What drives long-distance dispersal? A test of theoretical predictions

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Abstract. Long-distance dispersal (LDD) may contribute disproportionately to species persistence in fragmented landscapes, non-native invasions, and range shifts in response to climate change. However, direct data on LDD are extremely limited, leaving us with little understanding of why it occurs. I used six years of mark–recapture data on the stream salamander *Gyrinophilus porphyriticus* to test theoretical predictions of how variation in habitat quality affects LDD. Frequency of LDD was quantified using the kurtosis of yearly movement distributions from recaptured animals in a 1-km headwater stream. Temporal and spatial variation in habitat quality were quantified with spatially explicit data on the body condition and dispersion of individuals throughout the study stream. Using information-theoretic model selection criteria, I found that LDD increased during periods of low average body condition and low spatial variation in body condition. Consistent with basic theory, my results indicate that temporal variation in habitat quality is critical to initiating dispersal, and that LDD increases when animals must move farther to encounter higher-quality habitat. This suggests that information on how habitat quality varies in time and space can be useful for predicting LDD. More broadly, this study highlights the value of direct data on animal movement for testing dispersal theory.

Key words: amphibian; behavior; connectivity; Gyrinophilus porphyriticus; *habitat variability; headwater stream; kurtosis; leptokurtic; long-distance dispersal; movement; salamander; spatial ecology.*

INTRODUCTION

Dispersal is a fundamental process in demography and evolution (Clobert et al. 2001) and may be critical to the persistence of species in human-impacted landscapes (Hanski and Gilpin 1997). Defined as unidirectional movement away from an origin, dispersal in most animals and plants is characterized by many individuals that remain close to their origin and few individuals that move far from that location (Mayr 1963, Endler 1977). A surge of interest in these rare, long-distance dispersal events has been fueled by evidence that they contribute disproportionately to species persistence in fragmented landscapes (e.g., Tittler et al. 2006), nonnative invasions (e.g., Caswell et al. 2003), and range shifts in response to climate change (e.g., Higgins and Richardson 1999), three of our most pressing conservation issues. Although methods for observing movement in individuals are improving (Holden and Blackburn 2006), empirical research on long-distance dispersal (LDD) remains limited by detectability and by the difficulty of assessing population-level variation in movement distances (Trakhtenbrot et al. 2005, Nathan 2006). As a result, we know very little about why LDD occurs.

Theoretical models predict that spatial and temporal variation in habitat quality are important causal factors of dispersal (Johnson and Gaines 1990, Dieckmann et

al. 1999, Clobert et al. 2001). Dispersal is predicted to occur when habitat quality varies both temporally and spatially (Hastings 1983, McPeek and Holt 1992, Friedenberg 2003): temporal variability promotes movement away from an initial location; spatial variability creates the possibility that dispersal will be rewarded with increased fitness. Empirically, dispersal may be related to temporal and spatial variation in habitat quality at occupied sites, as represented by the performance of individuals at those sites, or by variation in the availability and spatial distribution of suitable sites (i.e., those meeting a minimum threshold of quality), as represented by the dispersion of individuals among potential sites. These predictions also pertain to LDD, but unlike models where dispersal is a categorical response (stay vs. move), any attempt to understand what controls LDD must address dispersal distance as well.

Theory suggests that dispersal distance should increase as spatial variation in habitat quality decreases because individuals must move farther to encounter habitat of significantly higher quality than their initial location (Palmer and Strathmann 1981, Levin et al. 1984, Hovestadt et al. 2001, Muller-Landau et al. 2003). In natural systems, this relationship may vary with behavior (Bowler and Benton 2005), the influence of passive forces (e.g., wind, water currents; Nathan et al. 2002), and stochastic events (Carlquist 1981). But because habitat quality affects both the probability of initial, post-dispersal establishment and the long-term fitness consequences of dispersal (Nathan 2005), the

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negative relationship between spatial variation in habitat quality and dispersal distance should be robust to this variation. This prediction is consistent with observations of LDD between sites separated by large areas of consistently unsuitable habitat (i.e., "jump dispersal"; Peterson and Fausch 2003).

