2012-04-01

Dispersal behavior correlates with personality of a North American fish

Josh E. Rasmussen

Mark C. Belk
Brigham Young University - Provo, mark_belk@byu.edu

Dispersal behavior correlates with personality of a North American fish

Josh E. RASMUSSEN[1*], Mark C. BELK[2]

[1] U.S. Fish and Wildlife Service, Klamath Falls, OR 97603, USA

[2] Department of Biology, Brigham Young University, Provo, UT 84602, USA

Abstract The process of dispersal is determined by the interaction of individual (intrinsic) traits and environmental (extrinsic) factors. Although many studies address and quantify dispersal, few evaluate both intrinsic and extrinsic factors jointly. We test the relative importance of intrinsic traits (exploration tendency and size) and extrinsic factors (population density and habitat quality) on dispersal of a medium-sized western United States minnow, southern leatherside chub *Lepidomeda aliciae*. A generalized linear model with a binomial response was used to determine the probability of individuals dispersing one year after tagging. Medium-sized individuals that were more prone to explore novel environments were 10.7 times more likely to be recaptured outside of their original capture area after a year (dispersal) compared to non-explorer individuals of the same size class. Differences between explorer classifications within the small and large size classes were negligible. Open habitat within 50 m upstream also increased the probability of dispersal relative to controls. Relative location within the study reach, and population density were not significantly related to dispersal probabilities of individuals. Our results indicate that understanding of personality may illuminate patterns of dispersal within and among populations [*Current Zoology* 58 (2): 260–270, 2012].

Keywords Temperament, Behavioral phenotype, Exploration, *Lepidomeda*, Personality-dependent

Simply defined, dispersal is the movement of an organism from one location to another, although it is often difficult to specify minimum spatial and temporal bounds that delineate when the process has occurred. The consequences of this simple action are often important at an individual level (Réale et al., 2007), and potentially have ecological and evolutionary roles for populations (Gresswell and Hendricks, 2007; Hassel and Nay, 1985) and communities (Bohonak, 1999; Bowler and Benton, 2005; Hanski and Gaggiotti, 2004; Ronce, 2007). For example, dispersal may mitigate negative interactions between ontogenetic stages or close relatives (Stenseth and Lidicker, 1992), affect metapopulation dynamics (Tallmon, Luikart and Waples, 2004), or be the mechanism of range expansion for a species (Fausch and Young, 1995; Neely and George, 2006). However, the inclination to disperse (or not) may not be homogenous among individuals of a population (Clobert et al., 2009; Godinho et al., 2007; Gresswell and Hendricks, 2007; Knaepkens et al, 2005).

Drivers of animal dispersal operate, singly or together, as an individual responds to surrounding habitat, such as resource availability, population, community, or environmental factors (Bowler and Benton, 2005;

Fausch and Young, 1995; Fraser et al.,1999). Individuals may respond differently to varying levels of stimuli based on intrinsically determined thresholds (McMahon and Matter, 2006). Varying thresholds and adaptive responses to dispersal triggers among individuals within a population or among species within a community produce a range of responses to the same ecological conditions. If differences in fitness or survival are associated with dispersal, natural selection will likely affect these intrinsic thresholds and adaptive responses over evolutionary time scales (Bowler and Benton, 2005; Diekmann et al., 1999; Dodson, 1997). Through the complex operations of the endocrine and nervous systems, individuals assess motivational levels (e.g. hunger, stress, fear) and their environment (Brown and Braithwaite, 2004; Clobert et al., 2009), including the presence of predators (Fraser et al., 1999), habitat (Fausch et al., 1995), or resources (e.g., food, space, or potential mates, see Belanger and Rodriguez, 2002; Lawrence, 1987). This information about the surrounding environment may be obtained directly through exploratory behavior or indirectly through social interactions (Clobert et al., 2009; Cote and Clobert, 2007b; Dall et al., 2005; Danchin et al., 2004; Valone and

---

Templeton, 2002), and can provide either prompting or suppressing stimuli for dispersal (Gowan and Fausch, 2002). Information is critical for an organism to be able to occupy the optimal patch in heterogeneous environments (Fausch and Young, 1995), but it is often unclear how much area individuals are able sample or assess through either private or public information (Danchin et al., 2001). An individual's intrinsic traits certainly interact with these extrinsic factors, and therefore also substantially affect dispersal (Bowler and Benton, 2005; Clobert et al., 2009).

