

Explaining Leptokurtic Movement Distributions: Intrapopulation Variation in Boldness and Exploration

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ABSTRACT: Leptokurtic distributions of movement distances observed in field-release studies, in which some individuals move long distances while most remain at or near their release point, are a common feature of mobile animals. However, because leptokurtosis is predicted to be transient in homogeneous populations, persistent leptokurtosis suggests a population heterogeneity. We found evidence for a heterogeneity that may generate persistent leptokurtosis. We tested individuals of the Trinidad killifish *Rivulus hartii* for boldness in a tank test and released them back into their native stream. Boldness in the tank test predicted distance moved in the field releases, even after effects of size and sex were removed. Further, data from a 19-mo mark-recapture study showed that individual growth correlated positively with movement in a predator-threatened river zone where the *Rivulus* population is spatially fragmented and dispersal is likely to be a hazardous activity. In contrast, no such correlation existed in a predator-absent zone where the population is unfragmented. These results show that a behavioral trait, not discernible from body size or sex, contributes to dispersal and that a component of fitness of surviving "dispersers" is elevated above that of "stayers," a fundamental assumption or prediction of many models of the evolution of dispersal through hazardous habitat.

Keywords: boldness, movement, dispersal, leptokurtic, exploration, *Rivulus*.

Many important ecological processes depend on movements made by individuals, for example, gene flow (Endler 1977; Kot et al. 1996; Bohonak 1999), metapopulation

dynamics (Hastings and Harrison 1994), and the reduction of local extinctions (Brown and Kodric-Brown 1977), and the frequency distributions of movement distances for many taxa are typically leptokurtic (Dobzhansky and Wright 1943; Mayr 1963; Endler 1977; Shields 1982; Paradis et al. 1998; Gomez and Samora 1999). Leptokurtic distributions (higher central peak and larger tails than a normal distribution) that persist over time are counter to the predictions for random walks in homogeneous populations because the central limit theorem predicts that the distribution of distances moved should approach normality with repeated draws (samplings) of individuals if draws are from the same population. Okubo (1980) and Skalski and Gilliam (2000) proposed a population heterogeneity hypothesis to explain leptokurtic distributions, drawing from the fact that leptokurtic distributions can be generated as the composite of two or more normal distributions with similar means and contrasting variances. Heterogeneity in movement behavior could derive from differences among sexes, age, or social status (Ketterson and Nolan 1985; Quinn and Brodeur 1991; Armstrong et al. 1997) or other properties of the phenotype. Behavioral or psychological assays could also reveal differences (Warren and Callaghan 1975; Verbeek et al. 1994), and detailed work might reveal a biochemical basis for the variation, as recently proposed for novelty-seeking behavior in humans (Benjamin et al. 1996; Ebstein et al. 1996). Differences in the variances of the normal distributions of movement distances generated by any of these factors, for example, sex, could produce, when plotted together, the observed leptokurtic patterns.

In a recent movement study of a tropical stream fish, Gilliam and Fraser (2001) found leptokurtic distributions of movement distances. Such leptokurtosis could potentially be explained by phenotypic or environmental heterogeneity, such as sex, habitat, predators, and season or a heterogeneity in an underlying behavioral trait affecting movement. Here, we hypothesize that variation in a behavioral trait, boldness, is a source of the observed lep-

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tokurtosis, operationally defining boldness as the propensity to move through and explore unfamiliar space (Russell 1983; Wilson et al. 1993). We evaluate this hypothesis in three ways. First, we statistically evaluate the leptokurtic pattern of dispersal distances observed in Gilliam and Fraser (2001) to ask whether the pattern persists when the effects of sex, season, microhabitat, and predators are removed from the calculation of kurtosis. If the leptokurtic distribution persists after eliminating these factors, the existence of interindividual variation in the propensity to move remains a possible source of the unexplained leptokurtosis. Second, we test for within-individual consistency in the propensity to move. Third, and most directly, we then perform explicit tests for a correlation between boldness and movement in the field. We do this by assaying fish for boldness in laboratory trials and recording distance dispersed in field releases, testing whether exploratory behavior in the laboratory assay predicts movement in the field.

One way in which possessing the bold phenotype could benefit an individual would be if exploratory movement from a patch led to improved feeding opportunities, as then manifested by increased growth and/or fecundity. However, the net advantage of such movement should be weighed against the cost of movement, such as the hazard of mortality during movement. A succession of metapopulation models of the evolution of evolutionarily stable dispersal behavior (e.g., Hamilton and May 1977; Frank 1986; Johst and Brandl 1999; Ronce et al. 2000) have been developed under the premise that expected fitness of “dispersers” equals expected fitness of “stayers,” that is, that $p_d w_d = p_s w_s$, where p indicates the probability of surviving some finite time interval, w indicates fitness given survival, and subscripts indicate dispersers or stayers, respectively (the inclusion of kin competition [e.g., Gandon and Michalakis 1999], avoidance of inbreeding [Shields 1982], and bet hedging [Karlson and Taylor 1995] modify the basic models). If dispersal is no more hazardous than staying, the models predict no enhancement of fitness by surviving dispersers relative to surviving stayers, but when movement is in a hazardous matrix between safer patches, such models predict evidence for higher fitness of surviving dispersers relative to surviving stayers. We test this prediction by contrasting the relationship between movement and an indicator of energy acquisition, individual growth rate, in contrasting populations (there is also evidence that growth and reproduction correlate positively in the study species *Rivulus hartii*; Fraser et al. 1999). In previous studies, we have examined spatial responses of a killifish, the jumping guabine, *R. hartii*, to a severe piscine predator, *Hoplias malabaricus*, finding that the presence of the predator converts a rather continuous distribution of *Rivulus* in streams (*Rivulus* at high density in pools, riffles, and

