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HABITAT QUALITY IN A HOSTILE RIVER CORRIDOR

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Abstract. Stream fish often occur in tributaries at high densities, and dispersal between tributaries must occur through the intervening river, whose attributes may differ from those of the tributaries. In Trinidad, tributaries of the Guanapo River have high densities of a killifish, *Rivulus hartii*, but the river also contains a strong piscivore that may affect the quality of the river as a movement corridor linking the adjoining tributaries. We hypothesized that *R. hartii* in the river, where they are scarce and confined to margins, would show stress as predicted for an animal in transit through a hostile corridor. We predicted that river fish would take in less food, grow more slowly, and contain fewer mature oocytes than tributary fish. We tested these predictions by comparing *R. hartii* from paired tributary and river sites for food intake, growth, and oocyte counts. We also asked whether *R. hartii* could spawn successfully in shallow water, such as at the river margins. To determine whether the river would satisfy criteria for its use as a movement corridor (movement along the river and movement in and out of tributaries), we marked 709 *R. hartii* in a 500-m stretch of river and two adjoining tributaries and recaptured them on seven sampling dates over a 15-mo period.

Contrary to our predictions, *R. hartii* in the river showed no stress in the form of reduced food intake, growth, or suppressed reproductive output. Instead, we detected no difference in food intake of *R. hartii* sampled from paired tributary–river sites, and river *R. hartii* displayed a greater growth rate and contained more mature oocytes than did their tributary counterparts. Laboratory and field studies also revealed that *R. hartii* can spawn viable eggs in shallow water that does not cover their bodies.

The movement study confirmed that the river has a conduit function for communication between tributaries, but the river also has a habitat function, as it contains resident individuals that grow and reproduce in the corridor. This means that movement of alleles and recolonization of local extinctions can occur via offspring of dispersers, rather than require successful movement of individuals directly between tributaries.

Key words: biotic factors; conduit; connecting habitat; corridor function; courtship; emigration; growth rate; Hoplias malabaricus; *oocyte production;* Rivulus hartii.

INTRODUCTION

The regional distribution of a species is often multimodal, consisting of patches of high abundance with intervening, connecting habitats containing saddles of low abundance or absence (Brown 1984). Genetic structure (Allendorf 1983, Meffe and Vrijenhoek 1988, Slatkin 1994, Mills and Allendorf 1996) and demographic structure (Kareiva 1983, Burkey 1989, Harrison 1991, Weins et al. 1993) among modes in such populations will depend on movement rates through the intervening habitat, and such movement will presumably depend on the properties of the intervening habitat (Beier 1993, Fahrig and Merriam 1994). In terrestrial landscapes, habitat elements that exist between larger patches may be strips that differ from their surroundings, i.e., corridors (Harris and Scheck 1991), which serve as conduits for the movement of animals between patches (Soule and Gilpin 1991). A corridor may also function as habitat (Forman 1995). Whereas the conduit function of intervening corridors has been well documented (Bennett 1990, Dmowski and Kozakiewicz 1990, Merriam and Lanoue 1990, Wegner and Merriam 1990, Saunders and Rebeira 1991, Harrison 1992, LaPolla and Barrett 1993, Leung et al. 1993, Hill 1995, Lindenmayer and Nix 1993, Downs et al. 1997), much less is known about the habitat function (Bennett et al. 1994, Forman 1995, Tiebout and Anderson 1997).

Understanding the habitat function will be important to models of regional population dynamics and gene flow. For example, a corridor that is unsuitable for feeding and reproduction may serve only as a conduit for the movement of individuals between modes. In this case, the probability of a successful recolonization of a mode that has become extinct would depend on the length of the corridor, or distance between modes, and the difficulty of the intervening terrain, e.g.,

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TABLE 1. A classification of corridors: S, survival; F, feeding; G, growth; R, reproduction.

Reproduce in corridor?	Feed in corridor?		
	No	Yes (≤ maintenance)	Yes (> maintenance)
No	S	F	G
Yes	SR	FR	GR

breaks, predators, and so on. However, a corridor may contain suitable habitat for both feeding and reproduction, and the corridor population, although at low density, may be a reproducing, self-sustaining local population, possibly even exporting individuals to and acting as a source (Pulliam 1988) for the modal populations. In this case, the local extinction of a usually modal site may be more readily recolonized from the corridor habitat, and alleles can travel among modal populations by incorporation into a corridor population, with eventual dispersal into the adjacent modal population.

For convenience, in Table 1 we designate the intervening, intermodal habitat through which animals only move, without feeding or reproducing, as S-corridors (for survival only); those in which feeding also occurs, but at levels not exceeding maintenance, as F-corridors; and those in which positive individual growth occurs as G-corridors. In addition, we designate those in which reproduction occurs as R-corridors. Cross-classifying the feeding category with the reproductive category yields six designations (Table 1). Perhaps the most common view of corridors in the ecological literature is to assume that they are S- or perhaps F-corridors. The existence of G-corridors could call for a different view of population genetics and dynamics. It may not be sufficient to account only for migration rates of individuals among sites, because the presence of growth in the corridor raises the possibility that individuals may arrive at one site from another at a larger body size, which implies higher reproductive value if reproductive value is positively related to body size. Thus, the loss of mass of dispersers to predation can be ameliorated by a gain in mass by those that survive. Similarly, reproduction in R-corridors ameliorates loss of individuals and raises the possibility of communication between modal patches via descendants of dispersers rather than dispersers themselves.

With respect to fish, we lack a precise aquatic analogue for the typical terrestrial corridor, e.g., a strip of forest connecting two larger forested patches. This is because a river that connects two tributaries of lower order will normally be wider and contain a greater volume of water than either tributary. For the purposes of this paper, we refer to a river connecting tributaries as a corridor that can function both as a conduit for the movement of individuals and as habitat for the production of individuals. In previous studies we identified a multimodal distributional pattern (Gilliam et al. 1993, Fraser et al. 1995), in which the tributaries (modes) of a dendritic drainage basin contained high abundances (1–12 individuals/m^2) of a prey fish, the killifish *Rivulus hartii* (Rivulidae), whereas the main, connecting river (corridor), contained very low densities of the prey fish (0.07 *R. hartii*/m^2).

