

Risk taking not foraging behavior predicts dispersal of recently emerged stream brook charr (*Salvelinus fontinalis*)

ALLAN H. EDELSPARRE,^{1,†} ROBERT L. MCLAUGHLIN,¹ AND MARCO A. RODRÍGUEZ²

¹Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario N1G 2W1 Canada

²Département des sciences de l'environnement, Université du Québec à Trois-Rivières,
C.P. 500, Trois-Rivières, Québec G9A 5H7 Canada

Citation: Edelsparre, A. H., R. L. McLaughlin, and M. A. Rodríguez. 2013. Risk taking not foraging behavior predicts dispersal of recently emerged stream brook charr (*Salvelinus fontinalis*). *Ecosphere* 4(6):73. <http://dx.doi.org/10.1890/ES13-00013.1>

Abstract. Several hypotheses predict that individual differences in migration and dispersal are related to individual differences in routine behavior associated with foraging and risk taking. We tested whether short-term dispersal of recently emerged brook charr *Salvelinus fontinalis* was correlated with differences in activity during prey search in the field (a measure of foraging tactic) or in the time taken to exit a dark tube into an unfamiliar field environment (a measure of risk taking). For one sample of fish, we tested whether an individual's propensity to disperse in a standardized dispersal test in the lab was correlated with its activity during prey search and its exit times in the field. For another sample of marked, released and recaptured fish, we tested whether an individual's minimum displacement distance over 6 days in the field (a measure of dispersal in the field) was related to its propensity to disperse in the lab. For the first sample, an individual's propensity to disperse in the lab was correlated with risk taking only, but, contrary to expectation, individuals with long exit times (risk-avoiders) dispersed farther than those with short exit times (risk-takers). For the second sample, dispersal in the field was also correlated with propensity to disperse in the lab, but, contrary to expectation, individuals with greater displacements in the field displayed lower propensities to disperse in the lab. Our findings demonstrate that individual differences in juvenile dispersal are related to differences in risk taking behavior, but not in foraging tactic, and that the nature of this relationship can depend on environmental context. These findings are consistent with the hypothesis that individuals differing in risk taking behavior can contribute disproportionately to ecological processes involving long-distance movement.

Key words: boldness; brook charr; dispersal; foraging behavior; leptokurtosis; Markov process; movement ecology; personality; risk taking; *Salvelinus fontinalis*.

Received 14 January 2013; **accepted** 7 February 2013; **final version received** 21 May 2013; **published** 21 June 2013.
Corresponding Editor: E. García-Berthou.

Copyright: © 2013 Edelsparre et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

† **E-mail:** a.edelsparre@mail.utoronto.ca

INTRODUCTION

There is growing interest in understanding how animal movements observed at small spatial and temporal scales, and the mechanisms responsible for them, are related to movements observed at larger spatial and temporal scales

(Jones et al. 1980, Morales and Ellner 2002, Samu et al. 2003). For individuals, there is interest in determining whether movements at small spatial and temporal scales can be used to predict a lifetime track or significant parts of it (Nathan 2008, Nathan et al. 2008). Such predictions would be particularly valuable in situations where

significant parts of an individual's lifetime track are difficult to measure directly. Conversely, when observations of movements are remotely sensed at large spatial and temporal scales, with corresponding error, there is interest in inferring sub-components of movements that are associated with foraging within a patch vs. searching for patches (Morales et al. 2004), or with diurnal foraging movements along migratory routes (Jonsen et al. 2006). For populations, there is also interest in understanding whether the movement of individuals measured at small spatial and temporal scales can explain key features of models that summarize the distribution of distances moved by individuals within a population. Distributions of movement distances are frequently leptokurtic, with more individuals near the center (high peak) and extremities (fat tails) of the distribution than expected from a normal distribution (Dobzhansky and Wright 1943, Paradis et al. 1998). Individuals in the high peaks are considered important to processes responsible for promoting local adaptation and biodiversity (Kerr et al. 2002, Gros et al. 2006). Individuals in the fat tails are considered important to processes responsible for the spread of invasive species and diseases (Kot et al. 1996, Dybiec et al. 2009), and to gene flow among populations (Ahmed et al. 2009). Understanding these ecological processes will likely involve understanding the mechanisms generating inter-individual differences that influence the magnitude of the high peak and the fat tails (Kerr et al. 2002, Dybiec et al. 2009).

There is theoretical justification, but limited empirical support, to expect that movements at small spatial and temporal scales are linked to movements at larger spatial and temporal scales, although contrary perspectives exist. Grinnell (1931) hypothesized that dispersal and migration evolved as extensions of smaller scale movements that make up routine daily activities, such as foraging. This hypothesis was based on observations that resident birds covered as much distance during their routine daily activities within a home range as did migratory birds during a day of continuous flight. Similarly, in a review of the ecological implications of animal temperament, Réale et al. (2007) hypothesized that migratory and dispersal movements would be outcomes of elemental temperament behav-

iors, such as general activity, boldness or risk taking, and sociability. In great tits (*Parus major*), individuals with bold temperaments explore farther than individuals with shy temperaments (van Oers et al. 2004) and in the common lizard (*Lacerta vivipara*) more social individuals of a population settle under high population densities and disperse under low densities while less social individuals do the reverse (Cote and Clobert 2007). From a contrary perspective, Fausch et al. (2002) cautioned against linking movement responses that describe different foraging tactics in stream fishes to movement at large spatial and temporal scales. Fausch et al. (2002) hypothesized that movements over large spatial and temporal scales (e.g., dispersal between patches), differ distinctively from the foraging, predator escape, and mating movements displayed once patches of suitable resources are encountered.

There is also theoretical justification to expect that movement of individuals observed at small spatial and temporal scales can explain the high peaks and fat tails of distributions of movement distances (Gurarie et al. 2009). Skalski and Gilliam (2000) and Rodríguez (2002) hypothesized that alternative patterns of foraging tactics exhibited by stream fishes, such as recently emerged brook charr (McLaughlin et al. 1992), could provide an explanation for the high peaks and fat tails of the distributions observed in the dispersal movements of several stream fishes, including brook charr (Skalski and Gilliam 2000, Rodríguez 2002, Coombs and Rodríguez 2007). The mechanisms involved remain unclear, but individuals that are more active during prey search could be acquiring the added energetic resources necessary for dispersal. Alternatively, Fraser et al. (2001) hypothesized that the high peaks and long fat tails of movement distributions could arise if individuals differ in their willingness to take risks and move into unfamiliar habitat. Bold individuals of Trinidad killifish (*Rivulus hartii*) exhibited longer dispersal distances in the field than shy individuals, consistent with their hypothesis. Although this notion is intuitively appealing, risk-dependent dispersal may depend on the environmental context, including predation risk (Cote et al. 2010a).

We tested whether foraging tactics and risk taking behavior (small scale movements) exhibited by recently emerged brook charr (*Salvelinus*

fontinalis) in the field were related to dispersal in the field (large scale movements). By dispersal we mean the movement of individuals from natal areas leading to spatial spread irrespective of whether the environment is homogenous or patchy (Turchin 1998, Clobert et al. 2001). Our study focused on stream fish because small streams can be conceptualized as one-dimensional habitats, making movement easier to quantify and model (Skalski and Gilliam 2000, Rodríguez 2002). Our study focused on recently emerged brook charr, because individuals at this life stage in Mykiss Lake, Ontario, Canada have been classified as “slow” and “fast” dispersers (Coombs and Rodríguez 2007). Furthermore, recently emerged brook charr in still-water pools along the bank of the Credit River show pronounced individual differences in foraging behavior: some individuals tend to actively search for insects in the upper portion of the water column, while others tend to sit and wait near the bank and feed on crustaceans that pass by or emerge from the sediment (Grant and Noakes 1987a, McLaughlin et al. 1992; 1994; 1999). Individuals also differ in their willingness to take risks (Farwell and McLaughlin 2009).

We examined whether foraging tactics and risk taking were linked with dispersal in two parts. We first tested whether foraging tactics and risk taking were linked to an individual's propensity to disperse in a controlled laboratory environment. We then tested whether an individual's dispersal distance in the field was related to its propensity to disperse in the controlled laboratory environment. We combined the findings between parts to infer how foraging behavior and risk taking were related to short-term dispersal in the field (Arnold 1983). We also compare our findings from the laboratory and field assays of dispersal and discuss the implications of our findings for future studies relying on laboratory assays of dispersal.

METHODS

Quantification of activity during prey search in the field

Field observations were made from 31 March to 25 May in 2008 and in 2009. In 2008, observations were made in still-water pools at the North Branch of the Credit River, upstream of

Highway 24 near Caledon, Ontario (43°52' N, 80°00' W) and the West Branch of the Credit River, 2 km north east of Erin, Ontario (43°45' N, 80°07' W). In 2009, all observations were made in still-water pools at the West Branch of the Credit River because the North Branch study site did not have still-water pools due to high flows. Pools ranged from 0.04–4 m² in surface area (\bar{x} = 1.04 m²) and 4–51 cm in depth (\bar{x} = 20 cm).