other habitats) to a fragmented spatial structure with *Rivulus* in patches of complex structure (cobble) or refugia (rain pools or flood pools separated from the main river and the predator) embedded within the predator-occupied matrix (Fraser et al. 1995). Further, in a previous mark-recapture study (Gilliam and Fraser 2001), we found that patches in the predator zone showed temporal variability in occupancy, with numerous patches unoccupied during any sampling period (Fraser et al. 1999; J. F. Gilliam and D. F. Fraser, unpublished data). Owing to the presence of temporarily empty patches in the predator zone, together with the apparently hazardous matrix, we anticipated that growth might positively correlate with movement there and that the correlation would be absent, or weaker, in the relatively homogeneous, apparently more saturated predator-absent zone (Fraser et al. 1995). We used our mark-recapture data to evaluate this possibility.

Methods

Subjects

The freshwater killifish, *Rivulus hartii*, is widely distributed in Trinidad (Phillip 1998). We studied it in the Northern Range Mountains where it is most abundant in slow-flowing or still waters that are free of piscivorous fish. In streams with piscivores, such as *Hoplias* and the pike cichlid, *Crenicichla alta*, the killifish, which is a nonschooling, solitary forager, tends to be confined to the shallow margins, especially those containing cobble or organic material that afford cover (Fraser et al. 1995). It also avoids predation by flipping into flood pools or rain pools. *Rivulus* is active at all times of the day but is most easily caught at night when it can be dipnetted from shallow water. The diets of mature *Rivulus* (≥ 30 mm total length) consist primarily of allochthonous input from the terrestrial environment such as ants and flying insects (Seghers 1973; Fraser et al. 1999).

We studied *Rivulus* in two adjacent river drainages, the Guanapo and Turure, on the southern versant of the Northern Range Mountains. We conducted a marking study of *Rivulus* in the Guanapo River in the forested Heights of Guanapo. We collected *Rivulus* for laboratory assays from the Guanapo and Turure Rivers.

Analyses of Moves in the Long-term Mark-Recapture Study

Kurtosis of Movement Distributions. We conducted a 19-mo mark-recapture study in the headwaters of the fourth-order Guanapo River in the Northern Range Mountains of Trinidad, West Indies, from January 1996 through July 1997, as previously reported (Gilliam and Fraser 2001),

Table 1: Summary statistics, chronology, and methods for testing boldness in the four cohorts of *Rivulus* from Trinidad, West Indies

Cohort	Origin	N	Total length (mm \pm SE)	Date collected	Date assayed for boldness	Date field tested	Location of field test	Indices of boldness
1	Guanapo River	41	43.1 \pm 1.0	May 1998	Oct. 1998	Oct. 1998	Guanapo River	Rank index
2	Guanapo River	42	49.4 \pm 1.1	Oct. 1998	Dec. 1998	Jan. 1999	Guanapo River	Rank index
3	Turure River	44	60.2 \pm 1.1	Aug. 1999	Jan. 2000	Jan. 2000	Experimental stream	Bold index Rank index
4	Turure River	47	52.9 \pm 1.8	Jan. 2000	Mar. 2000	Mar. 2000	Experimental stream	Bold index Rank index

with recaptures at approximately 2-mo intervals representing the sum of about 60 day/night movement periods. The study contrasted two sites: an upper zone free of strongly piscivorous fish and a lower zone containing highly piscivorous fish species (Gilliam et al. 1993). Within each zone, movement distributions (arbitrarily, positive values assigned to upstream moves and negative values to downstream moves) were strongly leptokurtic, suggesting some source of heterogeneity. To ask whether the leptokurtosis could be removed by dividing the data into more homogeneous groups, we decomposed the movement distributions into 16 cells generated by four binary factors: predation regime (predator zone, predator-absent zone), sex (male, female), season (wet, dry), and habitat (the river proper vs. occupancy of isolated side pools adjacent to the river channel). We also used body length as a covariate within each cell. For the classification by season, we extracted recapture events that recorded movement within a wet season or within a dry season, eliminating recapture events for which the previous capture was not in the same season. For the microhabitat classification, we extracted "main river" moves as those fish that were in the main river channel at a given capture and then subsequently in any location, that is, the main river, an isolated side pool, or a tributary; similarly, "isolated pool" moves were moves by fish that were in an isolated pool in the capture prior to the recapture. Because recaptures were at approximately 2-mo intervals, we standardized the movement as meters per 60 d. The categorization and screening yielded 426 moves for analysis. Within each of the 16 cells, we then regressed signed distance moved (positive = upstream) on body length and calculated the kurtosis of the residuals as the statistic g_2 (Zar 1999). Values of $g_2 > 0$ indicate leptokurtosis, with $g_2 = 0$ corresponding to a normal distribution. We tested the sample kurtosis values (g_2) by comparing them with tabled critical values for $P = .05$ (Zar 1999).