We determined that the presence of the predator fish, *Hoplias malabaricus* (Erythrinidae), in the main river can cause many of the prey to leave the river site, and that the remaining individuals are confined to river margins (Fraser et al. 1995; Power et al. 1985 found a similar shift to river margins in a temperate system), or sometimes shallow locations in elevated riffles. Long gaps (e.g., 50–200 m) between individual prey fish along river margins often occurred, especially in the vicinity of walled ''canyon'' pools in which shallow, cobbled edges were lacking. Further, manipulations of the predator in experimental streams showed that such severe intimidation by the predator resulted in reduced reproductive output and growth; the presence of the predator even shifted adult *R. hartii* growth from positive to negative values (Fraser and Gilliam 1992).

These observations suggest that the river habitat may be an S- or F-corridor, i.e., that chronic predation threat in the river habitat precludes growth and reproduction, and that all fish found there are in transit. In this view, transients may either successfully move into a predator-free tributary, or fail to transit the predator-threatened habitat, where they either remain or suffer predation. In this study we assessed (1) movement of *R. hartii* within the river habitat and movement into and out of tributaries, and (2) the quality of the river habitat revealed by comparison of *R. hartii* in the predator-threatened river with those in the predator-released tributaries, i.e., those in the modal patches. We asked the following questions: (1) Do Rivulus exhibit all three movements necessary for the river to act as a corridor for movement between tributaries, i.e., movement from tributary to river, movement along the river, and movement from river to tributary? (2) Is the incidence of empty guts greater in the river fish than the tributary fish? (3) Do river and tributary fish differ in the amount of food in their guts? (4) Does positive growth occur in the predator-threatened river habitat, and is it depressed relative to tributary growth? (5) Do mature oocytes occur in river fish? (6) Do *R. hartii* perform courtship and spawn viable eggs in extreme shallow margins or edges to which they are restricted in river habitat?

The hypothesis that the river functions as a corridor would be supported by a positive answer to Question 1. The hypothesis that predator-threatened river *R. hartii* are stressed relative to predator-released tributary *R. hartii* is addressed by the remaining five questions, which also appraise whether the river corridor is an S- or F-corridor.

METHODS

Study site

The study was done in the Heights of Guanapo watershed on the southern versant of the Northern Range Mountains of Trinidad. The watershed contains a major drainage, the fourth-order Guanapo River, with numerous connecting lower order tributaries. Our movement study was done in a 500-m stretch of river and the lower stretches of two connecting tributaries, here designated Tributary 1 and 2. The lower sections of each tributary differed from one another with respect to the location of the first waterfall blocking the upstream movement of *H. malabaricus.* Tributary 1 contained a 110-m section from below its first barrier waterfall to its confluence with the main river, and we found that *H. malabaricus* occasionally invaded this section (from none to two *H. malabaricus* were found in Tributary 1 on each of the sampling dates of the study). Tributary 2 contained several barrier waterfalls within 20 m of the main river and was predator-free on each sampling date of the study. *R. hartii* were abundant in both tributaries. For the food and oocyte studies, additional river–tributary pairs were sampled from the 3-km stretch of river downstream of the movement study.

Movement

To assess movement (Question 1), we marked *R. hartii* in the 500-m stretch of river and two adjoining tributaries, starting in January 1996, and at ~2-mo intervals thereafter, through March of 1997, for a total of seven sampling dates during which marked fish were recaptured. In all, 709 *R. hartii* were marked over this period. We searched for *R. hartii* after dark, between 1830 and 2400. *R. hartii* were dipnetted, anesthetized in tricane methanesulfonate (MS222), measured for total length, and marked by injecting with a small dot (~1 mm diameter) of elastic polymer that fluoresces under ultraviolet illumination (Northeast Marine Technology Incorporated, Shaw Island, Washington, USA). We used seven body positions and five colors (red, orange, green, blue, and yellow) to generate a three-dot code that uniquely marked each fish. We marked fish >32 mm total length (TL) using 3 mL tuberculin syringes with 29-gauge needles.

Using recaptured fish, we estimated per capita emigration from tributaries to river (E_T) and emigration from river to tributaries (E_R) for each of the seven recapture periods. Per capita emigration was calculated as $n/(N + n)$, where n = number of recaptured fish that had left the source during the period, and N = number of recaptured fish still present in the source at the end of the period. In calculating E_T, we pooled the number that emigrated from Tributaries 1 and 2 (n) and also pooled the number that remained in Tributaries 1 and 2 (N) to calculate a single estimate for each date. We used a paired t test on log-transformed data to test H_0: $E_T = E_R$. Some *R. hartii* were recaptured more than once, and in such cases we used only the first recapture interval in statistical analysis and figures regarding movement and growth.

Stomach contents

To assess stomach contents (Questions 2–3) we collected 8–9 *R. hartii* from each of six paired tributary and river sites in January 1995, and 15 *R. hartii* from each of four additional tributary–river paired sites in January 1997. A paired site consisted of a short stretch of tributary (10–50 m) above the downstream-most barrier waterfall, and a section of the main river in the vicinity of the tributary mouth. Collections were made by dipnetting during early evening, when *R. hartii* feed actively. *R. hartii* were killed immediately by anesthesia (MS222), measured for TL, and preserved. Contents of stomachs were examined under a dissecting microscope. Each prey item was identified to taxonomic group and its average width and maximum linear body dimension measured to the nearest 0.1 mm. The volume of each prey item was calculated by treating it as a cylinder. This method excludes appendages and only approximates the true volume, but we considered it to be adequate for the purpose of comparing river with tributary sites. We calculated the total volume (cubic millimeters) of food in each stomach by summing the individual prey volumes. The percent occurrence of a given taxon in the diet of tributary or river fish was calculated as follows. First, the percent occurrence of taxon i at each of the 10 replicate sites ($k = 1, \ldots, 10$) was calculated as $P_{ik} = n_{ik}/N_k \times 100\%$, where n_{ik} = number of stomachs containing taxon i at site k, and N_k = number of stomachs examined at site k. Second, the mean percent occurrence of taxon i ($P_i = \Sigma P_{ik}/10$) and its standard error were calculated from those 10 values.