I used six years of mark–recapture data on movement in the stream salamander *Gyrinophilus porphyriticus* to test the basic theoretical predictions that temporal variation in habitat quality is critical to initiating dispersal, and that LDD increases when spatial variation in habitat quality is low and animals must move farther to encounter higher-quality habitat. The study system has two properties that allowed for these empirical tests: (1) vagility of *G. porphyriticus* is low, so surveys can detect dispersal events that are long-distance and rare relative to the majority of movements (Lowe 2003), and (2) *G. porphyriticus* is constrained to linear habitats of streams and riparian zones (Lowe et al. 2006b, Greene et al. 2008), minimizing detection-related bias in measurements of dispersal distance. In two-dimensional landscapes, the probability of detecting marked animals declines with movement distance (Koenig et al. 1996). But when movement is along linear habitats, like stream corridors, and sampling is consistent throughout these habitats (e.g., from bank to bank), detection probability does not decline with movement distance.

METHODS

Study species and site

G. porphyriticus belongs to the family Plethodontidae, the lungless salamanders. This species is found in small, cool, well-oxygenated streams along the Appalachian uplift, from central Alabama, USA to southern Quebec, Canada (Petranka 1998). Larvae are strictly aquatic and the larval period is estimated to be 3–5 years (Bruce 1980). Adults are highly aquatic, but forage terrestrially at night (Greene et al. 2008). During the day, larvae and adults are found in interstitial spaces among the larger substrate particles of the streambed. In the northern Appalachians, larval size range is 26–80 mm snout–vent length (SVL), adults can reach 120 mm SVL, and both stages feed primarily on invertebrates (Greene et al. 2008).

The study site was Merrill Brook, a fishless, first-order stream in Dartmouth College's Second College Grant, located in northern New Hampshire, USA. Merrill Brook flows into the fourth-order Dead Diamond River; a wetland at the confluence serves as a barrier to brook trout (*Salvelinus fontinalis*) that might enter Merrill Brook from the larger river. Sampling occurred throughout a 1 km long section of Merrill Brook that started at the confluence with the outflow wetland and ended 1000 m upstream of that point, encompassing the perennial portion of the stream. Undisturbed headwater streams in New Hampshire display low conductivity (12.0–15.0

µS/cm), slight acidity (pH of 5.0–6.0), high dissolved oxygen content (80–90% saturation), and moderate midday temperatures in the summer (13.0–17.0°C) (Likens and Bormann 1995). Sampling throughout Merrill Brook matched these data. Other salamanders encountered in Merrill Brook included *Eurycea bislineata* and *Desmognathus fuscus* (both Plethodontidae).

Survey methods

Salamander surveys of Merrill Brook were conducted during three-day periods in mid-June, mid-July, and mid-August of 1999–2004, resulting in a total of 18 surveys. A cover-controlled, active search sampling method was used: moving upstream, I turned rocks within the channel and along the edge measuring between 64 and 256 mm in diameter (cobble); surveys continued until 1200 rocks had been turned. The even distribution of cobble allowed for a constant effort of just over one rock per meter of stream length, so surveys provided spatially explicit information on individual attributes of salamanders encountered throughout the stream, as well as data on occupancy in each meter of stream (i.e., spatial structure of suitable habitat). An aquarium dip-net was used to capture salamanders, including those flushed by the current.

All unmarked *G. porphyriticus* larvae and adults encountered were individually marked by subcutaneous injection of fluorescent elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA) and marked individuals were recorded. Retention of these marks is high throughout the life of the animals. The longitudinal position (distance from the confluence, m), length (SVL, mm), and mass (mg) of all individuals encountered were recorded. All surveys of Merrill Brook were conducted by the author to eliminate among-observer sampling variation.

Quantifying long-distance dispersal

I used data from individuals marked and recaptured within the same year (June–August surveys) to derive six independent movement distributions for *G. porphyriticus*. In Merrill Brook and 15 streams where shorter mark–recapture studies were conducted (1–2 years) there were no differences in movement distributions related to size, life history stage (i.e., larva vs. adult), or sex, and no within-year variation in movement distributions associated with stream flow (Lowe 2003, Lowe et al. 2006a). These previous findings allowed me to pool data across sizes, life-history stages, sexes, and months to generate population-level movement distributions for each year. They also suggest that movement distributions of *G. porphyriticus* are not subject to life-history related and environmental "noise" that could complicate analyses of the drivers of LDD. Recaptured individuals that were marked in previous years were not included in movement distributions because it was not possible to associate movement with a specific year.