Intrinsic traits commonly considered in dispersal analysis include age (Downs et al., 2006; Ekman, 2007), sex (Croft et al., 2003; Eikenaar et al., 2008), and reproductive status (Andreu and Barba, 2006). However, lesser studied intrinsic traits may also contribute to dispersal, such as social status (Aragon et al., 2006), morphology (O'Rian et al., 1996), or personality, also called temperament in the literature (Cote and Clobert, 2007a; Cote et al., 2010; Réale et al., 2007). For example, mosquitofish *Gambusia affinis* that were identified as more asocial than the population norm tended to disperse greater distances (Cote et al., 2010), and mosquitofish from populations characterized as more asocial or bold overall also dispersed more often regardless of their individual personality type (Cote et al., 2011). Boldness of Trinidad killifish *Rivulus hartii* was also found to be positively correlated with dispersal distance (Fraser et al., 2001). Duckworth and Badyaev (2007) also showed that dispersal tendencies and aggression were linked in western bluebirds *Sialia mexicana*. However, Bell and Stamps (2004) observed that individual personality of sticklebacks *Gasterosteus aculeatus* was not stable over time, but that the correlation between behaviors was stable. For example, as individual sticklebacks aged they may not always be the most aggressive, but at a given period the most aggressive individuals were also typically bolder toward predators. In general, the field of personality-dependent dispersal is expanding rapidly as greater evidence emerges of the relationship between personality types and dispersal (Cote et al., 2010).

Study of animal personality has increased in recent years (Conrad et al., 2011; Sih et al., 2004). Although individual behavior has often been regarded as infinitely flexible (Dingemanse and Réale, 2005), animals regularly express similar behavioral responses across a range of situations, suggesting limited plasticity (Budaev, 1997; Schürch and Heg, 2010; Sih et al., 2004; Wilson and Godin, 2009). Individual behavior can be assessed

across five axis of personality (Réale et al., 2007): boldness, exploration, activity, aggressiveness, and sociability. Natural selection can operate across these axes to affect the ecology and evolution of populations and species (Réale et al., 2007). For example, rates of exploration were linked to survival and reproduction of great tits (*Parus major*; Dingemanse and Réale, 2005), and boldness in ewe bighorn sheep *Ovis Canadensis* was correlated with age at first reproduction, reproductive output, and survival (Réale et al., 2000; Réale and Festa-Bianchet, 2003).

The exploration axis addresses the inclination of an individual to explore a novel space (Conrad et al., 2011; Réale et al., 2007). Multiple species of fish have been shown to exhibit consistent exploration behavior over time (Budaev, 1997; Coleman and Wilson, 1998; Cote et al., 2010; Schürch and Heg, 2010; Wilson and Godin, 2009, 2010). However, few studies have examined the relationship between this personality trait and dispersal directly (Conrad et al., 2011; Fraser et al., 2001). Here we test the correlation of exploration personality of a North American minnow with dispersal behavior. Our specific hypotheses are twofold: 1) An individual's propensity to explore a novel environment is positively related to long-term dispersal behavior and 2) this propensity is independent of available information about the local environment. Specifically, we assess the effect of extrinsic factors (i.e., population density and habitat quality) and intrinsic traits (i.e., exploration tendency and size) on the probability of dispersal in southern leatherside chub *Lepidomeda aliciae*. For the purposes of this research we define "dispersal" as any relevant translocation of an individual, as in the movement from one patch to another. We avoid use of the term "movement" to minimize confusion with the concept of motion of a physical body, as in the movement of the caudal peduncle.

1 Materials and Methods

1.1 Study site

This study was conducted with southern leatherside chub in portions of Salina Creek located in Salina Canyon near Salina, Sevier County, Utah, USA. The creek captures runoff from the Wasatch Plateau (elevation approximately 2000 m above sea level), and flows west until discharging into the Sevier River. Yearly peak flows in Salina Creek occur during May and June, and are driven by snowmelt runoff. Historic (1963–2011) maximum flows for this creek were 12.3 m^{3}s^{-1} (U.S. Geological Survey water Gauge 10205030). Base flows,

approximately 0.26 m^{3}s^{-1}, occur from August through April each year. The median flow during this study was comparable to long-term data, 0.27 m^{3}s^{-1}; the maximum instantaneous flow during the study was 3.51 m^{3}s^{-1}. Portions of the creek through the study section have been channelized or modified by the addition of large culverts that pass beneath the interstate highway, which runs roughly parallel to the stream through the canyon.

