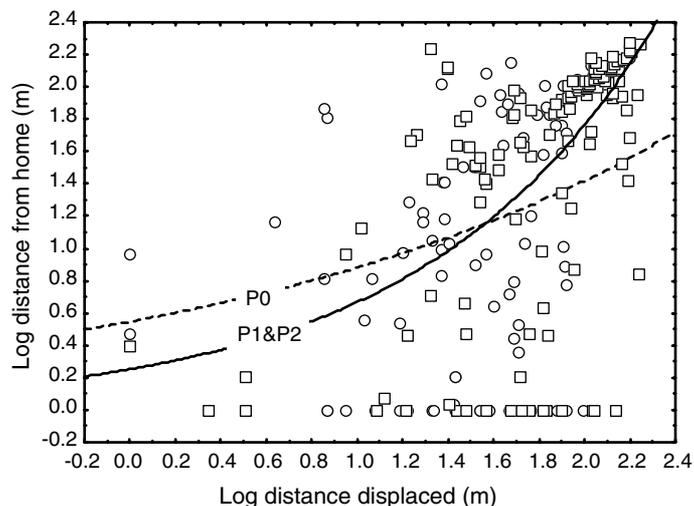
We recaptured >45 fish in each study zone. As predicted, the predators *Hoplias* and *Crenicichla* significantly reduced the homing success of *Rivulus* (P0 vs. P1 + P2 combined, Wald Statistic = 18.34, $p<0.001$). Figure 3 shows that homing success was strongly related to the distance displaced both in the presence and absence of the predators (Wald statistic = 46.33, $p<0.001$), although P0 fish reached closer to home on average than did those in the predator zones (mean \pm SE: P0 = 8.4 \pm 0.12; P1&P2 = 26.3 \pm 0.10; Wald Statistic = 4.43, $p=0.035$). We displaced few *Rivulus* to distances > 125 m in the P0 zones relative to the number we displaced >125 m in the predator zones. However, restricting the analysis to displace-

ments of ≤ 125 m yields virtually identical results. Figure 3 shows that homing failure was common to all zones, not just P1/P2. For example, a total of 59 of 94 recaptures failed to home in the combined P0 zones. However, of the 59, 26 were found in pools, apparently having found the pool habitat a suitable stopping point. Factors that make a pool a suitable stopping point are unknown, but the ‘‘absorbing effect’’ of pools was completely absent in the P1 and P2 zones, as we never found *Rivulus* in river pools that were accessible to the predators.

Discussion

Our results show support for the hypothesis that within and between-patch movement rates will be elevated at some intermediate level of threat, but depressed at higher levels. However, our findings apply only to the smaller size class of *Rivulus*. The river displacement study showed that while the presence of the single predator *Hoplias* (P1) lowered the probability of successful homing relative to that in the predator-absent zone, the addition of *Crenicichla* (P2) did not further lower the probability of homing for *Rivulus* of any size. Matthews (1998) notes the pervasiveness of homing behavior in freshwater fish, but there is little known about the ecological factors that affect homing success. Our results suggest an important role for predation and the quality of habitat encountered after displacement.

Fig. 3 Homing success as a function of displacement distance for *Rivulus* in the predator absent zones (P0) of the Turure and Guanapo River study areas, and in the combined predator zones (P1+P2); circles: P0, squares: P1&P2. Exponential fit lines shown for informational purposes



Elevated movement in the predator zone may operate within the broader context of the diel temporal patterning of threat, in which the diel activity pattern of predators, complementary in this system, proximally affects longitudinal movement. In experimental stream observations Fraser and Gilliam (1992) found that *Rivulus* tended to be active during the day when *Hoplias* was quiet and partially concealed on the bottom. In recent studies (Fraser and Gilliam unpublished) in the experimental stream facility, we have similarly noticed that in contrast to night, *Rivulus* in the day will readily cross pools containing *Hoplias*. The correlation of the activity pattern of the prey with the temporal patterning of threat is well known and not unique to this system (e.g. Lima and Bednekoff 1999; Sih et al. 2000; Reeb 2002). The correlation is especially well documented for zooplankton communities in lakes (e.g. Lampert 1993). The elimination of the temporal pattern of threat by the addition of the second predator with a contrasting activity pattern, diurnal + nocturnal threat, complementing rather than augmenting the first, may be common in stream ecosystems, although to our knowledge, this is the first reported case.