We calculated the diversity of prey items for each tributary and river site using the Shannon-Weaver index of diversity, $H' = -\Sigma p_i \ln p_i$, where p_i is the proportion by number of prey in category i and the summation is taken across prey categories. We used a two-tailed, paired t test to compare the 10 paired tributary–river Shannon-Weaver indices.

We compared the volume of food, the dependent variable, in stomachs of the tributary and river fish by a two-way ANCOVA with the covariate being fish length and the independent variables being location (tributary vs. river, treated as a fixed effect) and block (tributary–river pairs 1–10, treated as a random effect). Differences among the 10 tributary–river pairs might reflect a variety of sources of variation, e.g., position along river, or the year the sample was taken. Accordingly, we use the paired structure to control for such variation among the tributary–river pairs (block effect treated as a random factor), and we tested for the location effect (river vs. tributary) using the location × block variance as the error term (error df = 9, derived

from the $N = 10$ pairs). Stomach volumes were log transformed for analysis.

Growth

To assess growth rates in tributary and river sites (Question 4) we did two growth experiments, a short-term experiment in Tributary 1, and a subsequent long-term experiment in Tributary 2 using the recapture data from our movement study. The short-term experiment was done in July 1995 in Tributary 1 above the barrier waterfall at 110 m. We marked *R. hartii* in two pools, separated by a riffle (pool 1: $N = 15$, mean TL (± 1 SD) = 46.5 $\pm$ 6.9 mm; pool 2: $N = 13$, mean = 45.1 $\pm$ 9.6 mm). In the river site we marked 20 *R. hartii* in a 100-m stretch of river (mean = 42.1 $\pm$ 11.9 mm). We used the same marking procedures as in the movement study. We recaptured fish 16 d later.

The long-term experiment (15 mo) used the fish that we used in the movement study, comparing growth in the predator-free Tributary 2 to growth in the 500-m stretch of river. We had initially intended to replicate this study by including Tributary 1. However, the predator *H. malabaricus* appeared in the lower section of the tributary on the second recapture date, precluding its use as a predator-free tributary.

We analyzed Experiments 1 and 2 separately. We compared the instantaneous per day growth rate $[\ln(TL_{recap}) - \ln(TL_{initial})/(d_{recap} - d_{initial})]$ in the tributary vs. river using a one-way, fixed-effects ANCOVA design in which fish length was the covariate and location (river, tributary) the independent variable.

Oocytes

To assess oocytes (Question 5), we used the same fish from the 10 paired tributary–river sites used for stomachs, but made an additional collection in March 1997 of 10 female *R. hartii* from each of four additional paired sites. Thus, in all, we sampled *R. hartii* from 14 paired tributary–river sites. All ovaries contained oocytes in various stages of maturity. Because oocytes are spawned at 1.75 mm diameter (D. F. Fraser, *unpublished data*), we operationally treated those >1.75 mm in diameter as being spawnable, as measured under a dissecting microscope fitted with an ocular micrometer.

To compare the number of mature oocytes in the tributary and river fish, we used an ANCOVA design with fish length as the covariate and the independent variables location (tributary vs. river, fixed effect) and block (tributary–river pairs 1–14, random effect). As with the stomach analysis, we used this design to control for variation between the tributary–river pairs (block effect). Oocyte counts were log transformed for the analysis.

Spawning in shallow water

To determine whether *R. hartii* can spawn and produce viable eggs in shallow water (Question 6), such as in river margins, and, if so, whether there is a reduction in number or in viability of eggs, we did tests first in laboratory aquaria and then in a natural stream in Trinidad. In preliminary tests in aquaria, we readily determined that *R. hartii* would attempt to spawn in water shallower than the depth of their bodies. Because *R. hartii* in predator-released habitats, unlike those in predator-threatened habitats, have access to both deep and shallow water, we further evaluated their spawning behavior by doing a series of choice experiments in which *R. hartii*, collected from various localities in Trinidad, were given a choice between spawning in shallow vs. deep water. We also tested for the effect of light vs. dark on the behavior by doing the tests both in daylight and at night.

We divided a 30 $\times$ 80 cm aquarium into shallow and deep halves of equal length and surface area, but with one half 30 cm deep and the other 1 cm deep. The shallow half was made by raising a plexiglass floor to create the desired water depth. We found that *R. hartii* will readily deposit eggs in the frayed ends of a manila rope, 2.5 cm diameter, 10 cm long, and seem to prefer this to alternative sites such as sponge filters, substrate gravel, and glass walls of the aquaria. We searched any alternative sites, but rarely found eggs deposited outside of the spawning ropes. Hence, the ropes were a convenient tool for assaying egg production. Each half of the test aquarium contained one spawning rope placed on the bottom.

Subjects were seined from tributaries in three different drainages in the Northern Range Mountains: Marianne, Arima, and Guanapo. Prior to testing, the fish were maintained in the laboratory under a 12:12 (L:D) h cycle with artificial lighting, at a water temperature of 20°C. The fish were fed a mixture of commercial flake food, chopped beef liver, and canned tuna.

Twenty-four hours prior to testing, one male and one female were moved to separate holding tanks, the choice of subjects being arbitrary, as all were eventually tested. After 24 h of separation, the sexes were brought together again in the test tank. Courtship and spawning usually started within a few minutes. The spawning ropes were then periodically checked during the remainder of the day or night.