The section of the creek used in this study spanned approximately 15 km, dropping from an elevation 2018 m to 1757 m above sea level, a difference of 261 m (1.74 % slope). Aquatic habitats differed across this distance (Table 1). In general, the stream becomes less steep and more sinuous as it progresses downstream through the study site. This produces a gradient in substrate sizes, which are larger upstream (e.g., cobble and small boulders) and smaller downstream (e.g., sand and gravel). The middle reaches of the study site possessed substrate size transitional between these two groups. Densities of southern leatherside chub were found to be generally lower upstream and higher downstream, with the middle portion supporting intermediate densities (Table 1).

The native fish assemblage in Salina Creek is comprised of southern leatherside chub, mottled sculpin *Cottus bairdi*, speckled dace *Rhinichthys osculus*, and mountain sucker *Catostomus platyrhynchus*. Rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* have been introduced into the stream, but typically do not occur within the areas used for this study. Areas inhabited by these predators were purposely avoided to prevent confounded results since southern leatherside chub appear to be excluded by brown trout (Walser et al., 1999; Wilson and Belk, 2001). Competition for food resources between southern leatherside chub and other sympatric species probably insignificantly affects southern leatherside chub dispersal behavior because southern leatherside chub feed on items suspended in the flow of the stream and the others are primarily demersal or benthic feeders (Sigler and Sigler,

1996).

Southern leatherside chub are a medium-sized cyprinid (maximum standard length [SL] approximately 145 mm) that historically inhabited streams and lakes within the Bonneville Basin of the western United States. The probability of occurrence of southern leatherside chub is negatively associated with water velocity (Wilson and Belk, 2001). In contrast, water depth is positively associated with southern leatherside chub abundance (Walser et al., 1999; Wilson and Belk, 2001). Substrate size was found by Wilson and Belk (2001) to be negatively associated with both occurrence probability and abundance, but Walser et al. (1999) found southern leatherside chub to more commonly occur in heavily silted areas. In addition, this population of southern leatherside chub exhibits mainly short-distance dispersal. In a separate four-year mark-recapture study, 95% of recaptures were less than 100 m from year to year, but a small fraction of individuals were recaptured within 1 km up- or downstream (J. Rasmussen, unpublished data).

1.2   Sampling methodology

Within the 15 km of the study section, twelve 1-km segments were delineated (Fig. 1). Some portions of the stream were excluded due to the presence of large culverts that would likely disrupt natural dispersal behavior or act as complete barriers to passage. At the center of each 1-km segment a 25-m segment (target segment) was further delineated from which southern leatherside chub were captured. After capture these fish were assayed, tagged, and subsequently returned to the same 25-m segment. Sampling and marking were conducted from August through November 2005. Initial sampling consisted of a three-pass depletion procedure using a backpack electro-shocker within each 25-m target segment. Captured fish that were to be used in the study were held (typically < 1 hr) using aerated tanks with approximately 85 L of water until testing and tagging could be completed. Sampling efforts at individual sites were grouped by arbitrary divisions within the stream,

Table 1   Metrics of the downstream third (downstream), middle third (midstream), upper third (upstream), and complete study section

	Slope (%)	Sinuosity	Width (m)	Density	Substrate
Downstream	0.92	1.10	6.4 (1.4)	196.3 (83.0)	Sand, Gravel
Midstream	1.91	1.04	6.9 (0.9)	74.5 (80.7)	Gravel, Rubble, Cobble
Upstream	2.17	1.03	6.0 (0.7)	42.5 (8.3)	Cobble, Small Boulders
Overall	1.74	1.06	6.4 (1.0)	167.8 (91.5)	