Consistency within Individuals. Because we had more than one record of movement for many of the fish in the mark-recapture study, we could also analyze movement by in-

dividual fish to test for consistency of movement behavior within fish. We extracted fish from our mark-recapture study for which we had at least two records of movement using the first two observations for fish with more than two recorded movements, yielding 141 individuals (90 from the predator-absent zone and 51 from the predator-present zone). We calculated the strength of the repeatability of behavior within subjects by calculating a partial correlation between the distance moved in the first and second moves, treating each fish as a replicate and controlling statistically for predator zone, sex, and length.

Correlation of Growth and Movement. Instantaneous growth rate per 60 d was calculated as $\text{growth} = [(\ln \text{final total length} - \ln \text{initial total length}) / (\text{days between capture})] \times 60 \text{ d}$. We used a general linear model to ask whether there was a relationship between growth and movement by fish occupying the river. Distance moved was standardized to meters per 60 d and transformed as $\log_{10}(|x| + 1)$. Thus, the general linear model had growth as the dependent variable, and our primary interest was in tests for the main effect of movement, plus the movement times predator-zone interaction. Sex and length were analyzed as additional independent variables. Hence, the analysis had four main effects (predator zone, movement, sex, and length) and one interaction (predator zone \times movement). Significance level was set at $\alpha = .05$.

Laboratory Assays and Field-Release Experiments

Subjects. We made four collections of *Rivulus*, two each from the Guanapo and Turure Rivers, as detailed in table 1. We refer to these collections as cohorts 1–4. The cohorts were collected and tested in chronological order, and fish from each were assayed for propensity to explore unfamiliar space in the aquarium. Guanapo cohorts 1 and 2 were field tested in the Guanapo River, while Turure cohorts 3 and 4 were field tested in a field experimental-stream facility in Trinidad.

Subjects were maintained in 76-L aquaria in the laboratory and at the field site and were fed a mixture of

commercial flake food and canned tuna fish that was dispersed throughout the tank to facilitate access by all fish. Fish were marked by injecting them subcutaneously with a dot of a colored elastomer (Northwest Marine Technologies), with color and position of the mark uniquely identifying individuals (details in Gilliam and Fraser 2001).

Tank Assay. Our tank assay for boldness, described below, is a variant of the classical open field test of animal psychologists (Walsh and Cummins 1976; Csanyi and Gerlai 1988) and was recently employed by Budaev (1997b) to test for personality in the guppy *Poecilia reticulata*. Traditionally, the subject is placed in a novel open space from which escape is prevented by surrounding walls, and the behaviors elicited are measured. Our modification places the subject in a familiar refuge whose environment exactly duplicates that of the holding tank and measures behaviors associated with moving in and leaving the refuge to enter the novel open space beyond. We recognize that this single test likely reflects the total effect of several personality traits that are contributors that could be disentangled through a multivariate design (e.g., Maier et al. 1988; Budaev 1997b). Gosling (2001) provides a detailed review of the dimensions of animal personality.

To assay for boldness, we used a long, glass aquarium tank (120 cm long \times 30 cm deep \times 30 cm wide) that contained a refuge (25 cm) at either end; the intervening gap was unstructured and brightly lighted by overhead incandescent light (75-W bulb) plus normal laboratory fluorescent light. The start refuge (left side) was covered by an opaque cover and was divided into a front and rear section by a red-clay, three-hole brick (holes positioned vertically) that had an artificial aquarium plant placed in each hole. The floor of the refuge consisted of dark, aquarium-style gravel. The back side of the aquarium, away from the observer, and left end of the refuge were covered with black plastic sheeting that, in combination with the overhead opaque cover, resulted in a dimly lighted refuge. The front, or observer's side, was unobstructed, and an observer seated quietly 2 m from the tank could observe all parts of the tank simultaneously without disturbing the fish. The right refuge was structured like the left.

All subjects were acclimated for 15–21 h in batches of five to 10 fish by confining them to the refuge with an opaque, glass partition. After the acclimation period, which was always overnight, fish were transferred to a community tank where they were held prior to testing. All fish were fed ad lib. the evening before but not on the day of testing. Tests were done during the afternoon.

Each subject was tested individually by gently releasing it into the back of the refuge at the far left corner. As a

general rule, subjects remained motionless for a few minutes. Initially, all subjects were timed by stopwatch for time to cross out of the refuge and time to cross the intervening gap to the opposite refuge. We later realized that the brick dividing the refuge was important to the question of boldness. Thus, for Turure cohorts 3 and 4, we noted the amount of time spent in front of the brick. Also, a subject was judged to have crossed out of the refuge when >50% of its body was over a plane formed by the edge of the refuge, which was defined by the opaque cover and the dark gravel. A fish was judged to have crossed the gap between the refuges when its tail fin had passed the midway mark. Tests lasted 20 min.