Field tests were done in the third-order Ramdeen Stream (Fraser and Gilliam 1992) and one of its first-order tributaries during July and August 1994. We chose five pools in each stream based on the criteria that each pool contained a shallow beach and that it contained at least five mature female *R. hartii*. Because our previous work (D. F. Fraser and J. F. Gilliam, *unpublished data*) has shown that mature, unthreatened *R. hartii* remain in home pools for extended periods (weeks), we made no attempt to restrict movement of subjects by screening. However, we did modify pools by removing organic debris and rocks to minimize the number of alternative spawning substrates. Six spawning ropes, held in position by a stone placed on one

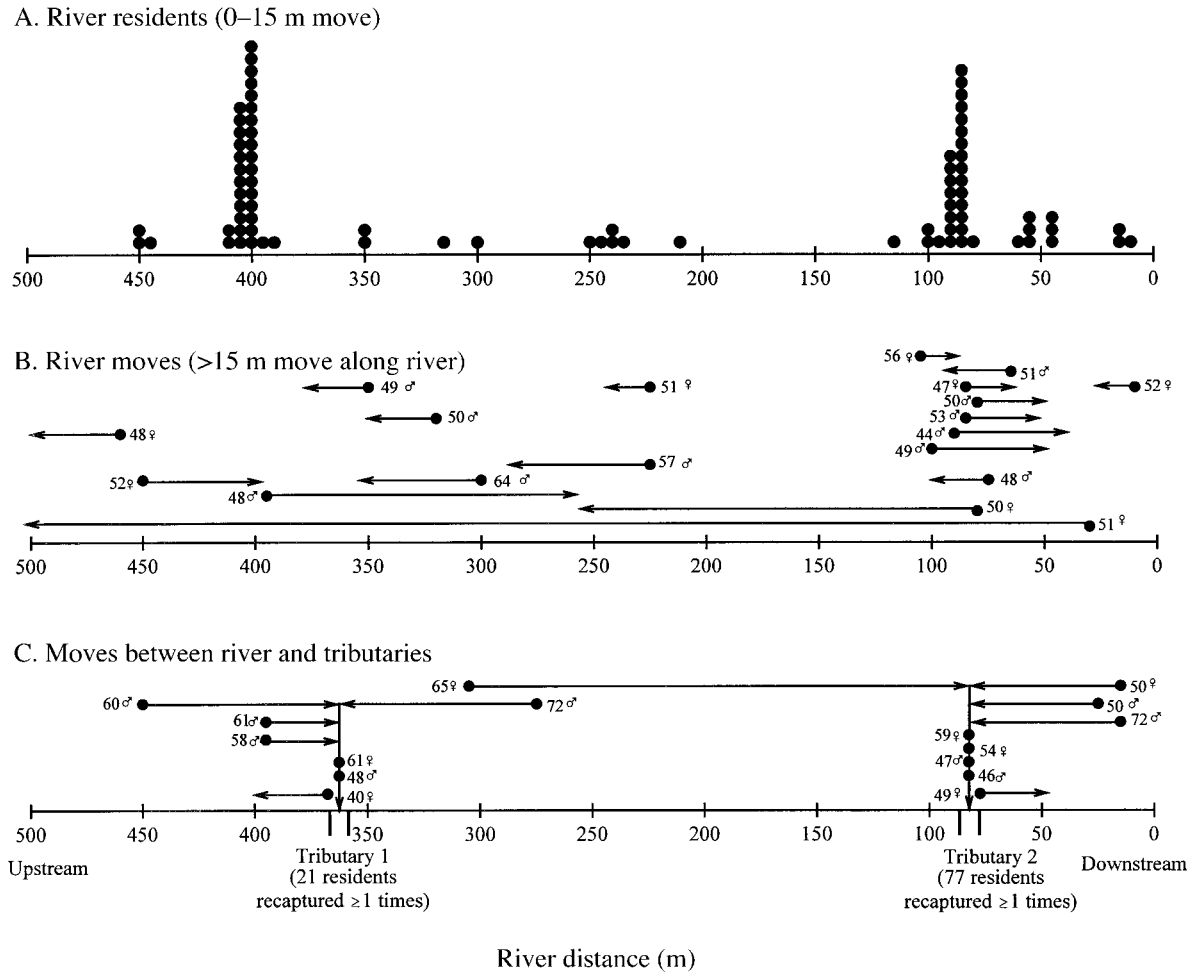

FIG. 1. Movement of marked fish in the Guanapo River study area. Each dot represents a single fish. For individuals recaptured more than once, only the first recapture is plotted. (A) *R. hartii* that stayed within 15 m of initial capture site. (B) *R. hartii* that moved >15 m from initial capture site; arrow shows beginning and end of move. (C) *R. hartii* that moved into or out of Tributaries 1 and 2; numbers of fish recaptured that stayed in each tributary are given for that tributary below the *x* axis. In (B) and (C), total length (mm) of fish at time of recapture is given at the beginning of each arrow. The figure shows that three criteria for corridor function were satisfied: movement along river, movement into tributaries, and movement out of tributaries.

end, were set in the shallow beach, 0.5–3.0 cm deep, with most of the rope exposed above the water level, and six were placed in the deeper part of the pool, usually the middle, which varied in depth from 8 to 20 cm. We checked the spawning ropes for eggs prior to sunrise, 0430–0530, and prior to sunset, 1630–1730, for a period of 14 d.

We evaluated the laboratory experiments comparing the diurnal vs. nocturnal proportion of eggs laid shallow by *R. hartii* derived from three locations (Marianne River, Ramdeen Stream and the Guanapo River), using a 2 × 3 ANOVA, with proportion laid shallow, the dependent variable, arcsine square root transformed prior to analysis. In the field experiments we combined the results from the two small streams and analyzed the proportion of eggs laid shallow using a *t* test.