Slope and sinuosity (stream distance / valley distance) were calculated across the entire section. Stream width and population density are mean values with standard deviations in (). Population density is the mean number of southern leatherside chub per 25 m. The substrate value indicates a qualitative assessment of predominant substrate type throughout the section.
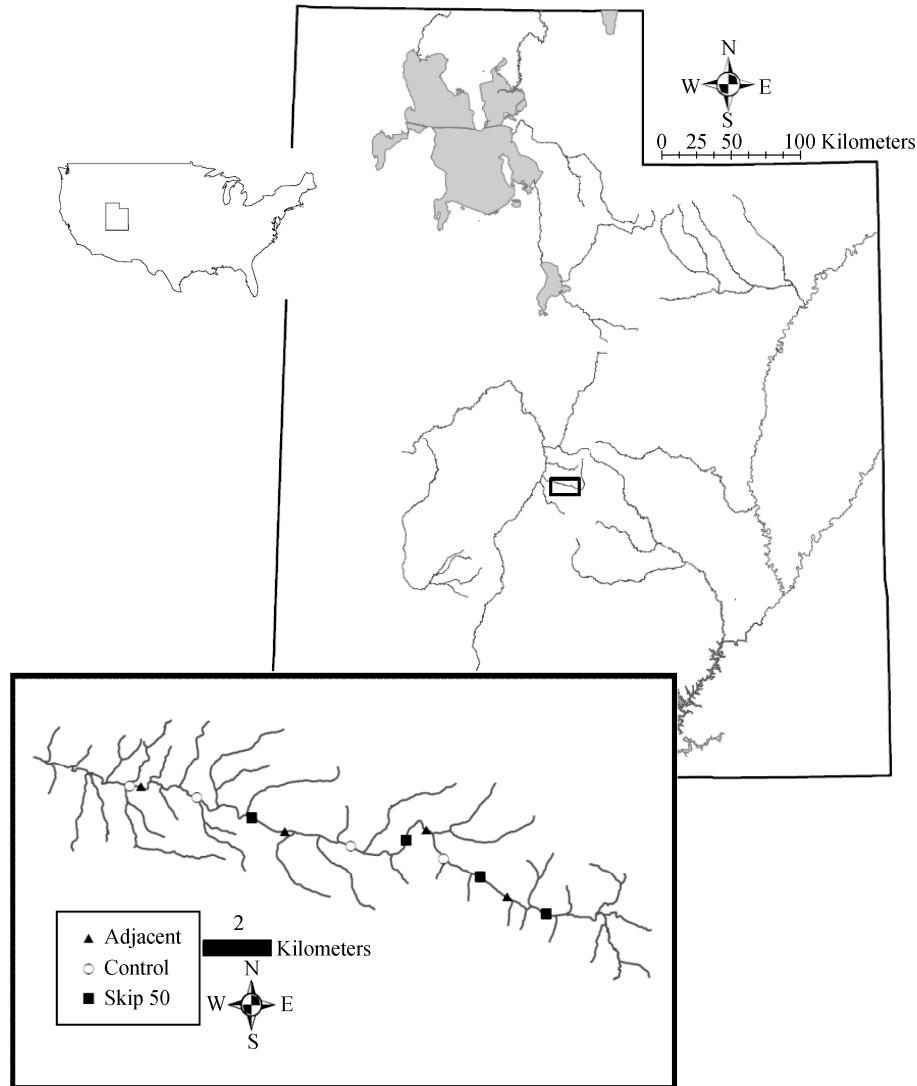
Fig. 1   Locations of the 12 study segments along Salina Creek in central Utah
Sites were grouped into groups of four as part of the position variable included in the analysis. The lowest the four sites were classified as "downstream;" the central four sites were classified as "midstream;" and the top four streams were classified as upstream. The stream flows from east to west (right to left).

i.e. all downstream segments were sampled before moving to midstream sites, and lastly upstream sites; but sampling order within a division was randomized.

Individuals greater than 40 mm SL ($n = 1,044$) from the 25-m target sections were assessed (Table 2) on the promptness with which they explored a novel environment (exploration/avoidance behavioral axis; Réale et al., 2007). These personality assays were conducted using a portable swim chamber (Fig. 2) in the field. The minimum length (40 mm) represents most age-1 individuals and is the smallest size that could be captured reliably. Swim chambers were constructed from white, five-gallon buckets with an opaque bowl weighted with a cobble-sized rock from the stream and positioned in

the center thereby creating a circular swim track approximately 100 mm in depth with a minimum (e.g. interior) circumference of 440 mm (140 mm in diameter) and a maximum (e.g. exterior) circumference of 839 mm (268 mm in diameter). Inconspicuous hash marks were placed around the swim chamber to facilitate estimation of the distance swum during the test. Individuals were placed inside the swim chamber and allowed to acclimate for two minutes. Following the acclimation period, we tallied the distance swum by the fish during one minute.