As with the smaller *Rivulus*, we documented higher movement rates for larger *Rivulus* in the zone with *Hoplias* (P1) compared to the zone with no piscivorous fishes, as we found in the earlier study (Gilliam and Fraser 2001). In contrast to the response of the smaller fish, the addition of *Crenicichla* in P2 neither added to this response, by increasing movement above P1, nor did it suppress movement as predicted by the ITH. The finding of a plateau effect for larger fish was not surprising, given that larger *Rivulus* appear to be relatively safe from attacks by *Crenicichla*, and shows a consequence of relative predator–prey body sizes in shaping the predator–prey interaction (e.g., Woodward and Hildrew 2002). Nevertheless, the behavior of *Rivulus* of all sizes in *Hoplias*-threatened zones of the Guanapo River (previous study) and *Hoplias* and *Crenicichla* zones of the Ture River is strikingly different from that in the predator-absent zones of those rivers. As we have previously shown (Fraser et al. 1995), threat is accompanied by dramatic shifts out of the main stream into edge areas. *Rivulus* is most abundant in raised riffle sections and along edges that are carpeted by cobble, rocks, and woody debris or where there are

large obstructions with hiding places, e.g. stumps and partially buried logs with leaf snags (Fraser et al 1995; Fraser and Gilliam unpublished). The immediacy of threat is also evident when capturing *Rivulus* by dip net, which we note anecdotally is much more difficult in predator zones where *Rivulus* are quick to exhibit protean escape behaviors. Given these strong responses to a clearly identifiable environmental factor, predation threat, it is not surprising that the behavioral responses can be generalized to movement behavior.

While the ITH was useful for understanding movement behavior in the headwaters of the Ture River, its utility in different systems and over different spatial scales is not known. We note that our results are dependent upon our definition of the vulnerable size range of prey, and additional studies are needed to determine whether the observed strong effect on the small fish will extend to the full size range of this taxon in more severe regimes, e.g. sites with higher predator richness and/or densities. Further, variables such as the distance between riffle refugia, (Table 1), will increase along the river continuum (riffle to riffle spacing is normally 5–7 times channel width at bankful discharge, Leopold et al. 1964) interacting with predators to affect the extent of longitudinal movements of *Rivulus*, e.g. a positive correlation of movement distances with an increase in refuge spacing. Here we suggest a preliminary model that makes qualitative predictions for movement along the stream gradient (Fig. 4).

A preliminary model

The Ture River varies from being very steep with numerous pools, but no riffles to a low elevation river with increased flow, larger pools and large, widely-spaced riffles. The level of threat changes along this gradient and is depicted by the numbered arrows, 1–5, in Fig. 4. We make a distinction between movements such as exploration for habitat selection and resources, and forced movements due to environmental events. Movement increases sharply with the appearance of one predator taxon that is active over a portion of the diel cycle. This is due to the creation of a now hostile matrix separating refugia. Prey fish are forced to move further to reach refugia, which they may do during the predator-inactive period of the diel cycle. As the spacing of riffle refugia steadily in-

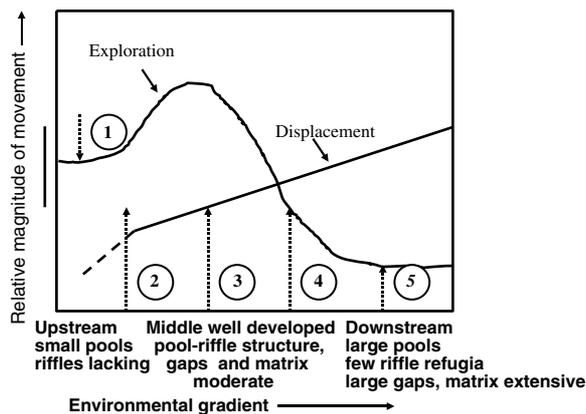


Fig. 4 Preliminary conceptual model that predicts movement of individual fish in relation to attributes of the environmental gradient, increasing pool size and spacing of riffle refugia in the river continuum. Arrows indicate the addition of predator taxa along the gradient. Lines show predicted movement, voluntary, e.g. exploration, searching for resources, and forced displacements, e.g. drying or flooding of refugia. Dashed portion of displacement line indicates uncertainty about its position in this area