I used the kurtosis of population-level movement distributions to measure the frequency of LDD in each year (Skalski and Gilliam 2000, Fraser et al. 2001). Because of the energetic cost and risks associated with dispersal, movement distributions are often leptokurtic (kurtosis [γ_2] > 0), with higher central peaks and larger tails than normal distributions (Johnson and Gaines 1990, Paradis et al. 1998). This pattern results from high concentrations of observations around a distance of 0 and relatively few long-distance dispersers. But kurtosis is a continuous parameter and, therefore, a useful index of the specific frequency of LDD in a population (Gosset 1908): as the frequency of LDD increases, kurtosis increases.

Although kurtosis is scale-free, its use as an index of LDD relies on the assumption that, for a given species, average dispersal distance increases with kurtosis. If this assumption is correct, then intraspecific variation in kurtosis reflects variation in both the frequency of LDD and the scale of movement (Skalski and Gilliam 2003). I tested this assumption by examining the relationship between kurtosis and average distance of movements >5 m in each year. This threshold was based on the conservative assumption that movements ≤5 m may represent within-home-range activity, as opposed to dispersal. I could not avoid undersampling the tails of movement distributions given basic constraints on sampling area (Koenig et al. 1996), but by sampling the same 1000 m of stream in all surveys, I generated length-standardized kurtosis estimates that were comparable across years (e.g., Skalski and Gilliam 2003).

Quantifying variation in habitat quality

To quantify temporal and spatial variation in habitat quality at occupied sites, I used means and standard deviations of body condition of individuals marked but not recaptured in each year. Mean condition values represented variation among years in habitat quality at occupied sites. Analyses in Lowe et al. (2006a) show that condition varies significantly among years. Because each salamander was associated with a specific position along the stream, standard deviations represented within-year spatial variation in habitat quality at occupied sites. I used size-corrected mass (log-transformed), the residuals from the linear regression of log-transformed mass and SVL, as the index of body condition. This index is positively related to growth rate and reproductive potential in G. porphyriticus (Lowe 2003, Lowe et al. 2006a), and it meets the assumptions underlying the use of linear regression for its calculation (Green 2001). The close relationship between body condition and local habitat quality in G. porphyriticus is also supported by the high sensitivity of amphibians to their local environment, and by the high proportion of individuals that never move from the point of capture (Lowe 2003).

To quantify temporal and spatial variation in the availability of suitable sites—another important measure of habitat quality—I used means and standard deviations of the Morisita dispersion index (Morisita 1959). Values of this index >1.0 indicate increasing aggregation of salamanders into a subset of suitable sites (10 m long reaches), which could be caused by spatial variation in flow, substrate conditions, or prey availability. Mean yearly values of this index (from June–August surveys) represented variation among years in the overall availability of suitable sites, assuming that aggregation increases as availability of suitable sites decreases. Standard deviations represented within-year variation in the availability and distribution of suitable sites (Matthews et al. 1994, With et al. 1997). There is no evidence that aggregation is beneficial in G. porphyriticus, and the Morisita Index is robust to variation in the number of individuals observed in each survey (Myers 1978, Hurlbert 1990). To eliminate non-independent observations, recaptured individuals that were marked in previous years were not included in calculations of yearly means and standard deviations of body condition and the Morisita Index.

Statistical analyses

Akaike's information criterion adjusted for small sample size (AIC_c) and the information-theoretic approach (Akaike 1973, Burnham and Anderson 2002) were used to select the best model of kurtosis from a set of univariate and multiple linear regression models. Models included up to three of the following four variables: mean and standard deviation of body condition, representing habitat quality at occupied sites, and mean and standard deviation of the Morisita dispersion index, representing availability and distribution of suitable sites. This approach identifies the model that represents the data adequately with as few parameters as possible, thus making a trade-off between potential bias caused by having too few parameters and poor precision of parameter estimates caused by having too many parameters. Models in the candidate set were first ranked by AIC_c differences (ΔAIC_c; Burnham and Anderson 2002), the difference between AIC_c for each model and that for the model with the lowest observed AIC_c. The best model has $\Delta AIC_c = 0$ and only models with $\Delta AIC_c < 4.0$ have substantial support (Burnham and Anderson 2002). Relative likelihood of each model in the candidate set was estimated with AIC_c weights, which sum to 1.0 for all models in the candidate set. To increase normality, kurtosis values were square-root transformed.