Each individual was given an identifying batch mark of visible implant elastomer (Northwest Marine Technologies Inc., Shaw Island, Washington, USA) reflecting

Table 2   Summary of data for each study segment beginning at the most downstream

| Manipulation	Explorer	Non-explorer	Recaptured	Outside
Control	7	102	44	12
Adjacent	24	81	23	15
Control	46	132	53	20
Skip	30	185	52	21
Adjacent	5	50	23	22
Control	4	20	5	4
Skip	28	147	33	17
Adjacent	2	23	6	6
Control	1	41	10	4
Skip	2	32	12	10
Adjacent	2	44	7	7
Skip	1	35	3	3
Total	152	892	271	141

Columns include density manipulation applied to each site, exploration phenotype categorization based on the field personality assay at each site, total number recaptured, and the number of individuals recaptured outside of the original 25-m tagging section (Outside). Summing the numbers in the explorer and non-explorer columns provides the total number of southern leatherside chub captured and tagged at each site.

exploration phenotype (by color) and original size bin (by location of mark). Fish were binned into two groups based on the exploration/avoidance phenotype: Non-explorer – little or no exploration within the allotted time (86% of the individuals tested), and Explorer – exploration amounting to at least 1 entire lap in the swim chamber in the allotted time (14% of the individuals tested). This break point was chosen *a priori* based on preliminary testing which indicated a natural grouping. Fish were also binned into three size classes, small

(< 65 mm SL; 21%), medium (64–84 mm SL; 55%) and large (84 mm SL; 24%). To apply the tag, small groups of 10 individuals or less were anesthetized in a bath containing a non-lethal dose (100 mg/L) of MS-222 (Argent Chemical Laboratories Inc., Redmond WA) prior to tag insertion. Fish then recovered in a holding tank with aeration until all individuals completely recuperated, typically 30 min, and then were released near the midpoint of the 25-m target section.

In addition to the personality assay, we manipulated southern leatherside chub densities upstream of the 25-m target segment. These manipulations consisted of 1) no density manipulations made – Control, 2) removal of southern leatherside chub from the 50 m immediately upstream of the target segment – Adjacent, and 3) removal of southern leatherside chub from the stream 50 – 100 m upstream of the target segment, but densities were undisturbed in the 50-m stretch immediately upstream of the target segment – Skip. The density manipulation was assigned *a priori* to each segment. Capture of southern leatherside chub from the manipulated 50-m segments, where required, occurred immediately following sampling of the 25-m target segment using the same methodology. Fish from the removal segments were quickly transported in aerated tanks to other sites within Salina Creek beyond the bounds of the study (> 2 km upstream of the uppermost segment).

Re-sampling occurred approximately one year later, August to October 2006. The re-sampling protocol was similar to the original capture sessions with the exception that instead of three-pass sampling, only two passes were conducted on the majority of the distance, and part of the re-sample consisted of only one pass. In addition to the original 25-m target segment, 150 m downstream and 300 m upstream were sampled at each site. Areas
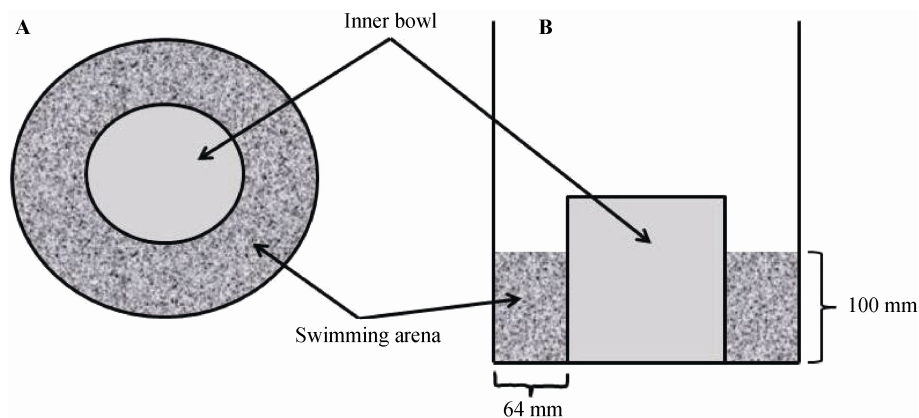
Fig. 2   Portable swim-chamber used to assess exploration phenotype of southern leatherside chub *Lepidomeda aliciae* from the top looking down into the chamber (A) and a cross-sectional cutout (B)