Activity during prey search was quantified daily between 09:00 and 18:00 using focal animal sampling (Altmann 1974). Upon arrival at a pool, the observer (AHE) would lay down close to the bank and wait 5–10 minutes for individuals to resume normal foraging behavior. If disturbed by an observer approaching the bank, recently emerged brook charr leave the pool or seek refuge at the stream bottom, or under the bank or other available structure. It takes 2 minutes on average for charr to return and resume foraging (Grant and Noakes 1987b). On each sampling day, the observer attempted to observe and capture two individuals that were less active and two individuals that were more active during prey search to ensure that each daily sample included individuals exhibiting different levels of activity during prey search.

Behavior of the focal individual was recorded on a mini-cassette recorder. The duration of observation was 20 minutes for 154 out of 158 individuals captured. Durations for the remaining four individuals ranged from 7.45 to 17 minutes due to poor weather conditions. Once an observation started, behavior of the focal individual fish was recorded every 5 seconds. During a 5-second interval, an individual's behavior was recorded as a *move* if the individual moved a body length or more or *no move* if it moved less than a body length. The observer also recorded whether that behavior was associated with an attempt to capture a prey item (foraging attempt) or aggression towards or from another conspecific. A foraging attempt entailed a conspicuous, rapid change in direction and speed towards a potential prey item (during *move*) or an adjustment in hovering position to intercept a prey item (during *no move*). Aggression entailed a rapid chase directed towards another individual or an escape response away from an aggressive individual. Five-second intervals not including a foraging attempt or aggression were considered

prey search and these 5-second intervals were used to calculate the proportion of time spent moving during prey search for each individual, following earlier studies on this system (McLaughlin et al. 1994, Farwell and McLaughlin 2009). After an observation, the observer attempted to capture the focal individual using two dip nets (18 × 25 cm). Capture success was not recorded in 2008. Sixty nine of 100 focal individuals were captured in 2009. Captured fish were held individually in a labeled 1-L glass Mason jar with a mesh cap placed in a shaded section of the stream away from where the focal observations were made.

Quantification of risk taking in the field

Risk taking was quantified using a refuge-exit experiment similar to those used by Fraser et al. (2001), Brown et al. (2005), and Farwell and McLaughlin (2009). The experimental arena consisted of a clear Plexiglas aquarium (55 × 26 × 35 cm) with an open top and a 1-mm² mesh bottom set in a pool at the river's edge. Within the arena was a vertical, free-standing opaque PVC tube (32 cm high and 12 cm diameter) with a 2-cm wide opening that could be opened manually by pulling a sliding door upwards. The tube was positioned at one end of the experimental arena with the opening facing the opposite end and providing a view of an unfamiliar but natural stream environment.

Experimental trials commenced approximately 30 minutes after an individual was captured. An experimental trial involved placing a captured individual into the tube from the top. The individual was given 10 minutes to adjust to its new surroundings and the sliding door was then opened. This procedure provided the individual with a refuge in the tube and a choice between staying in or exiting from the tube. An observer positioned approximately 90 degrees to the tube opening, recorded the time the individual took to exit the tube (exit time). Exit time was assumed to reflect an individual's assessment of the relative risk of remaining in the tube versus the risk of exiting into a novel, natural environment. If an individual did not exit the tube after 1800 seconds, the trial was ended and an exit time of 1800 seconds was recorded. The term risk avoider and risk taker have been assigned in terms of whether individuals' exit time suggested

they perceived the risk of the unfamiliar, natural environment, as being more or less risky, respectively, relative to the risk of remaining in the dark tube.

Each individual was tested under two treatments. One treatment quantified the time an individual took to exit the PVC tube in the absence of a novel object. A second treatment quantified the time the individual took to exit the PVC tube in the presence of a novel object (white Plexiglas plate; 36 × 22.5 cm) placed on the bottom of the aquarium extending 36 cm away from the base of the tube opening. In 2008, each individual was tested in the absence of a novel object first and in the presence of a novel object last. In 2009, the sequence of the treatments was randomized to minimize sequential effects. After the first trial the individual was netted and placed back into the tube for 10 minutes before commencement of the second trial. If an individual did not exit the tube during the first trial, the tube was removed and the individual was retrieved with a dip net. The individual was again placed in the tube for 10 minutes before the second trial. After completion of the risk taking experiment, each individual was placed back in its labeled Mason jar and returned to the shaded section of the stream. At the end of all treatments for a day, the captured fish were transported to the Hagen Aqualab, University of Guelph, where they were kept overnight in individual labeled containers with constant water flow, a water temperature of 10–12°C and 12:12 hour light/dark conditions.

Quantification of propensity to disperse in the laboratory

In 2008, propensity to disperse was quantified for each fish using a compartmentalized dispersal channel where individual fish could move away from an initial location by moving from one compartment to another. This approach has been used previously by Raleigh (1971), Northcote and Kelso (1981), and Bradford and Taylor (1997) to investigate dispersal and outmigration of other salmonid fishes, and by Fraser et al. (2001) and Rehage and Sih (2004) for dispersal in killifish and mosquitofish respectively. The dispersal channels were arranged side by side in an isolated room in the Hagen Aqualab. Black plastic screens hung along the lengths and ends

of the channels minimized any disturbance of the fish by observers. Each dispersal channel consisted of a green 4-m long PVC pipe (37.5 cm radius) cut in half along its length. To track the movement of fish, each dispersal channel was divided into 15 equally sized compartments (26 cm × 19 cm) labeled 1 to 15 (Bradford and Taylor 1997). The compartments were constructed by inserting dividers made from opaque PVC sheets. The dividers had a 2.5-cm diameter hole positioned 7.43 cm from the bottom and extending 4.8 cm from the wall. Hole position was determined based on earlier measurements of water column use by recently emerged brook charr in the lab (Wilson and McLaughlin 2007). The dividers were arranged so that the holes were on alternate sides of the dispersal channel from one divider to the next so that a test fish could not move through all compartments in a straight line and had to “seek out” the openings to move between compartments.

In 2009, two dispersal channels had compartments made from dividers with holes. Two other dispersal channels were modified by cutting away a third of each divider, thereby making the dividers more permeable to movement. These trials were conducted to determine whether results in 2008 were due to reluctance of individuals to pass through the holes.

Dispersal trials commenced between 10:30 and 11:30. Prior to the trials, each dispersal channel was emptied and refilled with oxygen-saturated water (10–11°C). An individual was randomly assigned to a dispersal channel, placed individually into compartment 1 with the opening blocked by an opaque PVC sheet, and given 30 minutes to adjust to its new surroundings. After 30 minutes, the PVC sheet was removed and movement of an individual from compartment to compartment was recorded by four overhead video cameras that each covered a 1-metre section of the dispersal channel. Movement between compartments was quantified for two hours, following Northcote and Kelso (1981), by recording times when the focal fish moved between compartments. Following the experiment, each individual was captured with a dip net, euthanized by an overdose of clove oil (60 mg/L), and measured for fork length (2008: 1.8–2.9 cm; $n = 59$; 2009: 2.1–3.3 cm; $n = 66$), and wet weight (2008: 0.04–0.32 g; 2009: 0.04–0.23 g).

Dispersal channels were drained and sprayed inside with fresh well-water to avoid transmission of any chemical cues released by test individuals between trials.

Quantification of dispersal in the field

Dispersal in the field was quantified in a mark-recapture study conducted between 25 May and 3 June 2009 in a 400-m stretch of the West Branch of the Credit River (43°46' N, 80°03' W). Brook charr were captured by electrofishing in five still-water pools (25 May to 28 May). An operator slowly approached fish in a pool with the anode, waited 2–3 minutes for fish to resume activity, applied electric current, and collected affected fish with a dip net. This approach ensured that fish did not leave the pool as a consequence of the electrofishing activity and allowed for capture of individuals hidden under structural cover and bottom debris. Each pool was electrofished using this method 6 to 7 times until few or no individuals were observed in a pool. Fish and pool locations were recorded using GPS (Magellan Mobilemapper 6).

The 92 captured brook charr (fork length range 3.1–5.8 cm) were individually marked using visual implant elastomer tags (North West Marine Technology, Inc.). Individuals were placed in a glass jar containing a clove oil solution until they lost equilibrium. Elastomer was then injected under the skin tissue at a pre-determined site. Individual marks were created by implanting two colors of elastomer (red and green) at a maximum of three of seven possible locations on an individual's body. Marked individuals were placed in a 20-L pail with aerated water and allowed to regain equilibrium before being released in their pool of capture. Fish were released by inserting a dip net with the fish into the water and allowing the fish to swim out.