creases along the continuum, prey movement reaches a maximum. Hypothetically, the addition of a second predator taxon slows movement by adding to the risk of mortality. If the temporal patterning of threat is removed because the second predator has a different and complementary activity pattern, as suggested for vulnerable fish in this study, the number of fish attempting or surviving movements should be further reduced. Additional increases in predator richness, which may include avian, reptilian and mammalian predators, combines with the steadily increasing distance between riffles along the continuum to further slow movement. Displacement events will assume greater importance in downstream areas, e.g. changes in temporary flood pools and filling due to siltation will force longer moves across hostile matrix habitat (Fig. 4). Finally, threat levels may render the stream habitats so hostile that *Rivulus* populations cannot maintain positive growth. We note that *Rivulus* may be nearly or completely absent from predator-rich, mainland rivers (Venezuela: Alex Flecker, personal communication) or limited to seasonally flooded but otherwise isolated forest pools (Costa Rica: Winemiller 1990).

In the model we make the assumption that the effects on movement of the prey are additive in that the addition of a predator may augment or complement the effects of those already present. Additive

effects of multiple predators have been observed in other taxa (e.g., Kotler et al. 1992; Gonzales and Tessier 1997), but this may not always be the case and predators may interfere with each other to the benefit of the prey (e.g., Sih et al. 1998; Vance-Chalcraft et al. 2004). Based on earlier findings (Gilliam et al. 2001), we also posit an important effect of refuge spacing on movement. We expect that inter-habitat spacing positively affects movement over relatively modest increases in spacing, but that larger spacing decreases the number of fish attempting or successfully completing movements between refugia. Lonzarich et al. (2000), working in a temperate stream, found that wider spacing among preferred pool habitat units decreased fish movement. Similarly, Schaefer (2001) documented lower movement rates of minnows across longer riffles in experimental streams. During the tropical wet season, rising water levels may lead to wider spacing of preferred *Rivulus* riffle habitats with similar effects.

The model emphasizes the likely increase in mortality cost associated with pool crossings at lower elevations, and leads to a prediction of declining voluntary movement as hazard increases in the environment at lower reaches. An alternative model posits that increased hazard leads to selection for exploratory behavior and also more movement, given that these behaviors result in (a) finding safer places in an overall increasingly hazardous environment, and (b) finding energetically rich patches which allow early and high reproductive output under high mortality. Genetic studies of population structure, which average movement across longer temporal scales than feasible with mark-recapture studies, might be an alternative way to distinguish between the hump-shaped ITH hypothesis predicted by the model, and the pattern of a plateau or increase in movement predicted by the alternative.

Our study finds support for the generality of the phenomenon of risk failing to completely suppress prey movement. *Rivulus* appeared to make voluntary moves in all zones of the river. While predation risk may act to suppress prey movement, it is not complete, and other factors such as local density effects on food or mate acquisition may promote movement of some individuals. Indeed, even the two-predator regime, coupled with the most dangerous habitat gaps, large canyon pools with no edge, failed to completely suppress movement across them. These findings are

not surprising in view of the well-documented behavioral response to risk in which it is clear that animals take risks and can balance costs and benefits in adaptive ways (e.g., Lima and Dill 1990; Magnhagen 1991; Kotler et al. 1992; Brown 1999). However, the longitudinal movement of prey through a hostile stream matrix is not well known, and the rules that apply to foraging and mating choices in certain other natural settings may not fully apply here (see Harvey et al. 2004 for example of a blocking effect).