greater than 100 m downstream and 200 m upstream of the 25-m target segment were only sampled with one pass. Capture efficiency with one and two passes is relatively high in this system, on average 79% and 86%, respectively (J. Rasmussen, unpublished data). More distance was re-sampled upstream than downstream of the 25-m target segment because southern leatherside chub in this system have been shown to have a high rate of recapture within 100 m of the capture site, but if dispersal does occur in this system it is predominantly upstream (M. Belk, unpublished data). The distance from the 25-m target segment was rounded for each recaptured fish to the nearest 10 m.

1.3 Statistical methodology

We used a generalized-linear model (GLM) with a binomial response to relate the probability of recapture outside of the original 25-m target segment to intrinsic and extrinsic predictors. Individuals recaptured outside of the original 25-m target segment were assigned a value of "1." Those recaptured within the original 25-m target segment were assigned a value of "0." Model fitting was performed using the *glm* and *lrm* (Harrell, 2007) functions within Program R version 2.8.1 (R Development Core Team, 2008). The full additive model included as fixed-effects the above mentioned density manipulations (Control, Adjacent, Skip), size class (Small, Medium or Large), personality (Non-explorer or Explorer), and stream position (Lower, Middle, and Upper). The estimated density of southern leatherside chub in the 25-m target segment was also included in the full model as a covariate. All possible two-way interactions between each of the fixed-effects were also assessed. To confirm that individual site effects were negligible, we also tested the effect of adding site as a random effect. Other common factors, such as age, sex, and reproductive status, were not included in our model because these traits were not readily distinguishable during the sampling period. Given the presumed binomial distribution of the response, the logit was used as the link-function. Significance of parameters in the model was determined by a drop-in-deviance test assuming a chi-squared (χ^2) distribution of deviances based on an *a priori* $\alpha = 0.05$.

The stream position factor and density covariate were included to account for variation created by the differences in habitat across the range of the study reach. The 12 1-km segments were grouped into three groups of four based on their relative position within the stream, i.e. downstream, midstream, and upstream (Fig. 1). Although these breaks were not determined quantitatively,

they do represent general differences in stream structure. Replication of the treatments within these designations was not balanced. The downstream division included two Controls, the midstream division included two adjacent density manipulations, and the upstream division included two Skip density manipulations. Besides these, each division also included one each from the other two density manipulations. Density was estimated for each 25-m target segment based on three-pass depletion methods and using Program CAPTURE (Pollock and Otto, 1983; White et al., 1978).

2 Results

No significant differences were observed among size classes in proportions of non-explorer and explorer individuals of the original captured fish ($n = 1{,}044$) ($\chi^2_{0.05, 2} = 2.75$, $P = 0.25$). Explorers were also similarly represented within each density manipulation type ($\chi^2_{0.05, 2} = 1.631$, $P = 0.44$). However, the proportion of personality types among stream position divisions was significantly distinct ($\chi^2_{0.05, 2} = 19.38$, $P < 0.001$). As one moves upstream the proportion of explorers identified by the personality assay decreased strongly. The proportion of explorers averaged 17.3% (standard deviation = 8.8%) of all individuals assayed in the downstream division, 12.4% (4.5%) in the middle division, and only 3.8% (1.6%) in the upstream division.

After one year, 271 marked individuals (26%) were recaptured (Table 1); this is consistent with other longer term mark-recapture studies in this system (J. Rasmussen, unpublished data). Fifty-two percent of the recaptured individuals were recaptured outside of the original 25-m target section where they had been captured and marked. Apparent mortality has been estimated to be approximately 50% annually for medium-sized individuals and approximately 40% for small and large size classes (M. Belk, unpublished data), and likely accounts for the many of individuals not recaptured. However, this estimate was not able to distinguish mortality from dispersal to areas that were not sampled for recapture. Differences of recapture rates of non-explorer and explorer individuals (approximately 25% for each) were not significantly different ($\chi^2_{0.05, 1} = 0.48$, $P = 0.49$). However, fish were more likely to be recaptured at Control segments (31.7%), than segments which received the Adjacent density manipulation (25.5%) and the Skip density manipulation (21.7%). This difference was significant between Control and Skip segments ($\chi^2_{0.05, 1} = 10.24$, $P = 0.001$), but not between Adjacent and either the Control or the Skip density manipulations

($P > 0.10$). Downstream sites, in general, had significantly higher recapture rates than upstream sites (28.3% and 24.0% respectively; $\chi^2_{0.05,1} = 4.15$, $P = 0.042$), but all other comparisons among stream position divisions (i.e., downstream versus midstream, and midstream versus upstream) were not statistically significant ($P > 0.16$).