In this assay, we observed that all subjects exhibited some level of fearfulness in the refuge. Subjects initially froze when released by dipnet into the back corner of the refuge and, after a latency period, began to move in the rear half of the refuge behind the brick. Almost without exception, subjects exhibited caution in moving to the front of the brick. They rarely swam over the top but tended to pass along the 4-cm space between the side of the brick and the tank wall. Those that moved to the front of the brick did so slowly and cautiously, often stopping alongside the brick with just their head and eyes extending beyond the front edge. Similarly, almost every subject stopped at the leading edge of the refuge and looked at the empty space before moving out of the refuge. Quick darts to the front and then to the back of the refuge were also characteristic of many individuals. The consistency of these behaviors that reflected fearfulness and the lack of any indication of feeding (subjects never attempted to bite at the substrate or any floating bits of debris at the surface or in the water column) suggest that the assay measures fearfulness or boldness in propensity to move beyond the refuge. However, we cannot completely discount the contributing role of any of a number of experiential variables that may affect our timed behaviors; for example, experience gained in the holding tanks prior to testing, manipulation of the subject by dipnetting and bringing it into the refuge, and experience of the experimental situation itself up to the instant at which the behavior is measured.

Indices of Boldness. A simple measure of boldness is the time from the start that it takes a fish to cross the gap. Behavior varied, however, with some boldly leaving the refuge within a few minutes of the start but never crossing over. To better express boldness over the full array of possible responses in the test, we derived two indices of boldness; the first was applicable only to Turure cohorts 3 and 4, for which we measured the total time spent in front of the brick, including time spent out of the refuge altogether.

We calculated the bold index (BI) for the i th individual as

$$BI_i = \left(\frac{t_i}{T} \right),$$

where t_i = time spent in front of the brick by the i th individual and T = total time in test.

The second index is based on the rank order of individuals within a cohort group (e.g., cohorts 1, 2, 3, and 4) with respect to crossing the gap, crossing out of the refuge, and time spent in front of the brick (including time spent out of the refuge). Rank order was calculated as follows: rank 1 is assigned to the individual crossing the gap in the least amount of time, 2 to the next shortest time, and so on, until all those crossing the gap are ranked. Then, continuing with the remaining fish, the next rank is assigned to the fish crossing out of the refuge in the shortest time, and so on, until all those that have crossed out of the refuge, but did not cross the gap, are ranked. Ranking continues with those remaining fish in the order of the most to the least time spent in front of the brick. Finally, the last rank is assigned to those remaining fish that never left the back of the refuge. All of those remaining fish are assigned the same, last rank (R). The rank index (RI) for the i th individual is then calculated as

$$RI_i = 1 - \left(\frac{r_i}{R} \right),$$

where r_i = rank of the i th individual and R = the last assigned rank in the sample. We had no ties, except for the lowest ranked category, but ties would have been treated by assigning each the same rank. Because we did not measure time in front of the brick for Guanapo cohorts 1 and 2, these cohorts were ranked only with respect to time to leave the refuge and time to cross the gap. Unlike the bold index, which can be used to compare different cohorts, the rank index is limited to within-cohort comparisons.

River-Release Experiments (Guanapo Cohorts 1 and 2). After assaying the fish for boldness, we conducted release experiments to determine their propensity to move away from the release point. We chose a 20-m stretch of river as the release site. The site was in the middle of a 200-m stretch of river that was devoid of waterfalls, contained cobble beaches, and had quiet water along most of the shoreline, which facilitated recapture of released fish. Prior to release, we searched the 200-m stretch and removed as many indigenous *Rivulus* as possible to reduce the chance of interference with the experimental fish. Cohort 1 ($n =$

41) fish was released in October 1998, and cohort 2 ($n = 42$) fish was released in January 1999 (table 1). We released the fish at 2000 hours and recaptured them 24 h later at night when *Rivulus* is easily caught with small aquarium dipnets. Because of the complexity of the river habitat, we chose 24 h, rather than some arbitrary longer interval, to facilitate recapture of as many fish as possible. Prior to release, we placed each fish individually in a quart-size, numbered, plastic bag at 1-m intervals and then gently released all fish among the cobbles. For the recapture, we intensively searched 300 m up- and downstream of the release area, but all recaptures occurred within 90 m of the individual release points. Each recaptured fish was identified by its unique mark.

Experimental-Stream Release (Cohorts 3 and 4). The river releases with cohorts 1 and 2 directly assess whether the laboratory assay predicts field dispersal, with the drawbacks that we could not recapture all individuals and the fate of missed fish is unknown. Therefore, we also used a field experimental-stream facility to measure movement distances using cohorts 3 and 4. The facility (more fully described in Fraser et al. 1995) consists of eight artificial tributaries, each with 0.42 m width and 2.7 m length, situated perpendicular to and elevated on a bank 0.8 m above an enclosed section of natural stream. For this study, we modified the facility with partitions to create experimental units in which fish would be released into one of the tributaries (the "home" tributary) and then could move up to 2.7 m downstream in the home tributary, descend a 2.5-m-long cascade into the natural stream, travel up to 4.3 m along the natural stream within a 0.9-m-wide enclosure, and ascend another 2.5-m cascade into a second tributary (the "sister" tributary) in which it could travel up to another 2.7 m upstream. Thus, a fish moving from the release point to the farthest point in the sister tributary could disperse a total of 14.7 m. Fish had many potential "stopping points" in the apparatus because we created realistic pools in the tributaries (three pools per tributary) and the natural stream (also three pools). These pools contained features typical of *Rivulus* habitat: gravel substrates and structure consisting of stones, woody branches, and leaves.