RESULTS

Movement

Fig. 1 shows that three criteria for demonstrating corridor function were satisfied. The study yielded 119 *R. hartii* for which the original capture or recapture or both occurred in the river. Of these 119 fish, 27 (22.7%) made moves >15 m along the river (Fig. 1B), while another 16 (13.4%) entered or left tributaries (Fig. 1C). However, the study also indicated that, in addition to functioning as a corridor, the river also functions as a habitat, because the remaining 70.6% of the fish remained in the immediate vicinity, within 15 m, of their original capture (Fig. 1A), indicating that the river contains individuals that can be considered residents. Fig. 1C shows that some of the 14 fish that entered tribu-

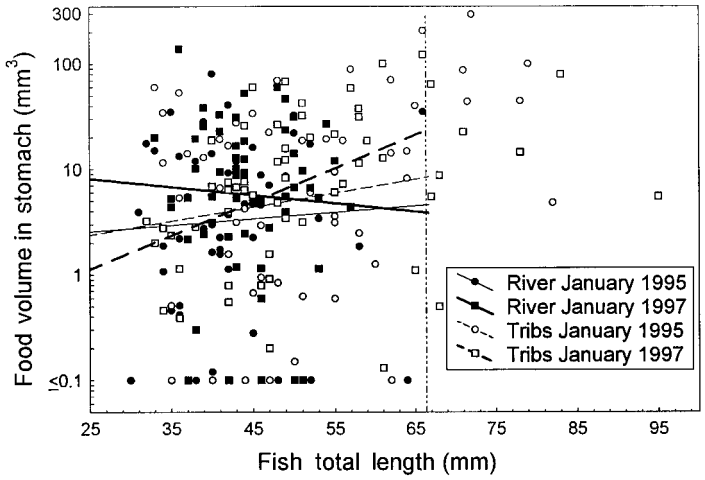

FIG. 2. Regressions of food volume in stomachs of *R. hartii* on fish total length, from river (N = 112) and tributary (N = 117) collections made in 1995 and 1997 (shown in key). The analyses revealed no differences between river-dwelling and tributary-dwelling fish in either food volume or the proportion of stomachs that were empty. Fish were collected from 10 paired river and tributary sites (not shown individually) collected in either 1995 or 1997 (shown). Statistical analysis was restricted to fish <67 mm TL (vertical line).

taries moved from somewhat distant locations along the river to enter tributaries, e.g., a 65-mm female moved 225 m downstream to enter Tributary 2, while 6 *R. hartii* entered tributaries from nearby river sites at or close to the tributary–river junction.

Of the 16 recaptured *R. hartii* moving into and out of tributaries, 14 entered tributaries while only two moved out. Converting these data to per capita rates for each sampling period yields estimates of tributary emigration (mean ± 1 SE = 0.006 ± 0.004 fish) and river emigration (mean = 0.081 ± 0.023). These estimates are not adjusted for any unestimated differences in mortality rates among sites, but suggest that the river may be a net exporter of *R. hartii* (t = −3.19, df = 6, P = 0.019). We note that three fish >70 mm TL were found in the river, of which two subsequently emigrated to the tributaries, suggesting a behavioral basis for the paucity of large fish in the river.

Stomach contents

Sampling of the 10 paired tributary and river sites confirmed a pattern that we had previously reported (Gilliam et al. 1993): The maximal length of the tributary-dwelling *R. hartii* is greater than the maximal length of the river-dwelling fish. Below, we will restrict our statistical analysis to the range of fish collected in the river in the diet study; i.e., <67 mm TL. Although we excluded the larger tributary-dwelling fish from the statistical analysis, we include them in Fig. 2 for completeness. Also, for simplicity and clarity in Fig. 2, we do not show separate symbols and regressions for each of the 10 paired sites; we depict the two sampling times (1995 and 1997), while using the full paired design in the statistical analyses.

Contrary to our initial hypothesis, river fish showed no higher incidence of empty stomachs than tributary fish: 9 of 112 river fish stomachs were empty, vs. 5 of 117 tributary fish stomachs (Yates corrected χ^2 = 0.83, df = 1, P = 0.36). Also contrary to our initial hypothesis, analysis of stomach volumes revealed no deficit in the mean amount of food taken by river-dwelling *R. hartii,* relative to those in the tributaries (Fig. 2). The stomach volumes of river fish did not differ significantly from those in the tributaries ($F_{1,9}$ = 0.43, P = 0.53). The block effect was significant ($F_{9,194}$ = 3.16, P = 0.001), with no significant interaction between location and block ($F_{9,194}$ = 1.63, P = 0.110). The amount of food increased with fish length (length as a covariate, $F_{1,197}$ = 14.11, P = 0.0002). Over all sites, the slopes of food volume regressed on length did not differ significantly between tributary and river sites ($F_{1,199}$ = 3.15, P = 0.08). Retrospective power analysis (Steidl et al. 1997) estimated the power to detect the observed-effect size for the river–tributary comparison to be 0.07. Adjusted means (±1 SE) were 0.915 ± 0.062 in the river and 0.848 ± 0.061 in the tributaries (the means reflect the $\log_{10}(X + 1)$ transformation), suggesting that a difference between river and tributary sites, if it exists but was undetected, is most likely to reflect higher mean food in the river, if the covariate is assumed to be homogeneous. However, we also note that higher sample size might reveal a nonhomogeneity in the covariate, since the data (Fig. 2) suggest that differences in mean intake, if present but undetected, may also be size specific.

Fig. 2 shows our 1995 and 1997 collections separately, but a separate analysis showed no significant difference between years ($F_{1,210}$ = 1.57, P = 0.21). All assumptions of the ANCOVA, homogeneity of slopes and variances, were met for this analysis. Tributary sites were all under closed forest canopy, whereas river sites tended to be more open, with canopy at the river edges. Tributary fish were observed foraging at all depths and distances from shore, but river fish were confined to river margins. Yet in both tributary and river fish aquatic dipteran larvae, ants, and winged insects (primarily dipterans) were the most frequent items by percentage occurrence in stomachs (Fig. 3). The