The preliminary model may help explain the movement behavior of tropical prey fishes along environmental gradients that are correlated with changes in predator communities. Our finding that movement behavior changes along the stream continuum may apply more generally, as other studies have predicted (Gorman 1986; Schlosser 1990) or documented (Albanese et al. 2004) differences in movement behavior between headwater and main stem fish populations. The phenomenon is worthy of additional study. In particular it would be useful to know whether the relationship between structural heterogeneity and the matrix, such as in the spacing of riffles, can ever become sufficiently unfavorable to rarify movement events. The importance of this occurrence is underscored by the high potential for unfavorable configurations in anthropogenically altered stream ecosystems (e.g. Paul and Meyer 2001). In Trinidad's rivers, patch loss and decreases in connectivity occur naturally with decreasing gradients as explained here. However, anthropogenic processes add to the loss of refuge patches and reduce the protective cover of remaining patches by altering the embeddedness of the cobble, and channelization may obliterate critical habitat patches without changing, i.e. reducing, the riskiness of the intervening matrix. Such changes in the habitat matrix are likely to affect the movement behavior of many fishes, which has important implications for conservation (Albanese et al. 2004).

Summary/conclusions

Conclusions stemming from this work corroborate and extend the main results of our previous work (Gilliam and Fraser 2001; Fraser et al. 2001). First, we have confirmed that elevated movement associated with the addition of the predator *Hoplias*, occurs in the Turure River as well as in the previously

studied Guanapo River, and therefore suggest that the phenomena are likely common to other drainages. Second, we find some support for our hypothesis that increased predation threat (>1 predator taxon) can slow population spread, although additional studies are needed to understand the generality of the ITH phenomenon and whether, under sufficiently severe predation, it would be independent of size in this taxon. Third, these findings emphasize the importance of the temporal patterning of threat by multiple predators, which may have a complementary rather than canceling effect on the prey's behavior (e.g. Sih et al. 1998). Fourth, we show a strong top-down (predator-dependent) component in the regulation of habitat-selection by *Rivulus*.

Acknowledgements We thank the late Roopchard (Boysie) Ramdeen of Verdant Vale for the use of Ramdeen Stream, the Asa Wright Nature Center (Simla and manager Ronnie Hernandez), and Dr. Mary Alkins-Koo for logistical support. We thank our stalwart Trinidadian field workers Ephriam Farfan, and Jose and Ramon Rodriguez and additional field workers, Ryan Baisley, Brian Baksh, Asbert Cuffy, Carl Fitzjames, Dan Nuckles, Jared Lendrum, Kelly Malchan, Jacob Miano, Jennifer Peloquin, Brandon Puckett, Wayne Rostant, John Saathoff, Chip Small, and Lauren Sokolik, and Sundar Dorai-Raj for statistical advice. The study was supported by the National Science Foundation.

References

- Albanese B, Angermeier PL, Gowan C (2003) Designing mark-recapture studies to reduce effects of distance weighting on movement distance distributions of stream fishes. *Trans Am Fish Soc* 132:925–939
- Albanese B, Angermeier PL, Dorai-Raj S (2004) Ecological correlates of fish movement in a network of Virginia streams. *Can J Fish Aquat Sciences* 61:857–869
- Angermeier PL, Winston MR (1998) Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology* 79:911–927
- Brown JS (1999) Vigilance, patch use, and habitat selection: foraging under predation risk. *Evol Ecol Res* 1:49–71
- Culp JM, Scrimgeour GJ (1993) Size-dependent diel foraging periodicity of a mayfly grazer in streams with and without fish. *Oikos* 68:242–250
- Doncaster CP, Clobert J, Doligez B, Gustafsson L, Danchin E (1997) Balanced dispersal between spatially varying local environments: an alternative to the source-sink model. *Am Nat* 150:424–445
- Endler JA (1987) Predation, light intensity, and courtship behaviour in *Poecilia reticulata*. *Anim Behav* 35:1376–1385
- Fraser DF, Gilliam JF (1992) Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology* 73:959–970