Fish were recaptured on 2 and 3 June by electrofishing the entire stream from 500 m downstream to 100 m upstream of the pools where the fish were marked. Sampling further upstream was not feasible due to dense vegetation and deep water. Captured individuals were examined for elastomer tags and the recapture locations of 19 marked individuals were recorded using GPS. Each recaptured fish was placed in a 20-L aerated holding pail located in a shaded

area near the river bank until transported to the Hagen Aqualab. Fish collected on the two daily samples were held separately in holding aquaria (40 cm long, 30 cm wide, 30 cm high) in the lab (mean water flow of 6.7 ml sec^{-1} , water temperature of $10\text{--}12^\circ\text{C}$ and 12:12 hour light/dark conditions). On 4 June we commenced quantifying each individual's propensity to disperse in the channel as described above. For this experiment, dispersal channels had compartments separated by dividers with holes. Individuals were tested in a random order. Trials quantifying the propensity to disperse concluded on 11 June.

Modeling propensity to disperse

Testing predictions regarding the propensity to disperse required measures of activity during prey search and risk taking for each individual in the first part of the study, and of dispersal in the field for each individual in the second part of the study. Activity during prey search was quantified as the proportion of time each individual spent moving while searching for prey in the field. Risk taking was quantified as the time each individual took to exit the tube in the presence and absence of a novel object, providing two measures of risk. Dispersal in the field was quantified for each individual by calculating the minimum displacement distance between the edge of the pool of capture to the closest edge of the pool where a fish was recaptured using ArcGIS software (v. 9.3).

Predictions relating the propensity to disperse in the lab to activity during prey search, risk taking, and dispersal in the field were tested using multi-state Markov models. Multi-state Markov models accommodate serially correlated movement data and potential individual predictors to estimate individual rates of movement between compartments (Jackson et al. 2003, Patterson et al. 2008). The Markov approach has two additional advantages compared to simpler analyses that use total displacement (distance covered by the fish over the entire trial, irrespective of direction), or net displacement (distance between the initial location and the location at the end of the trial) to characterize movement. First, where simpler analyses fail to account for stochasticity in individual fish movements, Markovian models consider that very different movement trajectories can lead to the same net

displacement, and characterize movements probabilistically. Second, the Markovian model with covariates accounts for variation in movement rates within and among individuals and integrates the information on movements of all fish, including the effect of covariates, in the likelihood. This approach therefore provides a unified treatment for quantifying movement rates and linking them to individual covariates. Although the Markovian model deals directly with movement rates, its parameters can be used to generate a probabilistic description of net displacements (dispersal kernels) at different times and for individuals that differ in covariate values. The Markovian approach thereby provides a principled means for connecting total displacement (as reflected by movement rates) and net displacement (as reflected by the dispersal kernel).

For each individual, a time series of locations within the dispersal channel was used to develop a matrix summarizing the movements (transitions) between adjacent compartments. Transitions were modeled as a homogeneous continuous-time Markov process (Jackson et al. 2003). A general model for the movement between compartments can be described by a transition intensity matrix, Q :

$$Q = \begin{pmatrix} q_{11} & q_{12} & 0 & 0 & \cdots & q_{1n} \\ q_{21} & q_{22} & q_{23} & 0 & \cdots & q_{2n} \\ 0 & q_{32} & q_{33} & q_{34} & \cdots & q_{3n} \\ 0 & 0 & q_{43} & q_{44} & \cdots & q_{4n} \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & q_{nn} \end{pmatrix} \quad (1)$$

where q_{rs} represents the instantaneous rate of movement to compartment s conditionally on occupying compartment r :

$$\lim_{\delta t \rightarrow 0} [Pr\{S_i(t + \delta t) = s | S_i(t) = r, F_t, Z\} / \delta t] \quad (2)$$

where F is the observation history of the process up to the time preceding time t , and, in models including descriptors of individual behavior from the field, the Z are predictors (covariates) that vary across individuals but are constant in time. The diagonal entries are

$$q_{rr} = -\sum_{s \neq r} q_{rs}. \quad (3)$$

q_{rr} represents the instantaneous rate of remaining

in compartment r and is always negative. In the models examined here the instantaneous rate of moving forward or backward is equal to q_{rs} and is assumed identical for all compartments. Q is estimated using maximum likelihood from observations of movement between compartments by individual i at time t . Q can be used to calculate a transition probability matrix $P(t)$

$$P(t) = \exp(tQ) \quad (4)$$

which yields probabilities of individuals being in specific compartments at specific times.

In models including measures of individual behavior in the field (predictors), rates of movement q_{rs} were modeled as a function of covariates Z (proportion of time spent moving in the field, exit times in the absence and presence of a novel object, and dispersal in the field) with parameters β following a proportional hazards formulation:

$$q_{rs}^i(Z_i) = q_{rs}^{(0)} \exp(\beta_{rs} Z_i) \quad (5)$$

where $q^{(0)}$ is a baseline value of q before considering individual differences in covariate values, and i indexes individuals. The R package *msm* (Multi-state Markov and hidden Markov models in continuous time) (version 1.2; Jackson 2011) was used to model movement between compartments in the dispersal channel.

Evaluating predictions

In the first part of the study, we fitted four multi-state Markov models, compared their performance using Akaike Information Criterion (Burnham and Anderson 2002), and determined whether the signs of predictor coefficients were consistent with our predictions. Akaike weights (w_i) were used to provide a probability that a given model was the best approximating model within the set of models (Burnham and Anderson 2002). The first model (M0) had a single q for all individuals, reflecting the hypothesis that propensity to disperse in the lab was unrelated to individual differences in field behaviors. The other three models represented movement rates as a function of individual covariates: proportion of time spent moving in the field (M1), exit time in the absence of a novel object (M2a), and exit time in the presence of a novel object (M2b). In these models the movement rate q differed among individuals as determined by parameter

β and individual covariate values in Eq. 5. We considered proportion of time spent moving and exit times in separate models because the hypotheses from the literature considered them separately. In addition, proportion and time spent moving and exit times were not related (2008: Spearman rank correlation, $R_s = -0.05$, $P = 0.7$; 2009: Spearman rank correlation, $R_s = -0.01$, $P = 0.9$).

For fish that dispersed in channels with holes, movement rates were estimated over the 2-hr period commencing when the PVC blocking the hole between compartment 1 and 2 was removed. For fish that dispersed in channels with open dividers, movement rates were estimated over 17 minutes. In both cases, the duration of trials was selected to attain adequate coverage of movement for all 15 compartments while reducing any potential effect of the far channel boundary on movement. For analysis, the proportion of time spent moving while searching for prey in the field was arcsine-square-root transformed, and exit times in the absence and presence of a novel object were natural log transformed, to reduce the influence of possible outliers. We included time squared as a variable in all models to allow for a change in movement rates over time (e.g., due to habituation or learning effects). Body size (fork length) was not included in any of the models because initial modeling revealed no relationship between body size and movement rate.

In the second part of the study, our prediction that individuals that dispersed farther in the field would exhibit greater propensity to disperse in the dispersal channel was tested by fitting and comparing two multi-state Markov models. The first model (M3) assumed a common q for all compartments and individuals and served as a baseline model for the hypothesis that propensity to disperse in the lab was unrelated to field dispersal. The second model (M4) assumed that movement rates in the lab were related to minimum displacement distances in the field. Movement rates were estimated over a 1-hr period to limit any effect of the far channel boundary on movement. At the time of these trials the fish were more mature and moved faster through the dispersal channel than fish from experiments in the first part of the study.

We examined whether the relationship be-

tween movement rates in the lab and each explanatory variable was consistent with our predictions, by plotting estimated instantaneous rate of movement q (min^{-1}) against proportion of time spent moving in the field, exit times in the absence and presence of a novel object and displacements in the field.

RESULTS

Foraging tactics, risk taking and propensity to disperse

Individuals differed markedly in their behavior in the field and in the dispersal channels. In 2008 and 2009, distributions of proportion of time individuals spent moving while searching for prey ranged from 0 to 1 and were similar for both years (Fig. 1A, B). There were no effects of size (fork length) or condition on the proportion of time spent moving while searching for prey (2008: size, $F = 35$, $df = 60$, $P = 0.6$, condition, $F = 0.0001$, $df = 60$, $P = 0.99$; 2009: size, $F = 0.02$, $df = 65$, $P = 0.88$, condition, $F = 0.02$, $df = 65$, $P = 0.9$). Exit times measured in the tube experiment ranged from 1 to 1800 seconds in the trials with the novel object absent in both years. Exit times ranged from 2 to 1800 seconds for the trials with the novel object present in 2008, and 1 to 1800 seconds for the trials with the novel object present in 2009. Exit times were repeatable; individuals that took longer to exit the dark tube in the absence of the novel object also took longer to exit the tube in the presence of the novel object in 2008 and 2009 (intra-class correlations: ICC = 0.63, $P < 0.0001$; and ICC = 0.31, $P < 0.0001$ respectively; Fig. 1C, D). There were no effects of size or condition on exit times (2008: size, $F = 0.68$, $df = 60$, $P = 0.41$, condition, $F = 0.94$, $df = 60$, $P = 0.33$; 2009: condition, $F = 1.16$, $df = 65$, $P = 0.28$) except for the 2009 trials where larger fish tended to exit faster relative to smaller fish (size, $F = 7.92$, $df = 65$, $P = 0.006$). Individuals also differed in propensity to disperse. Movement rates (q 's) of individuals in the dispersal channels ranged from 0–0.29 min^{-1} in 2008, from 0–0.51 min^{-1} in the 2009 experiment where dividers had holes, and from 0–2.15 min^{-1} in the 2009 experiment with open dividers. In all experiments there were individuals for which the 95% confidence limits of the q 's did not encompass the mean q across all individuals (Fig. 2).