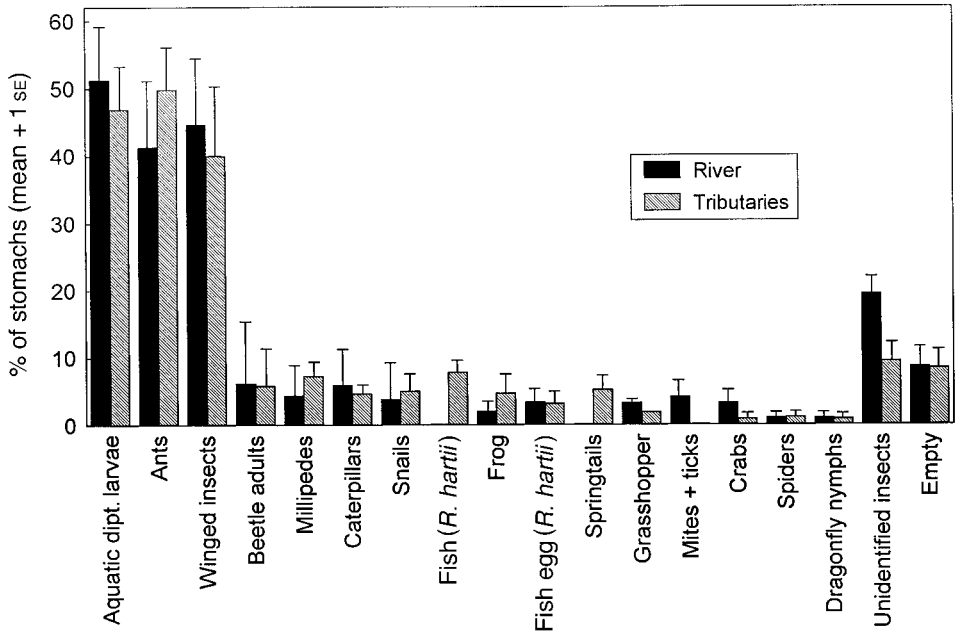

FIG. 3. Dietary items found in the stomachs of *R. hartii* from river and tributary locations. Diets were qualitatively similar, and diet diversity, as measured by the Shannon-Weaver Index, did not differ between river- and tributary-dwelling fish.

diversity of taxa consumed, calculated by the Shannon-Weaver index (H'), was similar for the 10 tributary (mean $H' \pm 1$ SE $= 1.57 \pm 1.39$) and river (1.59 ± 0.07) sites (paired $t = -0.19$, df $= 9$, $P = 0.86$).

Growth

Contrary to the hypothesis that the river is an S- or F-corridor in which individual fish fail to show positive growth, the river fish showed positive mean growth over much (Fig. 4, Experiment 1) or all (Fig. 4, Experiment 2) of the range of fish lengths occurring in the river corridor. Hence, we operationally classify the river as a G-corridor, while noting that the classification is most confidently applied to all but the largest fish found (Fig. 4). Further, mean growth of corridor fish was not depressed relative to the mean growth of tributary fish. Specifically, in Experiment 1, the ANCOVA yielded a significant main effect of location ($F_{1,22} = 22.12$, $P < 0.001$), but the slopes were not homogeneous ($F_{1,21} = 5.03$, $P = 0.036$), and the assumption of equal variances could not be met owing to the lack of variance in estimated growth rates of the tributary-dwelling fish (Fig. 4, Experiment 1). Hence, we also examine the 95% confidence interval for mean growth in the river, and we note that the confidence interval excludes zero growth for fish <52 mm TL. We conclude that mean growth of fish <52 mm TL in the river was greater than zero and greater than tributary fish. In Experiment 2, sample sizes were much larger and taken over a longer time period. In that experiment, the ANCOVA yielded a significant effect of location ($F_{1,327} = 55.36$, $P < 0.0001$), the covariate was not significant ($F_{1,327} = 0.28$, $P = 0.600$), and slopes were judged homogeneous ($F_{1,326} = 1.93$, $P = 0.166$). Inspection of the 95% confidence intervals for mean growth indicates that mean growth was positive in both locations over the full range of lengths found, and that the 95% confidence intervals for river and tributary fish do not overlap for fish length <67 mm. From Experiment 2, we conclude that river fish show positive mean growth at all sizes found, and that their mean growth exceeds the mean growth of tributary fish for TL <67 mm.

Oocyte counts

As with analyses for food, statistical analyses for oocytes were restricted to fish <67 mm TL. Fig. 5 shows each collection period separately, while the full paired structure (14 river–tributary pairs) is used in the statistical analysis.

Contrary to our initial predictions, Fig. 5 shows that river *R. hartii* produced mature oocytes. Moreover, the ANCOVA on oocyte counts revealed that river fish contained significantly more oocytes than did tributary fish ($F_{1,13} = 6.93$, $P = 0.021$). Oocyte counts increased with body size ($F_{1,170} = 60.33$, $P \leq 0.001$), and the slopes did not differ significantly between river and tributary locations (test for parallelism, $F_{1,166} = 0.00$, $P = 1.00$). Fig. 5 shows our 1995 and 1997 collections separately, but a separate analysis revealed no difference between the 1995 and 1997 collections ($F_{2,189} = 0.13$, $P = 0.87$). The proportion of fish with no mature oocytes did not differ between river and tributary sites

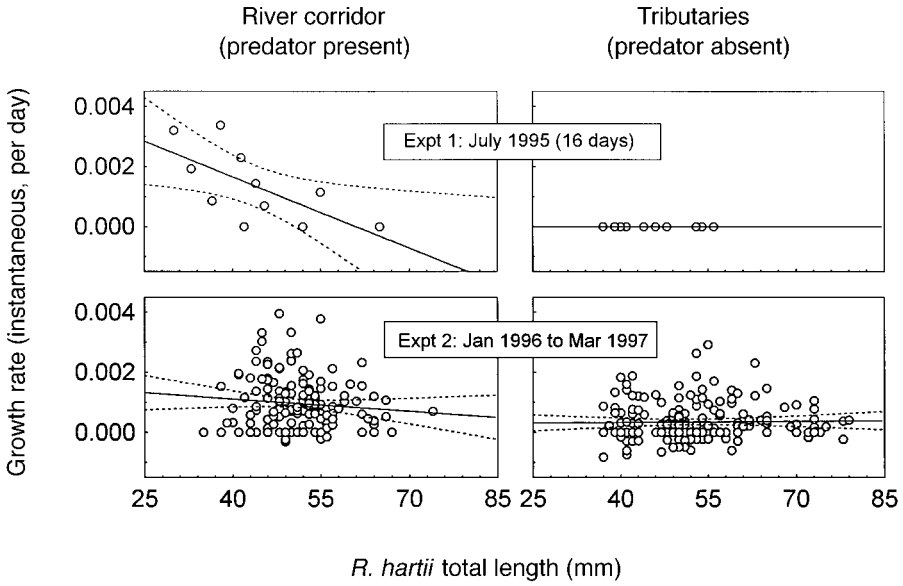

FIG. 4. Regressions of growth of *R. hartii* in the Guanapo River study area on fish total length. Dashed lines are 95% confidence limits for the regression line. Top: short-term study (Experiment 1) done in the river study site and in its paired Tributary 1 site above barrier waterfall. Bottom: long-term study (Experiment 2) done in the river study site and in its paired Tributary 2 site above barrier waterfall. Contrary to our initial hypothesis, the river fish did not show less growth than the tributary fish, and river fish <52 mm (Experiment 1) or <67 mm (Experiment 2) had higher mean growth than their tributary counterparts.