RESULTS

In all years, G. porphyriticus movement distributions were leptokurtic (kurtosis > 0; Appendix). Kurtosis was unrelated to number of recaptures in each year ($R = 0.24$, $N = 6$, $P = 0.64$), indicating that variation in sample size did not bias kurtosis estimates. Kurtosis was positively related to log-transformed average dispersal distance ($R = 0.82$, $N = 6$, $P < 0.05$). Also, modal movement distance was 0 m in all years, and there was

TABLE 1. Models of kurtosis of yearly movement distributions from *Gyrinophilus porphyriticus* larvae and adults in Merrill Brook.

Model	AIC_c	ΔAIC_c	AIC_c weight	Adjusted R^2	K
Mean Con, SD Con	−4.32	0.00	0.72	0.98	3
SD Con	−2.19	2.13	0.25	0.87	2
Mean Con	3.27	7.59	0.02	0.68	2
Mean Agg	4.93	9.25	0.01	0.58	2
SD Con, SD Agg	6.24	10.56	0.00	0.87	3
Mean Con, Mean Agg	6.29	10.61	0.00	0.87	3
SD Con, Mean Agg	7.23	11.55	0.00	0.84	3
Mean Con, SD Agg	9.37	13.69	0.00	0.78	3
SD Agg	10.70	15.02	0.00	0.00	2
Mean Agg, SD Agg	11.41	15.73	0.00	0.69	3
Mean Con, SD Con, Mean Agg	25.50	29.82	0.00	0.97	4
Mean Con, SD Con, SD Agg	25.62	29.94	0.00	0.97	4
SD Con, Mean Agg, SD Agg	36.15	40.47	0.00	0.81	4
Mean Con, Mean Agg, SD Agg	36.16	40.48	0.00	0.81	4

Notes: Second-order Akaike's information criterion values (AIC_c), AIC_c differences (ΔAIC_c), AIC_c weights, and number of estimable parameters including the intercept (K) are provided for all models. Mark–recapture surveys were conducted in June, July, and August of 1999–2004. Independent variables, calculated using data from new captures in each year (Appendix), include mean body condition (Mean Con), standard deviation of body condition (SD Con), mean aggregation (Mean Agg), and standard deviation of aggregation (SD Agg). Aggregation was quantified with Morisita's dispersion index (Morisita 1959).

no relationship between kurtosis and the frequency of 0-m observations ($R = 0.27$, $N = 6$, $P = 0.6$). This indicates that variation in kurtosis was primarily related to variation in the frequency of long-distance movements, as opposed to variation in the frequency of "stayers," further validating kurtosis as an index of LDD. Of the animals recaptured more than once over the six years ($N = 109$), only one moved from a capture location and subsequently returned to that location. None of the other animals moved and then returned to a previous location. This suggests that the majority of movements observed in this study were unidirectional dispersal events, as opposed to temporary movements.

There was no correlation among means and standard deviations of body condition and the Morisita index ($|R| \leq 0.7$, $N = 6$, $P \geq 0.10$), confirming that these variables were independent and that standard deviations were unbiased measures of heterogeneity in habitat quality (Downing 1986). There was also no correlation between number of new captures each year and the independent variables ($|R| \leq 0.75$, $N = 6$, $P \geq 0.09$; Appendix), confirming that the independent variables were not biased by differences in sample size.

The best model explained 98% of the variation in kurtosis of yearly *G. porphyriticus* movement distributions and included mean and standard deviation of body condition (Table 1). Consistent with a priori predictions, both mean and standard deviation of body condition were negatively related to kurtosis (Fig. 1). The best model fit the data almost three times as well as the second-best-fitting model. Model selection results were the same when Morisita dispersion indices were calculated for 5-m stream reaches. In a posteriori analyses, I found no relationship between the total number of captures in each year, including new captures and

recaptures (Appendix), and kurtosis ($F_{1,4} = 0.63$, $P = 0.47$, $R^2 = 0.14$), or between total recaptures and the independent variables ($F_{1,4} \leq 5.79$, $P \geq 0.08$, $R^2 \leq 0.59$). This suggests that salamander density was not an important determinant of LDD, or of spatial and temporal variation in body condition and dispersion.