Subjects were released in the most upstream pool of the home tributary, which we designated as a "refuge," with an opaque cover and twice the structure as the other sections. At the start of each test, at 2200–2400 hours, 10 fish were confined to the start pool by a blocking screen. After 1 h, the screen was lifted and the fish were free to move. After 20 h, we searched the tributaries and natural stream using headlamps, and all fish were typically recaptured within an hour. We occasionally missed an individual, but these were recaptured on a subsequent night and not used

in the analysis. Each of the 10 fish was scored for distance moved from the start refuge.

Analysis. We evaluated the relationship between the dependent variable, distance moved in the river or experimental-stream releases, and boldness in the tank assay (independent variable) by a general linear model, with fish length, sex, and cohort as additional independent variables. We tested for these four main effects, and also for a cohort \times boldness interaction, to ask whether the effect of boldness was consistent across cohorts. Boldness in the Guanapo River fish (cohorts 1 and 2) was given by the rank index and in the Turure River fish (cohorts 3 and 4) by the bold and rank indices. Distance moved was transformed as $\log_{10}(|x| + 1)$. Regression coefficients were tested by the t -test with $\alpha = .05$.

Results

Analyses of Moves in the Long-term Mark-Recapture Study

Kurtosis of Movement Distributions. When the overall leptokurtic distribution of movement distances was decomposed by considering residuals within each cell, controlling for length, leptokurtosis remained a feature of the residual distributions (table 2). Of the 16 possible combinations, nine had sample sizes >20 , which allowed testing for significance (kurtosis different from zero). The point estimate of kurtosis of the residuals was positive (positive = leptokurtic) for all nine cases, and seven of the nine differed significantly from zero. The results suggested some as yet undetected source of heterogeneity in movement, hence leaving viable the hypothesis of individual variation in the propensity to move.

Consistency within Individuals. Distances moved by individuals on successive recaptures in the field mark-recapture study were positively correlated. The simple correlation between the first and second moves, not controlling for predator zone, length, or sex, was $r = .38$ ($N = 141$, $df = 139$, $P < .001$). The partial correlation, controlling for predator zone, length, and sex, was $r_{\text{partial}} = .33$ ($N = 141$, $df = 136$, $P < .001$). Thus, the movement distance observed on the first interval was a predictor of movement distance on the second interval, and the positive correlation remains after removing effects of predator zone, length, and sex, which is consistent with the hypothesis of heterogeneity in movement behavior.

Correlation of Growth and Movement. As shown in figure 1, the growth rate of individuals was unrelated to movement behavior in the predator-absent zone of the river

Table 2: Kurtosis of the residual distributions for each category of sex, season, habitat, and predator

Sex, season, and habitat	Predators	<i>N</i>	Kurtosis	SE	<i>P</i>
Male:					
Dry:					
Main river	Absent	35	17.424	.778	<.01
	Present	23	.953	.935	>.05
Isolated pools	Absent	5	—	—	—
	Present	14	—	—	—
Wet:					
Main river	Absent	77	2.021	1.541	<.05
	Present	45	6.513	.695	<.01
Isolated pools	Absent	5	—	—	—
	Present	33	11.656	.798	<.01
Female:					
Dry:					
Main river	Absent	28	.698	.858	>.05
	Present	35	4.487	.779	<.01
Isolated pools	Absent	0	—	—	—
	Present	9	—	—	—
Wet:					
Main river	Absent	73	16.456	.555	<.01
	Present	15	—	—	—
Isolated pools	Absent	7	—	—	—
	Present	22	3.599	.953	<.05

Note: Dependent variable in the analysis of kurtosis is distance moved in the river per 60 d. Residuals are for each combination of sex, season, habitat, and predator with length as a covariate. A dash indicates sample size insufficient for testing significance of kurtosis.

but positively correlated in the predator zone. The general linear model revealed a main effect of distance moved on growth rate ($F_{1,538} = 6.90$, $P = .009$) and also a significant interaction between distance moved and predator zone ($F_{1,538} = 4.15$, $P = .042$), indicating that the slopes in the two panels of figure 1 differ. Within the predator-absent zone, the correlation was not significantly different from zero ($N = 372$, $r_{\text{partial}} = .06$, $P = .284$) but was positive in the predator zone ($N = 169$, $r_{\text{partial}} = .22$, $P = .004$). Predator zone and sex showed no effect in the analysis ($P = .394$ and $P = .706$, respectively), whereas length did have a significant negative effect on the growth rate ($P = .004$). These results support the hypothesis that growth benefits accrued from movement will be most evident in the fragmented, high-hazard environment.

Laboratory Assay and Field-Release Experiments

River Release (Guanapo Cohorts 1 and 2). We recaptured 16 (39%) cohort 1 fish and 27 (64%) cohort 2 fish. *Rivulus* that ranked high for boldness moved farther in the river than those that ranked low (fig. 2). The statistical analysis judged rank index to be statistically significant ($r_{\text{partial}} =$