Model comparison supported the hypothesis that propensity to disperse in the laboratory was related to behavior in the field. Baseline models that excluded the proportion of time spent moving during prey search in the field and exit times in the field ranked third among the set of competing models in all three experiments (Table 1). In each case the probability that the baseline model was the best approximating model from the model set was low (Table 1).

The hypothesis that propensity to disperse was related to the proportion of time spent moving during prey search in the field received the least support (Table 1). Models including proportion of time spent moving while searching for prey in the field ranked last in all model sets (Table 1). The results do not support the prediction that individuals spending a greater proportion of time moving in the field during prey search exhibited greater movement rates in the dispersal channels (Fig. 3).

Support was strongest for the hypothesis that propensity to disperse in the dispersal channel was related to risk taking. Models that included either exit times in the absence of the novel object or exit times in the presence of the novel object in the field were consistently ranked as the best approximating models (Table 1). In the 2008 experiment with dividers having holes and the 2009 experiment with open dividers, the model that included exit times in the absence of the novel object ranked higher than the models that included exit times in the presence of the novel object. In the 2009 experiment with dividers having holes, the model that included exit times in the presence of the novel object ranked higher than the model that included exit times in the absence of the novel object. However, in each experiment, individuals with longer exit times in the field exhibited greater movement rates in the dispersal channels than individuals with shorter exit times in the field, contrary to our prediction (Fig. 3).

The unexpected negative relationship between risk taking and propensity to disperse was likely not due to chance. In both experiments with dividers having holes, individuals with longer exit times in the tube experiment in the field exhibited greater movement rates in the dispersal channel than individuals with shorter exit times in the field (Fig. 3B, D). The negative relation-

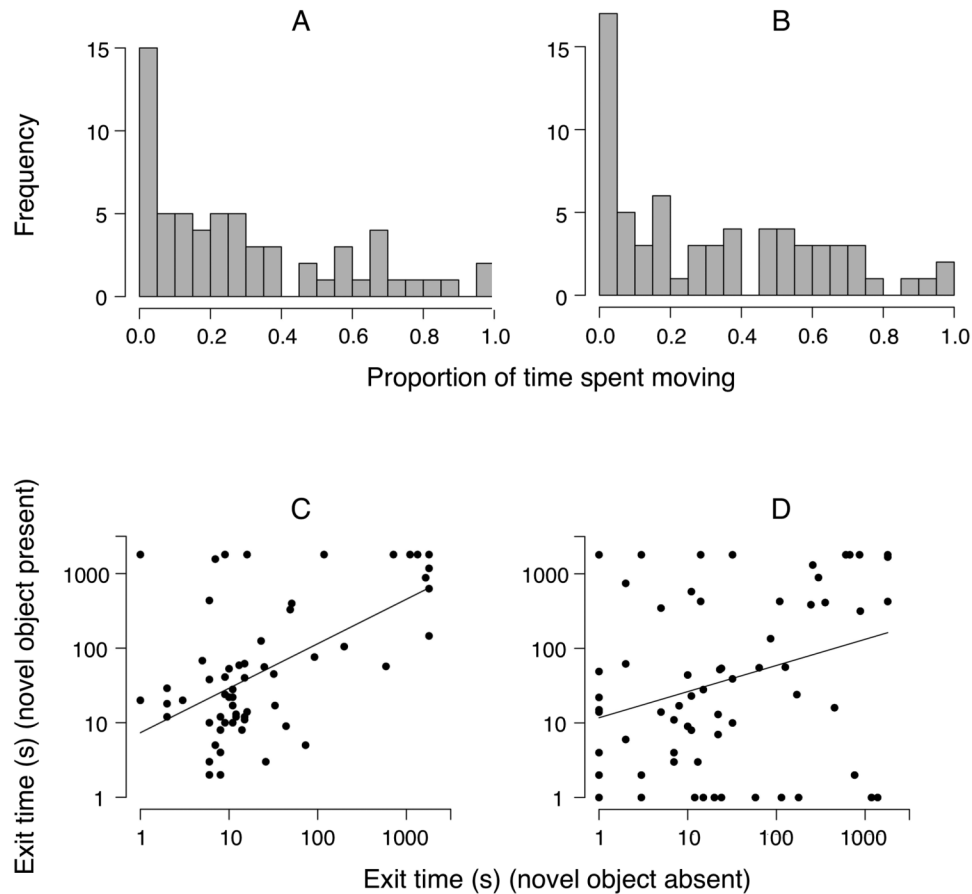


Fig. 1. Frequency distributions of proportion of time spent moving while searching for prey in the field during the (A) 2008 and (B) 2009 field seasons and exit times taken in the absence of a white Plexiglas plate (x-axis) and in the presence of a white Plexiglas plate (novel object) (y-axis) during the (C) 2008 and (D) 2009 field seasons.

ship between risk taking and propensity to disperse was also not an artifact of how individuals responded to the holes in the dispersal channel. When the dividers with holes were replaced by open dividers, individuals with longer exit times in the field continued to exhibit greater movement rates in the dispersal channel than did individuals with shorter exit times in the field (Fig. 3F vs. Fig. 3B and Fig. 3D).

Dispersal in the field and propensity to disperse

Minimum displacement distances measured in the field for 19 recaptured individuals ranged from 0 to 50 m. Sixteen individuals showed no displacement (0 m); the remaining 3 were recaptured in new pools with minimum displacement distances of 3, 34, and 50 m. The q 's

estimated for recaptured individuals ranged from 0 to 0.97 min^{-1} and there were individuals for which the 95% confidence limits did not encompass the mean q estimated across all individuals (Fig. 2D).

Our hypothesis that the propensity to disperse in the lab was related to dispersal in the field was supported. The model including minimum displacement distances from the field provided a significantly better fit than the model that did not include displacement distances in the field (Table 2). However, similar to the trials involving risk taking, displacement distance in the field was negatively related to propensity to disperse in the laboratory, contrary to our expectation (Fig. 4). A comparison of the probability distributions across all compartments in the dispersal channel revealed similar dispersal predictions for risk