Discussion

Over a six-year period, frequency of LDD in the *G. porphyriticus* population was closely related to temporal and spatial variation in habitat quality within the 1-km study stream. Kurtosis of *G. porphyriticus* movement distributions increased as mean yearly body condition decreased, indicating that LDD increased during periods of low overall habitat quality and, more broadly, that temporal variation in habitat quality was important to maintaining LDD in the population. In recaptured animals, the correlation between initial body condition and movement distance was positive and nonsignificant (Spearman rank correlation: $R_s = 0.18$, $N = 105$, $P = 0.06$), suggesting that the decision to disperse was based on current habitat quality at a site, not on an individual's prior performance at that site. There was also no relationship between change in body condition (recapture condition − initial condition) and movement distance ($R_s = -0.04$, $N = 105$, $P = 0.69$), supporting the assumption that dispersers were responding to variation in mean habitat quality, not causing variation in the index of habitat quality.

Kurtosis was negatively related to the yearly standard deviation of body condition. This result supports theory predicting that LDD should increase as spatial variation in habitat quality decreases because dispersing individuals must move farther to encounter habitat of significantly higher quality than their initial location
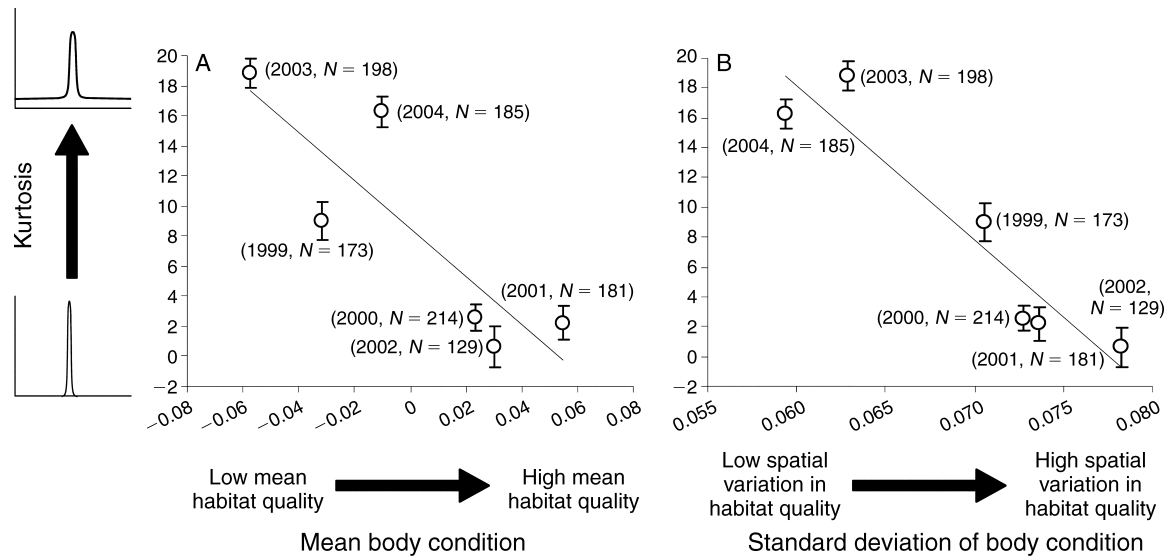
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Fig. 1. Relationships of yearly (A) mean and (B) standard deviation of body condition (measured as the residuals from the linear regression of log-transformed mass on log-transformed length) to the kurtosis ($\pm$SE) of yearly movement distributions of *Gyrinophilus porphyriticus* individuals. Body condition values are from individuals that were marked and not recaptured in each year (June–August of 1999–2004); body mass was originally measured in milligrams, and lengths in millimeters. Movement data are from individuals that were marked and recaptured in the same year. There is no correlation between mean and standard deviation of body condition ($R = 0.68$, $N = 6$, $P = 0.14$). In parentheses adjacent to each data point are the year and the total number of animals captured in that year, including new captures and recaptures. Standard errors of kurtosis estimates were calculated using methods in Cramer and Howitt (2004).