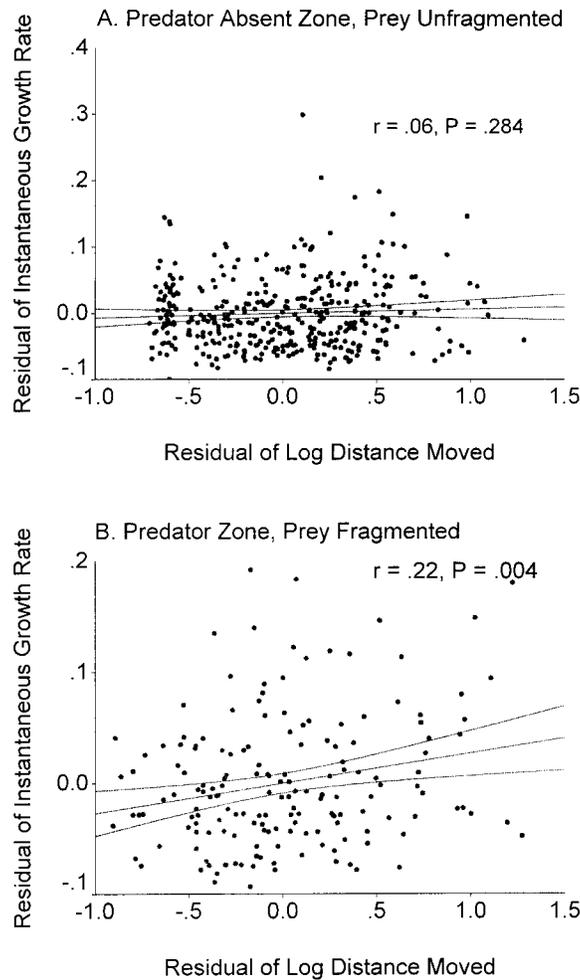


Figure 1: The effect of movement rate on growth rate in the 19-mo mark-recapture study in the Guanapo River. Figures show the residual effect of movement on growth with effects of fish length and sex removed. Regression and 95% confidence intervals for the mean are shown. No significant relation was found in the predator-absent zone (A), but a significant relation occurred in the predator zone (B), in which the fish were spatially fragmented and in a high-hazard environment (interpatch habitat hazardous).

.405, error $df = 39$, $P = .010$). The cohorts did not differ (cohort effect: $P = .478$; cohort \times boldness interaction: $P = .943$). Length and sex were also statistically insignificant at $\alpha = .05$ ($P = .059$ and $.111$, respectively). Figure 2 shows that the rank index of boldness (residual plot with effects of cohort, length, and sex removed) predicts distance moved. Boldness itself was uncorrelated with either length or sex (multiple regression of rank index on length and sex revealed no effect of either factor; length: $r_{\text{partial}} = -.123$, $t = -.78$, $P = .437$; sex: $r_{\text{partial}} = -.233$, $t = -1.52$, $P = .138$).

Experimental-Stream Release (Turure Cohorts 3 and 4). Consistent with results from the river release, figure 3 shows that the bolder fish in the experimental-stream release

moved farther than did lower ranked fish, as measured by either the rank index (fig. 3A) or the bold index (fig. 3B). The statistical analysis using the rank index indicated significant effects by the rank index ($r_{\text{partial}} = .453$, error $df = 75$, $P < .001$), with length and sex effects insignificant ($P = .054$ and $.665$, respectively). Also, the cohorts did not differ (cohort effect, $P = .375$; cohort \times rank index interaction, $P = .143$). The analysis using the bold index showed the same phenomenon: significant effects by the bold index ($r_{\text{partial}} = .484$, $P < .001$). However, here, length effects were also significant ($P = .030$) but not sex effects ($P = .249$). Again, cohort ($P = .175$) and the cohort \times bold index interaction ($P = .068$) were not significant. Figure 3 shows that both indices (with effects of cohort, length, and sex removed) predict distance moved.

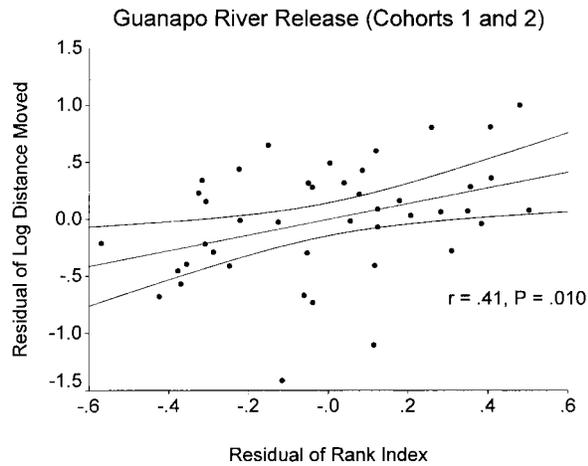


Figure 2: The effect of the rank index of boldness (calculated from the laboratory assay for boldness) on distance moved in the Guanapo River release (cohorts 1 and 2). The figure depicts the residual effect of the rank index, with the effects of cohort, fish length, and sex removed. Regression and 95% confidence intervals for the mean are shown. The figure shows that the laboratory assay predicted dispersal in the field.

As with cohorts 1 and 2, multiple regression revealed that neither the bold nor the rank indices were affected by length (length on bold: $r_{\text{partial}} = .159$, $t = 1.425$, $P = .158$; length on rank: $r_{\text{partial}} = .172$, $t = 1.546$, $P = .126$) or sex (sex on bold: $r_{\text{partial}} = -.055$, $t = -.483$, $P = .631$; sex on rank: $r_{\text{partial}} = .104$, $t = .923$, $P = .359$).

Overall, these results support the hypothesis that boldness, as assayed in small laboratory tanks, contributes to the movement observed in field releases. Length also influences movement, with the effect of length not attributable to a correlation with boldness, and vice versa.