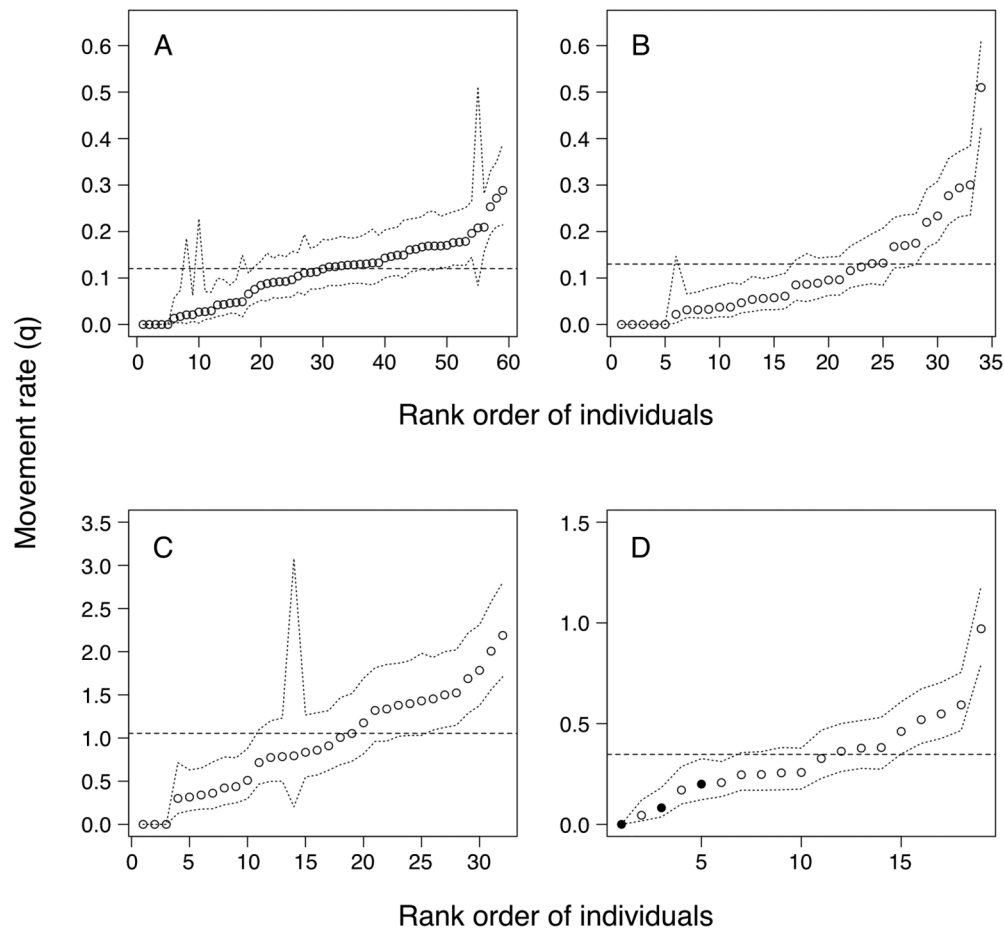


Fig. 2. Rank order of estimated movement rates q (min^{-1}) and 95% confidence intervals for individual brook charr (circles, ranked by movement rate along the x-axis): (A) dividers with holes, 2008 ($n = 59$ individuals); (B) dividers with holes, 2009 ($n = 34$ individuals); (C) open dividers, 2009 ($n = 32$ individuals); (D) dividers with holes, 2009 ($n = 19$ recaptured individuals); closed circles: displacement distance in the field > 0 (range 3–50 m); open circles: displacement distance in the field $= 0$ m. The dotted line represents the mean for all individuals used in the experiment.

takers and dispersers in the field and for risk avoiders and non-dispersers in the field (compare Fig. 5A with 5B).

DISCUSSION

Three main conclusions emerge from our findings. First, movements of individual brook charr expressed at smaller spatial and temporal scales can be related to movements of individuals expressed at larger spatial and temporal scales. Second, our results suggest that individuals that were more likely to take risks in our field experiment were also those most likely to

disperse from their pool of capture. This conclusion is supported by the observed relationships between risk taking and dispersal in the field to propensity to disperse in the lab. Third, individual differences in short-term dispersal were not related to individual differences in foraging tactics, because an individual's propensity to disperse in the lab was not related to activity during prey search in the field.

Demonstrating that movement behaviors measured at larger spatial and temporal scales can be predicted from movements measured at smaller spatial and temporal scales is valuable in several ways. Quantifying the lifetime tracks of most

Table 1. Model rankings based on the Akaike information criterion (AIC). M0: baseline model (no covariates included); M1: model including proportion of time spent moving while searching for prey in the field; M2a and M2b: models including exit times in the absence and in the presence of a novel object in the field, respectively. n : number of individuals; Δ AIC: difference between the AIC of the best approximating model and AIC score of each model; w_i : Akaike weight.

Model description:	AIC	Δ AIC	(w_i)	Parameters	n
A) Dividers with holes 2008					
Exit time (M2a)	7389.8	0	0.91	4	59
Exit time, novel object (M2b)	7394.9	5.1	0.07	4	59
Baseline (no covariates) (M0)	7398.6	8.8	0.01	3	59
Proportion of time spent moving (M1)	7400	10.2	0.01	4	59
B) Dividers with holes 2009					
Exit time, novel object (M2b)	4625	0	0.74	4	34
Exit time (M2a)	4627.3	2.4	0.23	4	34
Baseline (no covariates) (M0)	4632.8	7.9	0.02	3	34
Proportion of time spent moving (M1)	4634.5	9.5	0.01	4	34
C) Open dividers 2009					
Exit time (M2a)	1475	0	0.66	4	32
Exit time, novel object (M2b)	1477	2	0.25	4	32
Baseline (no covariates) (M0)	1479.5	4.5	0.07	3	32
Proportion of time spent moving (M1)	1481.5	6.5	0.03	4	32

animals is largely unfeasible because of the complexity of animal movements, and of limitations with current tracking technologies arising from the size, lifespan, and detection range of tags or marks. Predictions across scales could help overcome these challenges and extend the inferences made from movements that can be measured. Additionally, demonstrating a relationship between short-term dispersal and risk taking aids in understanding the basis for the leptokurtic distribution kernels that frequently characterize dispersal distances at the population level. Leptokurtosis in dispersal kernels has been attributed to underlying differences in behavior that involve routine daily activities (Fraser et al. 2001, Coombs and Rodríguez 2007). If this explanation holds, individuals comprising the fat tails of the distribution could be behaviorally distinct; inter-individual differences could then be important to understanding ecological processes such as colonization of new habitats or the spread of diseases (Kot et al. 1996, Dybiec et al. 2009, Cote et al. 2010b, Radinger and Wolter 2013). The ability to predict which individuals are likely to exhibit long distance movement, and the magnitude of such movements, could help understand key ecological processes by targeting individuals that are most influential to the process of interest (Sih and Watters 2005, Phillips et al. 2009). Finally, the demonstration of a link between risk taking and dispersal in the field

suggests that individual differences in basic personality traits can have important ecological implications. Personality refers to characteristics or qualities that form an individual's distinctive character (Réale et al. 2007). Risk taking and general activity have been proposed as elemental personality axes in animals (Réale et al. 2007). There is strong interest in whether personality traits influence more complex behaviors of ecological importance, including dispersal (Réale et al. 2007, Cote et al. 2010b).

Our findings regarding links between short-term dispersal and either risk taking or activity during prey search advance our understanding of the dispersal process because such correlations have been proposed previously, but tested rarely (risk taking) or not at all (foraging tactics). The proposed correlations are intuitively appealing, yet underlying complexities can easily be overlooked. For dispersal to be related to behaviors expressed at smaller spatial and temporal scales, three conditions must be met: (1) individuals must differ in the behavior of interest, (2) individual differences at smaller spatial and temporal scales must be related to an individual's propensity to move into and explore unfamiliar habitat (propensity to disperse), and (3) individual differences in the propensity to disperse must be realized as differences in dispersal distance in the face of heterogeneity in the physical, competitive, and predatory envi-