(Levin et al. 1984, Hovestadt et al. 2001, Muller-Landau et al. 2003). The strong relationship between spatial variation in body condition and kurtosis also suggests that salamanders were able to assess local habitat quality accurately during dispersal events, and based settlement decisions on that assessment. There was no correlation between means and standard deviations of body condition, confirming that temporal and spatial variation in habitat quality act independently to determine the frequency of LDD (Johnson and Gaines 1990, McPeek and Holt 1992). Kurtosis of *G. porphyriticus* movement distributions was highest when overall habitat quality was low and spatially consistent.

Long-distance dispersal in *G. porphyriticus* was unrelated to temporal and spatial variation in the distribution of suitable habitat, as represented by the dispersion of individuals in Merrill Brook. Mean Morisita dispersion indices ranged from 1.54 to 2.56 and coefficients of variation ranged from 0.16 to 0.71 (Appendix), indicating that salamanders were consistently aggregated in a subset of 10-m reaches, but that the level of aggregation varied considerably among and within years. The lack of correlation between body condition and spatial distribution strongly suggests that patterns of aggregation within the stream were unrelated to habitat conditions affecting short-term fitness (e.g., individual performance), and may instead be related to factors affecting long-term fitness (e.g., inbreeding risk; Szulkin and Sheldon 2008). Likewise, the drivers of movement in *G. porphyriticus* may vary with the scale of movement, where long-distance movements are in

response to conditions affecting short-term fitness (Table 1), but shorter movements are in response to factors affecting long-term fitness. This hypothesis brings together competing models of the evolution of dispersal—those emphasizing extrinsic environmental conditions (e.g., McPeek and Holt 1992), and those emphasizing inbreeding and kin competition (e.g., Perrin and Goudet 2001).

Intrapopulation variation in behavioral phenotypes can lead to leptokurtic movement distributions (Fraser et al. 2001). Specifically, the large tails of leptokurtic distributions can result from a subpopulation of bold "movers," whereas the high peaks are comprised of less-bold "stayers." Other phenotypic polymorphisms can produce leptokurtic movement distributions as well (e.g., Harrison 1980) and may contribute to the consistent leptokurtosis of *G. porphyriticus* movement distributions across sites and across time at the same site (Lowe 2003, Lowe et al. 2006a). However, independent of these possible phenotypic effects, my results show that habitat conditions affecting individual performance are important in determining the degree of kurtosis, and thus the frequency and extent of LDD. These results underscore the need for research on how ecological and evolutionary processes interact to produce dispersal polymorphisms.

This study suggests that information on spatial and temporal variation in habitat quality may be valuable for predicting LDD in diverse species and systems. Specifically, when key controls on habitat quality are known (e.g., vegetation structure, temperature, moisture), remote sensing and GIS data may be used to

predict both current distributions of endangered or invasive species and how those distributions will change due to LDD (Caswell et al. 2003, Trakhtenbrot et al. 2005). When proximal controls on habitat quality are unknown, as in the case of *G. porphyriticus*, fitness or condition indices may be equally useful for predicting the frequency and consequences of LDD. A recent Supreme Court opinion made protection of headwaters under the Clean Water Act contingent on evidence of connectivity to larger streams and rivers (Nadeau and Rains 2007). My results suggest that headwater tributaries where habitat conditions are temporally dynamic and spatially consistent are the most likely to be connected to downstream reaches by dispersal, thus deserving protection under this interpretation.

Efforts to understand why dispersal happens and its demographic and evolutionary implications have produced a large body of theory (e.g., Hamilton and May 1977, Hastings 1983, McPeek and Holt 1992). However, the difficulty of observing dispersal directly and the wide range of dispersal mechanisms and population distributions that exist make it difficult to test this theory, resulting in a gap between theory and empirical data on dispersal. Theory should outpace and inspire empirical research, but as emphasized in reviews (e.g., Johnson and Gaines 1990, Clobert et al. 2001, Nathan 2006), the persistence of this gap risks creating two, largely independent bodies of work on this important topic. In addition to elucidating the causes of LDD, I hope this study helps close this gap by showing the value of direct data on animal movement for testing basic dispersal theory. Using direct data on movement to test a priori predictions of the causes and consequences of dispersal, we can ensure that research on spatial ecology is both broadly informative and grounded in mechanistic understanding.

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APPENDIX

A table presenting summary data for *Gyrinophilus porphyriticus* individuals captured during surveys of Merrill Brook, a first-order stream in northern New Hampshire, in June, July, and August of 1999–2004 (*Ecological Archives* E090-097-A1).

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