Discussion

Hamilton and May (1977) and others (review of theories by Johnson and Gaines 1990; Holt and McPeck 1996) have postulated that some proportion of local populations should emigrate, suggesting that the propensity to disperse may be associated with a behavioral polymorphism. The rover-sitter phenotypes of *Drosophila* (Osborne et al. 1997; Sokolowski et al. 1997) may be an example of such a polymorphism, although its relevance to dispersal in nature is unknown. A probable dispersal morph has also been described for the naked mole-rat, *Heterocephalus glaber* (O'Riain et al. 1996). While theoretical work since Hamilton and May has explored what the evolutionarily stable strategy dispersal rate should be (e.g., Ronce et al. 2000),

we know of no empirical work that links behavioral assays to distance moved in nature. This study provides evidence of such a link. Distances moved in the natural and experimental streams were significantly related to boldness as indexed by either the rank index (reflecting readiness to explore the test tank) or the bold index (reflecting time spent in front of or out of the refuge).

The contribution of this personality trait, boldness, to movement in the field provides a concrete example of a behavioral source of population heterogeneity in movement as an explanation for leptokurtic movement distributions that we (table 2) and others have observed. Skalski and Gilliam (2000) addressed the issue of modeling lep-

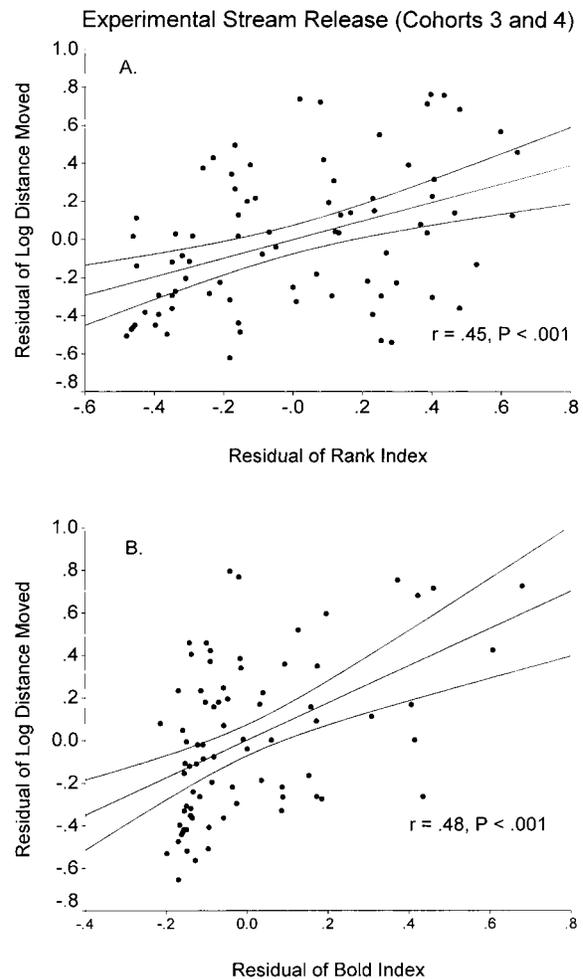


Figure 3: The effect of (A) the rank index and (B) the bold index on distance moved in the experimental-stream release (cohorts 3 and 4). The figure depicts the residual effect of the indices, with the effects of cohort, fish length, and sex removed. Regression and 95% confidence intervals for the mean are shown. Both indices derived from the laboratory assay predicted movement in the release.

tokurtic distributions generated from population heterogeneity. Finding persistent leptokurtosis in bluehead chubs *Nocomis leptoccephalus* over a 4-mo time interval, they postulated the existence of a population heterogeneity underlying the leptokurtosis and constructed a heterogeneity model to explain population movement distributions that fail to become normal with successive samplings. Their empirical data fit a model that assumed subpopulations of “fast” and “slow” fish. “Bold” and “shy” are examples of fast and slow categories in the Skalski-Gilliam model; other categories could be more immediately obvious phenotypic traits such as maturity, size, or sex (e.g., Nichols 1996). Skalski and Gilliam (2000), while modeling heterogeneity with two subpopulations, pointed out that some traits, of which boldness is an example, would be better modeled as continuous variables.

While we know of no other study linking a laboratory behavioral assay for boldness to field movement, there are many observational field studies that show variation in movement by individuals that is consistent, at least over short time intervals (one or a few days), with the existence of a behavioral heterogeneity. In fish, for example, McLaughlin et al. (1992) observed recently hatched brook charr *Salvelinus fontinalis* and found that a little more than half of the young charr in field streams spent >40% of the observation time moving within their home area in search of food, whereas 15% were stationary. Grant and Noakes (1987) and Armstrong et al. (1997) made similar observations. Wilson et al. (1994; see also Greenberg 1995) argued that a shy-bold continuum, while well established in human populations, is likely to exist in many taxa, argued for its relevance to many evolutionary and ecological questions, and proposed a framework for its study.

Once an individual initiates movement, for whatever reason, boldness may be an important factor influencing subsequent dispersal distance, which is important in a number of population phenomena. For example, Neubert and Caswell (2000) draw attention to the theoretical prediction that long- and short-distance dispersal governs invasion speed, even when long-distance dispersal is rare. The shape of the dispersal kernel, the probability-density function that gives the probability distribution of the location of an individual as a function of its starting location, in particular the nature of its tails, is important in determining a population's rate of spread (Kot et al. 1996). In the current context of boldness, selection resulting in high variance in boldness would produce a leptokurtic dispersal kernel with long tails, and initial colonists in a spreading population are likely to be bolder than average.