(29 of 93 with no mature oocytes in river, 36 of 103 in tributary, Yates corrected $\chi^2 = 0.17$, $P = 0.68$).

Ability to spawn in shallow water

The oocyte counts above establish that river fish can produce mature oocytes, but they do not address the issue of whether they can lay the oocytes successfully in the very shallow water of river margins where we often observe *R. hartii*. The laboratory results showed that *R. hartii* readily deposited their eggs in shallow water. They were indiscriminate with respect to depth during daytime spawning (proportion shallow, mean ± 1 SE = 0.59 ± 0.05), but at night *R. hartii* almost always spawned at the shallow site (proportion shallow = 0.98 ± 0.02) (Fig. 6). In addition, this significant time effect ($F_{1,74} = 67.75$, $P < 0.001$) was consistent across all three drainages (location effect, $F_{2,74} = 0.14$, $P = 0.87$; interaction effect, $F_{2,74} = 0.59$, $P = 0.56$).

The results from the field study were similar to the laboratory experiments (Fig. 6), even though we had little control over what was happening in the test pools, e.g., we could not control which fish were spawning eggs, nor did we know how many pairs were responsible for the eggs that we obtained from the ropes. As in the laboratory, the field fish were indiscriminate during the day (mean proportion spawned shallow = 0.49 ± 0.03), but spawned almost exclusively in the shallows at night (1.00). The proportion of eggs laid in

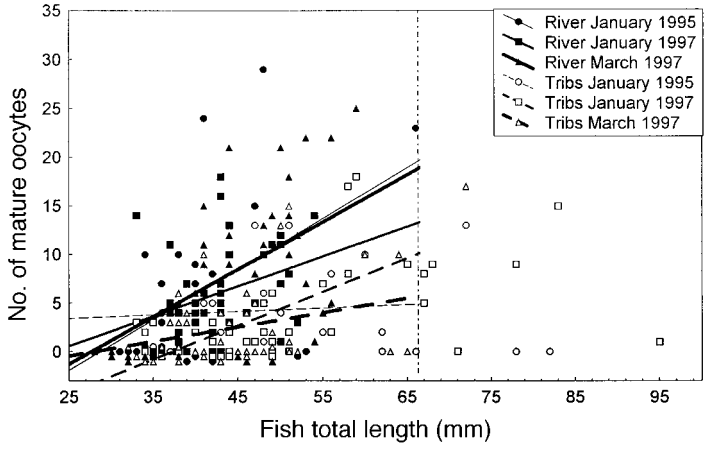

FIG. 5. Regressions of oocyte counts on fish total length for *R. hartii* collected from river and tributary locations in 1995 and 1997 (shown in key). River fish had higher mean oocyte counts than did their tributary counterparts (ANCOVA, $P = 0.02$). Fish were collected from 14 paired river and tributary sites (not shown individually). Statistical analysis was restricted to fish <67 mm TL (vertical line).

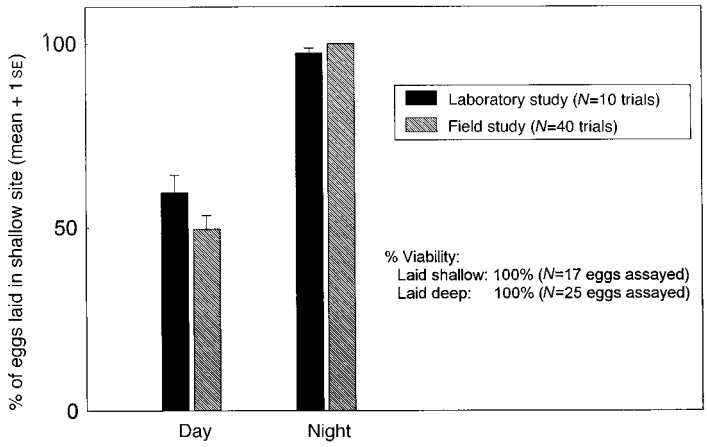

FIG. 6. Choices of spawning depth (mean + 1 SE) by *R. hartii* in laboratory and field experiments. Fish were indifferent between deep and shallow sites in the day but chose the extreme shallows at night. All eggs assayed were viable, regardless of the egg-laying site.

shallow habitat in daytime was significantly different from the proportion at night ($t = 5.05$, df = 18, $P < 0.001$). Assays on a subset of the eggs laid in shallow and deep water sites revealed that fertilization was successful in both sites (Fig. 6, 100% fertilization in each site).

Our field experiments were in predator-released zones of Ramdeen Stream and its tributary, and one may now ask if *R. hartii* spawns eggs in the predator-threatened Guanapo River, where the stomach and oocyte analyses were done. *R. hartii* eggs are difficult to find in nature, even in tributaries, but we have now occasionally found eggs in root masses and leaf packs along the Guanapo River. We reject the hypothesis that restriction of *R. hartii* in predator zones to the shallow river margins precludes successful spawning.

DISCUSSION

The results of this study indicate that the river habitat connecting tributaries serves both as conduit for the movement of *R. hartii* between tributaries and as habitat for the growth and reproduction of *R. hartii.* Although the density of *R. hartii* is low in the river relative to the tributaries, often with gaps of many meters between any two individual fish, the river population of *R. hartii* includes growing individuals capable of reproduction, and thus represents a potentially self-sustaining river population, rather than simply transients, as we initially hypothesized based on previous work (Fraser and Gilliam 1992, Gilliam et al. 1993).