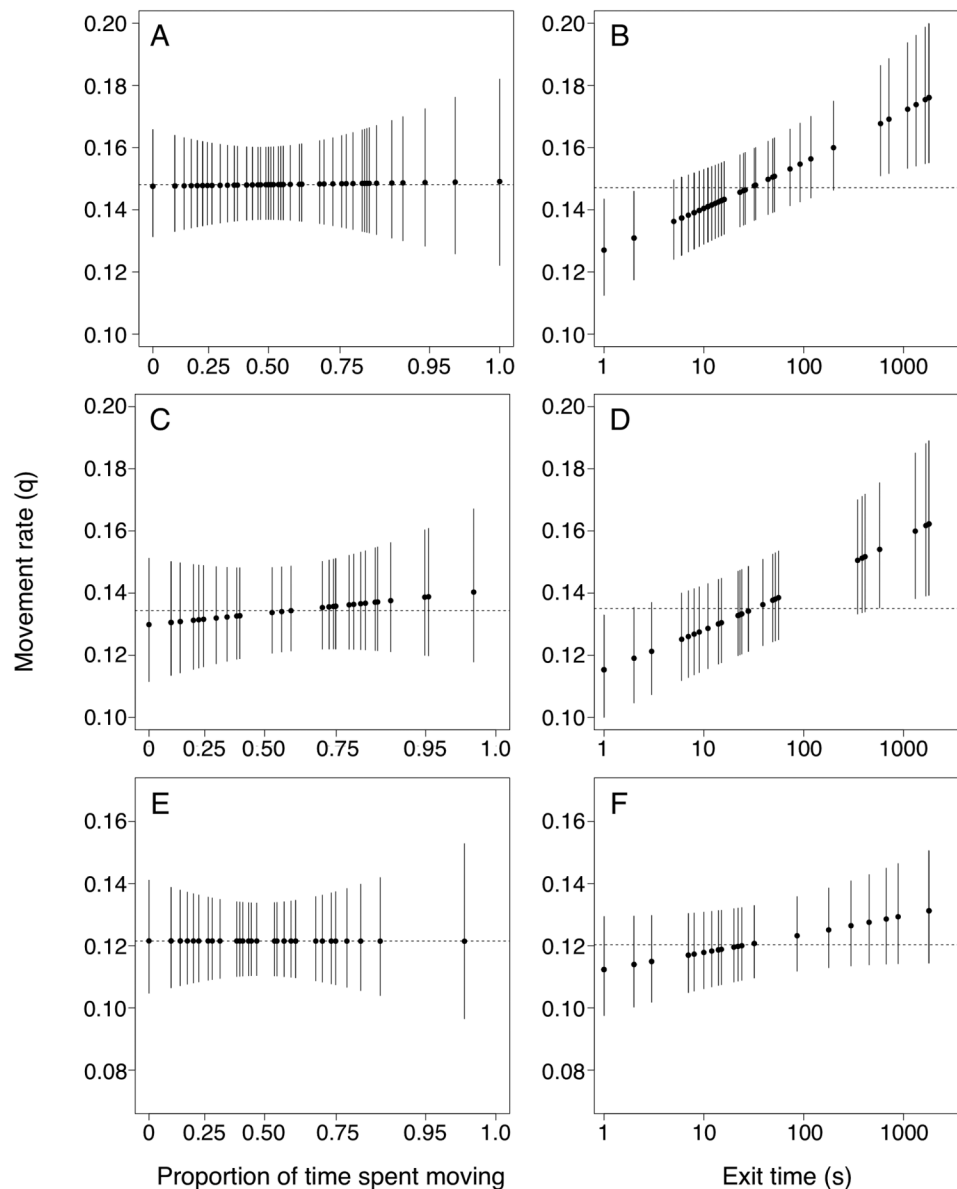


Fig. 3. Estimated movement rates q (min^{-1}) for each individual in the laboratory in relation to proportion of time spent moving while searching for prey in the field for three experimental trials: (A) dividers with holes, 2008 ($n = 59$); (C) dividers with holes, 2009 ($n = 34$); (E) open dividers, 2009 ($n = 32$). Estimated movement rates q min^{-1} for each individual in the laboratory in relation to exit times from the tube exit experiment in the field for three experimental trials: (B) dividers with holes, 2008 (novel object absent; $n = 59$); (D) dividers with holes, 2009 (novel object present; $n = 34$); (F) open dividers, 2009 (novel object absent; $n = 32$). Points and associated vertical lines represent estimated movement rate and 95% confidence interval. The dotted line represents the mean movement rate across all individuals.

ronments in which the individuals travel, as well as any physiological changes required for long distance movement (Dingle 2006). The link between risk taking and field dispersal in the

present study satisfies all three conditions. Conversely, activity during prey search was unrelated with propensity to disperse in the lab, whereas dispersal in the field and propensity

Table 2. Model rankings for models M3 (baseline without covariates) and M4 (minimum displacement distances in the field as a covariate). n : number of individuals; ΔAIC : difference between the AIC of the best approximating model and AIC score of each model; w_i : Akaike weight.

Model description	AIC	ΔAIC	(w_i)	Parameters	n
Displacement distance (M4)	2551.3	0	0.99	4	19
Baseline (no covariates) (M3)	2576.6	25.4	0.00	3	19

to disperse in the lab were correlated. These findings suggest that activity during prey search and dispersal involve different sensory, motivational, or energetic mechanisms as Fausch et al. (2002) cautioned. This outcome is plausible because the two forms of behavior involve different aspects of movement. Activity during prey search involves differences in the proportion of time individuals spend moving whereas dispersal involves differences in net displacements. Further examination of individual differences in risk taking and activity during prey

search as explanations for the slow and fast dispersers in lake and stream fishes is warranted because (1) heterogeneity in dispersal distances can be influenced by individual differences in behaviors other than those hypothesized, (2) individuals could be intrinsically similar in their propensity to disperse, but encounter different environmental conditions that affect how far they disperse (Fausch et al. 2002), in which case propensity to disperse and realized dispersal distances could be unrelated, or (3) individuals could be intrinsically similar in their propensity to disperse, but heterogeneity in realized dispersal distances is the outcome of two underlying movement processes that all individuals employ probabilistically during dispersal (Firle et al. 1998, Rodríguez 2002).

Contrary to expectation, there was a negative relationship between risk taking and propensity to disperse in the lab, and between minimum displacement distance in the field and propensity to disperse in the lab. These relationships were consistent across experimental trials and are unlikely to have arisen by chance. These outcomes indicate that caution is required when using dispersal channels to infer the dispersal of fishes in the field without proper validation. Previous studies have used similar channels to make inferences about fish dispersal (Raleigh 1971, Northcote and Kelso 1981), out-migration (Bradford and Taylor 1997), or invasiveness (Rehage and Sih 2004, Cote et al. 2010b) in the field, without verification that individual performance in the channel was consistent with the corresponding behavior in the field. Why performance in the dispersal channels was contrary to expectation remains unclear. Additional experiments revealed that the nature of the relationships was not due to differential preference for overhead cover or for structure in the water column, which could affect willingness to pass through holes (Appendix). Our interpretation is

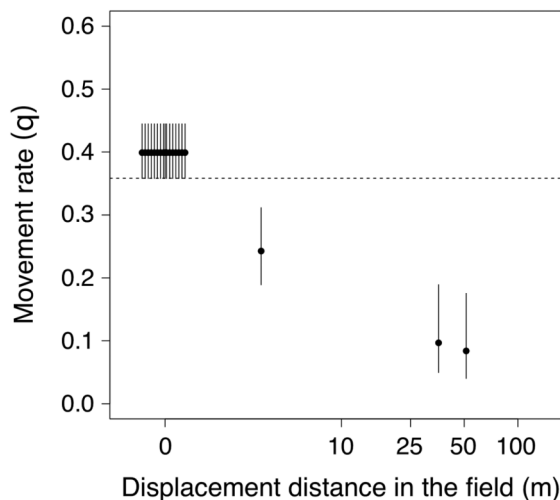


Fig. 4. Estimated movement rates q (min^{-1}) in the laboratory in relation to minimum displacement distances observed in the field for 19 individuals in dispersal channels with dividers having holes, 2009. Points and associated vertical lines represent the estimated movement rate and 95% confidence interval for a given value of displacement in the field. The dotted line represents the mean movement rate across all individuals. To improve visibility, displacement distances for individuals that never moved in the field have been slightly offset horizontally.

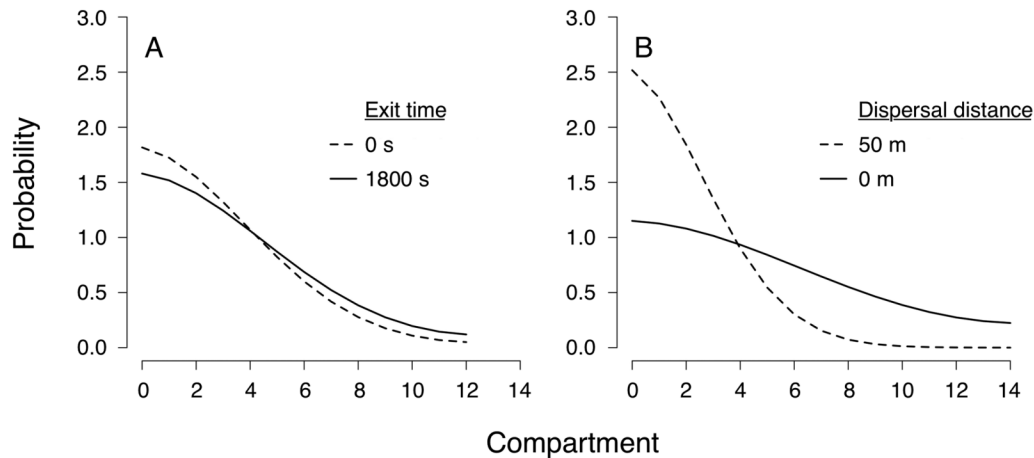


Fig. 5. Dispersal kernels for individuals from the tube exit experiment in (A) the field and (B) the mark recapture study. Curves represent estimated probability distributions for the location of an average individual (distance from the first compartment) 60 minutes after the onset of the experiment. (A) Distributions for a risk taker (solid black curve) and risk avoider (dashed curve) for the 2008 experiment (M2a). (B) Distribution for individuals that dispersed 0 (black curve) and 50 m (dashed curve) in the field (M4).

that the dispersal channel is so novel that the fish with long exit times from the tube experiment panic and move more hurriedly through the channel than do fish with shorter exit times from the tube experiment. However, this remains to be tested.

Our study has important caveats. One caveat is that we only measured dispersal over a short period of time. This was necessary because brook charr mortality during early life-stages is high and only a small fraction of the cohort can be marked; recapture rates over longer time periods can therefore be inadmissibly low. However, a study of dispersal of young-of-the-year brook charr from a lake population indicated that dispersal parameters estimated for the first two weeks following emergence predicted dispersal 12 weeks post-emergence (Coombs and Rodriguez 2007). A second caveat is that we addressed the relationship of short-term dispersal with foraging tactics and risk taking in separate steps, rather than directly (Arnold 1983). This was necessary because the time needed to measure foraging behavior and risk taking limited the number of fish that could be assessed and subsequently released, thereby reducing the chances of recapturing a suitable sample of known individuals. Although the two part

analysis involved two different groups of fish differing in body size (fork length range 1.8–3.3 cm vs. 3.1–5.8 cm) and age, potentially influencing behavioral scores in our assays (Biro 2012), the two parts of the study come together in a way that is logically coherent. A third caveat is that we only tested for relationships between short-term dispersal and measures of foraging tactics and risk taking. Dispersal may also be linked to aggressiveness and sociability (Cote and Clobert 2007, Duckworth and Badyaev 2007, Cote et al. 2010b). For brook charr, the rationale for linking dispersal to aggressiveness and sociability remains unclear. Brook charr can be aggressive towards conspecifics (McLaughlin et al. 1999), but aggressive interactions tend to be infrequent and subtle in still-water habitats (Biro et al. 1997, McLaughlin et al. 1999). Also, shoaling is one clear measure of sociability in fish (Cote et al. 2010b), but brook charr do not shoal. A final caveat is that the influence of personality traits on dispersal may be subtle and difficult to detect, as exemplified by the moderate effect of exit times (risk taking) on predicted dispersal distances in the laboratory.