A host of theoretical studies, as noted above, have explored conditions that can lead to the evolution of dispersal. For cases in which movement and boldness correlate, such models provide some guidance for speculation

regarding the evolution of mean boldness in populations in different environments. Two generalizations across many of the models (Dieckmann et al. 1999) are that dispersal rates (here, substitute “boldness” as a surrogate concept) should increase in environments with high patch-extinction rates (see Ronce et al. 2000 for a model with a different prediction) and that costs of dispersal, such as mortality, should decrease dispersal. In our empirical contrast of two environments in Trinidad that differ in the presence or absence of the predator (fig. 1; Gilliam and Fraser 2001), separate consideration of these two generalizations produce contrasting predictions. The first generalization predicts more movement and bolder fish in the predator zone than the predator-absent zone. The second generalization predicts the opposite, assuming that movement through the predator-occupied matrix is sufficiently hazardous relative to the hazard in the refugia and hazard during movement in the predator-absent zone is unlikely to differ from the hazard incurred by animals undergoing normal activities while not dispersing. We empirically resolved the question regarding movement, finding that movement was greater in the predator zone (Gilliam and Fraser 2001). However, it is not known whether boldness in exploration also differs between the contrasting environments (we note that a different assay, termed “tenacity” in feeding, did show higher tenacity in fish collected from high-hazard sites [Fraser and Gilliam 1987], but we agree with Coleman and Wilson [1998] who caution against assuming boldness in one trait infers boldness in another).

Our fieldwork suggests that movement by *Rivulus* is sometimes “spontaneous,” that is, as is typically assumed in the metapopulation models, not forced by deterioration of a local habitat due to environmental alteration. However, some moves are also clearly “induced” (hence our care in this study to correctly classify fish to habitat type in table 2) because *Rivulus* in isolated side pools flanking the river are subject to drying of the pools and also to obliteration of the refuge advantages of such habitats, such as when floods rearrange the substrate (we also recognize that many of the moves we categorize as spontaneous might actually be attributable to more subtle changes, such as food depletion). Our field releases, while not specifically designed to mimic such “forced” moves, are nonetheless suggestive of representing such an event if one views the field releases as an environmental change. The amount of movement that we recorded in our field releases (river and experimental streams) is more than would be expected over a 24-h period in the field by undisturbed *Rivulus* (Gilliam and Fraser 2001; J. F. Gilliam and D. F. Fraser, unpublished observations) but are in line with what we observe following environmental disruption.

We have no knowledge regarding the basis of the within-population variation in boldness in exploration in our

assays in terms of genetic and environmental contributions, but note that others have found differences in exploratory behavior in laboratory studies assaying different populations of the same species ("strains"; e.g., DeFries et al. 1974; Simmel and Bagwell 1983; Magurran 1990; Gershfeld et al. 1997). However, efforts to measure within-population heritability of the propensity to disperse in vertebrates have produced little or no convincing evidence for nonzero heritability (Waser and Jones 1989). We would anticipate substantial contributions of early experience to boldness (Huntingford et al. 1994) but have no convincing reason to posit zero heritability, especially in light of the known genetic contributions to movement behavior discovered by Osborne et al. (1997).

We found that boldness was not influenced by sex or length in either the Guanapo River fish released into the river (cohorts 1 and 2) or the Turure River fish released into the experimental streams (cohorts 3 and 4). However, in both field releases, length joined boldness as a significant predictor of distance moved. The cohorts were all collected in predator zones of rivers, and the positive influence of length on movement is consistent with our finding (Gilliam and Fraser 2001) that, in the predator zone but not the predator-absent zone, movement along the river was positively correlated with fish length and that larger fish were more likely to emigrate from the river to adjoining tributaries. However, the conclusion that length influenced movement in our releases is contingent on using absolute distance moved as the measure of movement. Rescaling distance moved to body lengths, that is, dividing meters moved by body length, retains a positive point estimate of the partial correlation but renders length nonsignificant in all three cases calculated (Guanapo River fish, rank index [$P = .107$, $r_{\text{partial}} = .256$]; Turure River fish, rank index [$P = .245$, $r_{\text{partial}} = .134$]; and bold index [$P = .258$, $r_{\text{partial}} = .130$]). The effect of boldness on movement was significant in all three cases ($P = .015$, $<.001$, and $<.001$, respectively). Viewed in the context of body lengths moved, boldness alone was a predictor of distance moved.

Overall, our results demonstrate that laboratory and mesocosm assays for a behavioral trait, boldness, expressed as the propensity to explore unfamiliar habitat, predicts initial dispersal in the field, thereby providing direct experimental evidence for a behavioral polymorphism that may underlie long-term dispersal behavior. The results also confirm, for the first time to our knowledge, the hypothesis that movement and an index of fitness (growth) should positively correlate when the intervening matrix between patches is rendered hazardous. More generally, our results extend in a new direction the growing body of evidence that boldness can be adaptive in a variety of ecological contexts (Fraser and Gilliam 1987; Wilson et al. 1994; Godin and Dugatkin 1996; Budaev 1997a).

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