- Fraser DF, Gilliam JF, Yip-Hoi T (1995) Predation as an agent of population fragmentation in a tropical watershed. *Ecology* 76:1461–1472
- Fraser DF, Gilliam JF, MacGowan MP, Arcaro CM, Guillozet PH (1999) Habitat quality in a hostile river corridor. *Ecology* 80:597–607
- Fraser DF, Gilliam JF, Daley MT, Le AN, Skalski GT (2001) Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *Am Nat* 158:124–135
- Gilliam JF, Fraser DF (2001) Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology* 82:258–273
- Gonzalez MJ, Tessier AJ (1997) Habitat segregation and interactive effects of multiple predators on a prey assemblage. *Freshwater Biol* 38:179–191
- Gorman OT (1986) Assemblage organization of stream fishes: the effect of rivers on adventitious streams. *Am Nat* 128:611–616
- Harvey BC, White JL, Nakamoto RJ (2004) An emergent multiple predator effect may enhance biotic resistance in a stream fish assemblage. *Ecology* 85:127–133
- Johansson J, Turesson H, Persson A (2004) Active selection for large guppies, *Poecilia reticulata*, by the pike cichlid, *Crenicichla saxatilis*. *Oikos* 105:595–605
- Kotler BP, Blaustein L, Brown JS (1992) Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann Zoologici Fennici* 29:199–206
- Lampert W (1993) Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Archiv für Hydrobiologie Ergebnisse der Limnologie* 39:79–88
- Leopold LB, Wolman MG, Miller JP (1964) Fluvial processes in geomorphology. W.H. Freeman and Company, San Francisco, U.S.A
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am Nat* 153:649–659
- Lonzarich DG, Lonzarich MR, Warren ML Jr (2000) Effects of riffle length on the short-term movement of fishes among stream pools. *Can J Fish Aquat Sci* 57:1508–1514
- Magnhagen C (1991) Predation risk as a cost of reproduction. *Trends Ecol Evol* 6:183–185
- Matthews WJ (1998) Patterns in freshwater fish biology. Chapman & Hall, New York, USA
- McCullagh P, Nelder JA (1989) Generalized linear models. Chapman & Hall, London, UK
- Paul MJ, Meyer JL (2001) Streams in the urban landscape. *Ann Rev Ecol Syst* 32:333–365
- Rahel FJ (2002) Homogenization of freshwater faunas. *Ann Rev Ecol Syst* 33:291–315
- Reebs SG (2002) Plasticity of diel and circadian activity rhythms in fishes. *Rev Fish Biol Fish* 12:349–371
- Schaefer J (2001) Riffles as barriers to interpool movement by three cyprinids (*Notropis boops*, *Campostoma anomalum*, and *Cyprinella venusta*). *Freshwater Biol* 46:379–388
- Schlösser IJ (1990) Environmental variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. *Environ Manage* 14:621–628
- Schultz CB (1998) Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. *Conserv Biol* 12:284–292
- Schultz CB (2001) Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82:1879–1892
- Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13:350–355
- Sih A, Ziemba R, Harding KC (2000) New insights on how temporal variation in predation risk shapes prey behavior. *Trends Evol Ecol* 15:3–4
- Vance-Chalcraft HD, Soluk DA, Ozburn N (2004) Is prey predation risk influenced more by increasing predator density or predator species richness in stream enclosures? *Oecologia* 139:117–122
- Vandermeer J, Carvajal R (2001) Metapopulation dynamics and the quality of the matrix. *Am Nat* 158:211–220
- Winemiller KO (1989) Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environ Biol Fishes* 26:177–199
- Winemiller KO (1990). Spatial and temporal variation in tropical fish trophic networks. *Ecol monogr* 60:331–337
- Winer BJ (1991) Statistical principles in experimental design. 3rd edn. McGraw-Hill Book Company
- Woodward G, Hildrew AG (2002) Body-size determinants of niche overlap and intraguild predation within a complex food web. *J Anim Ecol* 71:1063–1074