Despite these caveats, our study provides a set of novel and potentially valuable assessments of behavioral mechanisms linking movements ex-

pressed at different spatial and temporal scales. Our study tested whether dispersal behavior of fish in the field is related to activity during prey search and found no support for this hypothesis. This hypothesis had not been explicitly tested before and alternative hypotheses need to be considered more rigorously. Our study did support the hypothesis that individuals dispersing farther in the field were those more likely to take risks. This relationship demonstrates the potential to predict important components of an individual's lifetime track (Nathan et al. 2008) and to understand how key individuals disproportionately influence ecological processes such as spread of diseases and colonization of new habitats (Sih and Watters 2005, Cote et al. 2010b). Lastly, our study demonstrated that the relationship between different components of movement behavior expressed at different spatial and temporal scales can be complex and require deeper understanding of how individuals perceive and respond to risky situations.

ACKNOWLEDGMENTS

We thank the Department of Integrative Biology at the University of Guelph for partially funding this project and the Hagen Aqualab for providing support and facilities for the laboratory experiments. MAR and RLM thank the Natural Sciences and Engineering Council of Canada for financial support. We also thank Eric Smyth, Clayton Coppaway, Jeff Zeyl, Jennifer McCarter, Michelle Farwell, and in particular Tanya Pulfer for assistance in the field. We thank the Ontario Ministry of Resources for permission to collect fish for scientific purposes. Collections were made under Animal Utilization Protocol 08R34, University of Guelph. Finally, we thank Douglas Fraser and an anonymous reviewer for insightful comments on earlier versions of the manuscript.

LITERATURE CITED

- Ahmed, S., S. G. Compton, R. K. Butlin, and P. M. Gilmartin. 2009. Wind-borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. *Proceedings of the National Academy of Sciences of the United States of America* 106:20342–20347.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–266.
- Arnold, S. J. 1983. Morphology, performance, and fitness. *American Zoologist* 23:347–361.
- Biro, P. A., M. S. Ridgway, and D. L. G. Noakes. 1997. The central-place territorial model does not apply to space-use by juvenile brook charr *Salvelinus fontinalis* in lakes. *Journal of Animal Ecology* 66:837–845.
- Biro, P. A. 2012. Do rapid assays predict repeatability in labile (behavioral) traits? *Animal Behavior* 83:1295–1300.
- Bradford, M. and G. Taylor. 1997. Individual variation in dispersal behavior of newly emerged Chinook salmon (*Oncorhynchus tshawytscha*) from the upper Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1585–1592.
- Brown, C., F. Jones, and V. Braithwaite. 2005. In situ examination of boldness-shyness traits in the tropical poeciliid, *Brachyrhaphis episcopi*. *Animal Behaviour* 70:1003–1009.
- Burnham, K. and D. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag, New York, New York, USA.
- Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols. 2001. Dispersal. Oxford University Press, New York, New York, USA.
- Coombs, M. F. and M. A. Rodríguez. 2007. A field test of simple dispersal models as predictors of movement in a cohort of lake-dwelling brook charr. *Journal of Animal Ecology* 76:45–57.
- Cote, J. and J. Clobert. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B* 274:383–390.
- Cote, J., J. Clobert, T. Brodin, S. Fogarty, and A. Sih. 2010a. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B* 365:4065–4076.
- Cote, J., S. Fogarty, K. Weinersmith, T. Brodin, and A. Sih. 2010b. Personality trait and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society B* 277:1571–1579.
- Dingle, H. 2006. Animal migration: is there a common migratory syndrome? *Journal of Ornithology* 147:212–220.
- Dobzhansky, T. and S. Wright. 1943. Genetics of natural populations. X. Dispersion rates in *Drosophila pseudoobscura*. *Genetics* 28:304–340.
- Duckworth, R. A. and A. V. Badyaev. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences USA* 104:15017–15022.
- Dybiec, B., A. Kleczkowski, and C. A. Gilligan. 2009. Modeling control of epidemics spreading by long-range interactions. *Journal of the Royal Society Interface* 6:941–950.
- Farwell, M. and R. L. McLaughlin. 2009. Alternative foraging tactics and risk taking in brook charr (*Salvelinus fontinalis*). *Behavioral Ecology* 20:913–

- 921.
- Fausch, K., C. Torgersen, C. Baxter, and H. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *Bioscience* 52:483–498.
- Firle, S., R. Bommarco, B. Ekbom, and M. Natiello. 1998. The influence of movement and resting behavior on the range of three carabid beetles. *Ecology* 79:2113–2122.
- Fraser, D., J. Gilliam, M. Daley, A. Le, and G. Skalski. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist* 158:124–135.
- Grant, J. W. A. and D. L. G. Noakes. 1987a. Movers and stayers - foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. *Journal of Animal Ecology* 56:1001–1013.
- Grant, J. W. A. and D. L. G. Noakes. 1987b. Escape behavior and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1390–1396.
- Grinnell, J. 1931. Some angles in the problem of bird migration. *The Auk* 48:22–32.
- Gros, A., H. J. Poethke, and T. Hovestadt. 2006. Evolution of local adaptations in dispersal strategies. *Oikos* 114:544–552.
- Gurarie, E., J. J. Anderson, and R. W. Zabel. 2009. Continuous models of population-level heterogeneity inform analysis of animal dispersal and migration. *Ecology* 90:2233–2242.
- Jackson, C., L. Sharples, S. Thompson, S. Duffy, and E. Couto. 2003. Multistate Markov models for disease progression with classification error. *Journal of the Royal Statistical Society Series D* 52:193–209.
- Jackson, C. H. 2011. Multi-state models for panel data: The msm package for R. *Journal of Statistical Software* 38(8):1–29. <http://www.jstatsoft.org/v38/i08/>
- Jones, R., N. Gilbert, M. Guppy, and V. Nealis. 1980. Long distance movement of *Pieris rapae*. *Journal of Animal Ecology* 49:629–642.
- Jonsen, I. D., R. A. Myers, and M. C. James. 2006. Robust hierarchical state-space models reveal diel variation in travel rates of migrating leatherback turtles. *Journal of Animal Ecology* 75:1046–1057.
- Kerr, B., M. Riley, M. Feldman, and B. Bohannan. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* 418:171–174.
- Kot, M., M. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* 77:2027–2042.
- McLaughlin, R. L., M. Ferguson, and D. Noakes. 1999. Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sitting-and-waiting and actively searching. *Behavioral Ecology and Sociobiology* 45:386–395.
- McLaughlin, R. L., J. Grant, and D. Kramer. 1992. Individual variation and alternative patterns of foraging movements in recently-emerged brook charr (*Salvelinus fontinalis*). *Behaviour* 120:286–301.
- McLaughlin, R. L., J. Grant, and D. Kramer. 1994. Foraging movements in relation to morphology, water-column use, and diet for recently emerged brook trout (*Salvelinus fontinalis*) in still-water pools. *Canadian Journal of Fisheries and Aquatic Sciences* 51:268–279.
- Morales, J. and S. Ellner. 2002. Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology* 83:2240–2247.
- Morales, J., D. Haydon, J. Frair, K. Holsinger, and J. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85:2436–2445.
- Nathan, R. 2008. An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences USA* 105:19050–19051.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences USA* 105:19052–19059.
- Northcote, T. and B. Kelso. 1981. Differential response to water current by two homozygous LDH phenotypes of young rainbow trout (*Salmo gairdneri*). *Canadian Journal of Fisheries and Aquatic Sciences* 38:348–352.
- Paradis, E., S. Baillie, W. Sutherland, and R. Gregory. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67:518–536.
- Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. *Trends in Ecology and Evolution* 23:87–94.
- Phillips, B. L., P. G. Brown, and R. Shine. 2009. The evolution of growth rates on an expanding range edge. *Biology Letters* 5:802–804.
- Radinger, J. and C. Wolter. 2013. Patterns and predictors of fish dispersal in rivers. *Fish and Fisheries* doi: 10.1111/faf.12028
- Raleigh, F. R. 1971. Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. *Ecology* 52:291–297.
- Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.
- Rehage, J. and A. Sih. 2004. Dispersal behavior, boldness, and the link to invasiveness: a comparison of four *Gambusia* species. *Biological Invasions* 6:379–391.
- Rodríguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology* 83:1–13.