We can now operationally classify the river as a GR-corridor (growth and reproduction), rather than a S- or F-corridor (Table 1). We also recognize that spatial and temporal variability in predation intensity, food availability, and other variables within the river are likely to produce corresponding spatial and temporal variation in growth and reproductive activity, so a classification on a fine spatial or temporal scale could produce a shifting mosaic of corridor classifications within subdivisions of the river. However, we lack sufficient data to detail such within-river differences.

Given that the river contains *R. hartii* with positive individual growth and the capability of reproducing, and is not used solely as an S- or F-corridor, we should modify our view of its role in affecting the genetic structure of the tributary populations. If the river were an S- or F-corridor, the genetic isolation of a specific tributary could simply depend on the rate of arrival of individuals directly from other tributaries (Slatkin 1994, Forman 1995), where biotic and abiotic factors such as predators, habitat structure, and disturbances could affect movement rates and mortality through the corridor (Doak et al. 1992, Knappen et al. 1992, Gustafson and Gardner 1996). Similarly, regarding regional population dynamics, if the river were an S- or F-corridor, recolonization of a tributary after a local extinction could only occur by arrival of at least one male and one female born in other tributaries. However, given our finding, emigrants from tributaries may join reproducing river populations, resulting in these being mixtures of genotypes from many tributaries; genetic communication can occur via offspring of tributary emigrants, and recolonization can occur via the reproductive output of the river corridor itself. A more accurate general view may be to treat the system as an island–mainland model (mainland = river), albeit an unusual case, because the central mainland has a much lower density than the peripheral islands. The connecting river can be viewed both as a corridor among population modes, and as a central mainland that contains the genetic diversity of joining tributary populations, and in which predation threat may act as a *R. hartii* ''pump,'' as *R. hartii* leave the river due to predation threat (Fraser et al. 1995). The movement study suggests that the river may be a net exporter of *R. hartii,* but characterization of the river population as a source or sink would require measurement of four vital rates (births, deaths, immigration, and emigration; Pulliam 1988), and, as argued by Watkinson and Sutherland (1995), its classification may be difficult to discern.

The presence of reproductive *R. hartii* in predator-

threatened habitat and the elevated growth rates of *R. hartii* in the river over those in the tributaries would not be readily predicted by our previous finding that the presence of *H. malabaricus* could severely impact demographic rates and the behavior of *R. hartii*. *H. malabaricus* suppressed reproductive output and retarded the growth of adult *R. hartii,* but not juveniles (Fraser and Gilliam 1992). The experiments in Fraser and Gilliam (1992) emphasized the short-term behavioral suppression of growth and reproduction following a predator invasion of a site, and were designed to imitate predator effects in small headwater streams without a safe refuge. In contrast, the complex edge areas of rivers may offer relatively safe refugia where *R. hartii* may resume their normal daily activities.

We found higher oocyte counts in the river fish than the tributary fish, but interpretation of the result remains speculative. Higher counts do not imply higher daily production; they may indicate accumulation of oocytes, perhaps due to a lack of spawning opportunities due to predation threat in the river (e.g., sparseness of mates or safe spawning sites). Although we have no direct information on the availability of mates or spawning substrates in the river, the former may be the more severe constraint on spawning, because our shallow-water breeding experiments demonstrated that *R. hartii* can readily spawn in shallow refugia along the river margins. We also note that guppies, *Poecilia reticulata,* in high-predation sites in Trinidad evolve higher reproductive output than those in low-predation sites (Reznick et al. 1997), but we do not know whether *R. hartii* do the same.

Since the predator induces a spatially fragmented pattern of abundance (high tributary and low river population density when the predator is in the river; Fraser et al. 1995), an immediate hypothesis might have been that the predator also fragments the tributary populations dynamically, i.e., that there will be less gene flow and population-dynamic linkage among the tributaries when the predator occupies the river. However, spatial fragmentation by the predator might not imply dynamical fragmentation in this system. The predator might induce greater movement when spates flood shallow refuge pools within cobbled edges and raised riffles, inducing the prey to seek new, safe sites, relative to movement by the prey if the predator is absent from that section of the river (i.e., above the predator's upstream limit at a barrier waterfall in the river). Drying of such temporary refuge pools may have the same effect of greater movement by displaced prey if predators are present. Also, as we have already found in experimental mesocosms (Fraser et al. 1995), we can hypothesize that predators will increase the probability of river-to-tributary shifts. Thus, we can list two ways in which the predator may be a retarding force in movement of fish and/or alleles among tributaries: The predator can eat some of the potential dispersers, and it can discourage movement along the river (i.e., ''longitudinal'' movement along the river, as through steep-walled canyon pools). We can also list two ways in which the predator may act as a promoter of movement among tributaries: The predator may increase movement by inducing longitudinal movement by prey occupying side pools obliterated by flooding or drying (the prey may scatter along the river rather than remain in the now-exposed site), and the predator may increase the probability that *R. hartii* at the base of a tributary make shifts from the river into the tributary (''lateral'' movement).

Townsend and Crowl (1991; see also Crowl et al. 1992, Flecker and Townsend 1994 for discussion) did a broad survey of the fish of New Zealand streams. They suggested that predation by non-native brown trout, *Salmo trutta,* was the principal agent of spatial fragmentation in the distribution of a native stream fish, *Galaxias vulgaris,* but found no evidence for predator escape mechanisms in the native species, which they attributed to their historical lack of contact with predators. In such a case we might expect that the predator induces both spatial and dynamical fragmentation. In contrast, our earlier mesocosm experiment (Fraser et al. 1995) compared the between-tributary movement by *R. hartii* in the presence and absence of *H. malabaricus,* a native predator, and found that the retarding effect of the predator (some potential dispersers killed) was outweighed by its inducement of greater distance moved by surviving dispersers, including facultative lateral shifts into tributaries by the prey. The effect of the predator in producing spatial fragmentation of *R. hartii* is clear, but the net effect of the predator in decreasing or increasing dynamical fragmentation among tributaries in nature remains unknown.

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