- Samu, F., A. Sziranyi, and B. Kiss. 2003. Foraging in agricultural fields: local 'sit-and-move' strategy scales up to risk-averse habitat use in a wolf spider. *Animal Behaviour* 66:939–947.
- Sih, A. and J. Watters. 2005. The mix matters: behavioral types and group dynamics in water striders. *Behaviour* 142:1417–1431.
- Skalski, G. and J. Gilliam. 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. *Ecology* 81:1685–1700.
- Therneau, T. and T. Lumley. 2011. survival: Survival analysis, including penalised likelihood. R package version 2.36-10. <http://CRAN.R-project.org/package=survival>
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts, USA.
- van Oers, K., P. Drent, P. de Goede, and A. van Noordwijk. 2004. Realized heritability and repeatability of risk-taking behavior in relation to avian personalities. *Proceedings of the Royal Society B* 271:65–73.
- Wilson, A. D. M. and R. L. McLaughlin. 2007. Behavioral syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour* 74:689–698.

SUPPLEMENTAL MATERIAL

APPENDIX

Initial findings suggested that the propensity to disperse in the lab was related to risk taking, but, contrary to expectation, risk-avoiders (long exit times) exhibited greater dispersal propensities in the dispersal channel than risk-takers (short exit times). Two mechanisms could influence this negative relationship. Risk-avoiders could exhibit greater propensities to disperse in the lab than risk-takers if risk-avoiders were searching the dispersal channel for overhead cover. We therefore conducted an exit experiment in the dispersal channel having dividers with holes to test whether individuals remained longer in compartment 1 when overhead cover was provided than when no overhead cover was provided. Alternatively, risk-avoiders could have exhibited greater propensities to move through the dispersal chamber than risk-takers if they are more likely to associate with in-stream vegetation and debris in the field and therefore more likely to move through the holes in the compartment dividers. We therefore tested whether individuals differed in their affinity for in-stream vegetation and whether individuals displaying higher affinity for in-stream vegetation were more likely to move through the structural components within the dispersal channel than individuals with less affinity for structure.

Effect of overhead cover on exit from the first compartment

Forty individuals (2.2–3.4 cm fork length; 0.04–0.32 g wet mass) were dip-netted (18 × 25

cm) haphazardly from still-water pools at the West Branch of the Credit River during early May 2009. Following capture, individual fish were transported to the Hagen Aqualab in an aerated 20-L container and held together overnight in a holding aquarium. The following morning, individual fish were selected haphazardly from the holding aquarium, assigned randomly a dispersal channel, and placed into compartment 1. An opaque PVC sheet prevented the individual from exiting into compartment 2. The individual was given 10 minutes to adjust to its new surroundings. It was then given 1200 seconds to exit through the hole. An exit time of 1200 seconds was recorded if the individual had not left compartment 1 after 1200 seconds. Each individual was tested twice. One treatment measured the time taken to exit from compartment 1 into compartment 2 with a piece of cardboard covering compartment 1 (overhead cover) and another without cardboard covering compartment 1 (no overhead cover). The sequence of treatment was randomized and in each treatment the hole between compartment 2 and 3 was blocked to prevent individuals from exploring the dispersal channels. All treatments were recorded on video.

Quantification of affinity for structure

A laboratory experiment was used to determine whether individuals differed in their affinity for structure and whether any differences were related to the willingness to pass through the holes of the dispersal channel. The test arena consisted of 20 aquaria (40 cm long × 30 cm wide

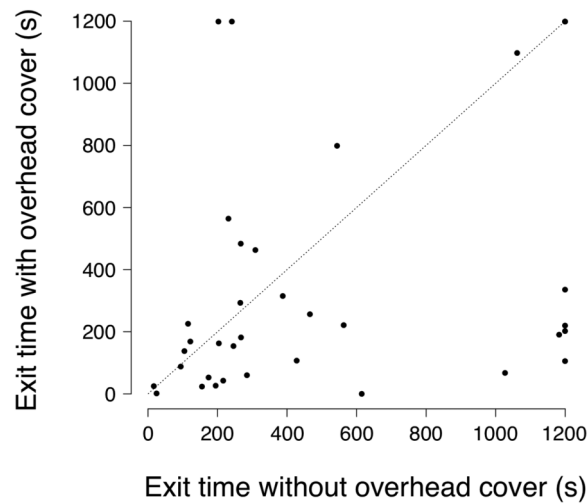


Fig. A1. Exit times from compartment 1 to compartment 2 for individual brook charr in the absence (x-axis) and presence of overhead cover (y-axis). Each point represents an individual. The diagonal (1:1) dotted line represents identical exit times in the absence and presence of overhead cover.

× 30 cm high; mean water flow = 6.7 ml sec^{-1} and water temperature = $10\text{--}12^{\circ}\text{C}$). The sides of the aquaria were opaque so that fish in adjacent aquaria could not observe one another. Simulated in-stream vegetation (structure) made from shreds of green plastic bags extending from the bottom to the water surface was placed at one

long end of the aquarium. Two lines were drawn on the aquarium bottom dividing the length of the aquarium into three equal-sized sections differing in their distance from the simulated in-stream vegetation. Black plastic bags were hung across the lengths and ends of the experimental setup to facilitate behavioral obser-

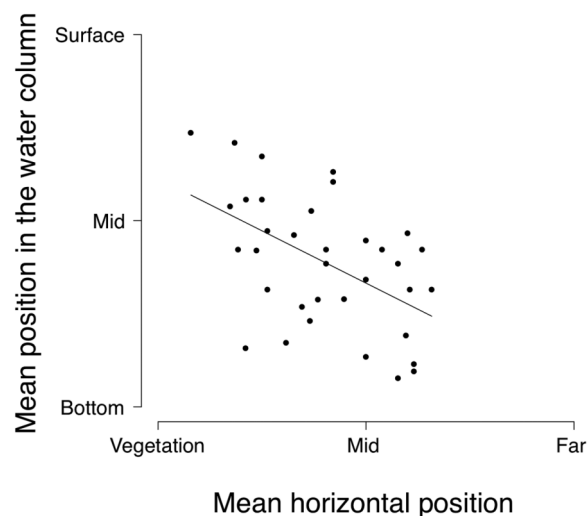


Fig. A2. Horizontal (x-axis) and vertical (y-axis) habitat use of individual brook charr relative to simulated in-stream vegetation. Each point represents the mean horizontal and vertical location of an individual. The solid line represents the regression equation relating mean vertical position (y) to the mean horizontal position (x) ($y = 2.789 - 0.562x$; $F = 11.75$; $df = 33$; $R^2 = 0.26$; $P = 0.002$).

uations with minimal disturbance by the observer (AHE).

Following the exit experiment, individual fish were assigned randomly and singly to an aquarium. Observations of the horizontal and vertical position of each fish in the water column were made twice daily between 08:00 and 10:00 and between 16:00 and 19:00 for 14 consecutive days. Horizontal position of an individual was scored as 1 if the fish was in the section closest to the simulated vegetation, 2 if the fish was in the middle section, or 3 if the fish was in the section farthest from the vegetation. Vertical position was determined by recording whether the fish was on or just off the bottom (1), just under the surface (3), or in the space between the bottom and surface (2). After 14 days, mean horizontal and vertical positions were calculated for each individual. For the duration of the experiment, fish were hand-fed (trout chow spread uniformly over the water surface) *ad lib* twice daily at times outside of the observation periods.

Statistical analysis

We used time-to-event analysis to test whether individuals remained longer in compartment 1 when provided overhead cover than when not provided overhead cover and to test whether individuals with greater affinity for structure were likely to exit more rapidly from compartment 1 (no overhead cover) than individuals with less affinity for structure. This form of analysis was appropriate because data represent-

ed time to a pre-specified event (exiting) and included durations where some trials ended before the event occurs (censored data). All time-to-event analyses statistically adjusted for fork length (body size) and were based on a Z test with a one-tailed alpha of 0.05. The R package survival (version 2.36-10; Therneau and Lumley 2011) was used for time-to-event analyses.

Results

We found no evidence that individuals in the dispersal channel were searching for overhead cover. Individuals did not remain longer in the first compartment when the overhead cover was available than when it was not available ($Z = 3.49$; $df = 37$; one-tailed $P > 0.95$). In fact, individuals left the first compartment sooner, on average when the overhead cover was available (median = 192 s) compared to when it was absent (median = 268 s) (Fig. A1). We also found no evidence that movement through the dispersal channel was influenced by affinity for in-stream vegetation and corresponding willingness to pass through the holes in the channel dividers. Individuals did differ in their affinity for simulated in-stream vegetation (Fig. A2). However, individuals with higher affinity for structure did not pass through the hole into the second compartment sooner than individuals with lower affinity for structure ($Z = -1.17$; $df = 33$; one-tailed $P = 0.26$).