Based on drop-in-deviance tests, the density covariate and size and position main effects did not explain a significant amount of variation (Table 3), but these were retained in the model as statistical controls for the estimation of the primary variables of interest, explorer classification (personality) and manipulation. Individual site effects (modeled as random effects) were negligible with a standard deviation of 0.08. Likewise, all interaction terms, with the exception of the size by personality term, were non-significant, and were not included in the model. Discrimination and calibration of the model were assessed using area under the receiver operator curve (ROC) and the Hosmer-Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow, 2000) and Somers' rank correlation index (D_{xy}) (Harrell, 2001). Based on ROC assessment, model discrimination was acceptable indicating that this model will perform approximately 76% as well on a separate dataset. Likewise, the Hosmer-Lemeshow goodness-of-fit statistic ($\chi^2_{0.05,8} = 9.95$, $P = 0.27$) suggests that the model discriminates well. Somers' rank correlation produced similar results ($D_{xy} = 0.563$), but this statistic was found to be slightly optimistic (0.059) based on bootstrapped replication (B = 150). Incorporating this bias produces a $D_{xy} = 0.502$. Comparison between observed and bias- corrected probabilities, based on bootstrapped replications, re-

Table 3   Statistical significance of variables included in the generalized linear model based on drop-in-deviance tests as compared to a chi-squared distribution

Variable	Drop-in Deviance (χ^2)	DF	*P-value*
Personality	15.29	3	<0.01
Manipulation	22.07	2	<0.01
Stream Position	2.43	2	0.30
Size	7.52	4	0.11
Density	0.19	1	0.67
Personality x Size	7.37	2	0.03

The response was whether individuals were captured outside of the original 25-m target segment (1) or not (0) after one year. Main effects include classification based on personality assay (Explorer or Non-explorer), density manipulation (Manipulation; levels are Control, Adjacent, or Skip), stream position (Downstream, Midstream, or Upstream), Size (Small, Medium, and Large), and Density, as a covariate. The drop-in-deviance, degrees of freedom, and subsequent p-values for the main effects include the factor plus any higher order factors (i.e. interaction terms).

vealed a mean absolute error of 0.03 in predicted probabilities.

Medium-sized individuals that were identified as explorers in our personality assay were 10.7 times (95% Confidence Interval: 3.2 – 36.1) more likely to have been captured outside of the 25-m target segments after one year (for our purposes termed dispersal) than individuals categorized as non-explorers of the same size class. Comparison of the odds ratios (OR) between explorers and non-explorers among size classes revealed that a greater disparity existed between medium-sized individuals compared to small (1.9) and large individuals (OR 0.7) (Table 4). Of the recaptured individuals

Table 4   Effect size and odds ratios of terms in the logistic regression model used to assess the probability of being recaptured outside of the original 25-m target segment after one year

Effect	Effect Size	Standard Error	Odds Ratio
Manipulation - Adjacent	2.17	0.47	8.7 (3.5 – 21.9)
Manipulation - Skip	0.66	0.49	1.9 (0.8 – 5.0)
Exploration – Small individuals	0.66	0.84	1.9 (0.4 – 10.1)
Exploration – Medium individuals	2.37	0.62	10.7 (3.2 – 36.1)
Exploration – Large individuals	−0.45	0.90	0.7 (0.1 – 3.7)
Position - Mid	0.74	0.51	2.1 (0.8 – 5.7)
Position - Up	1.15	0.83	3.2 (0.6 –16.2)
Density	−0.15	0.34	0.9 (0.4 – 1.7)

Due to a significant interaction between explorer personality and individual size (Table 3) effect sizes and odds ratios of explorers relative to non-explorers were calculated for each size. Manipulation effects were compared to the control; position effects were compared to downstream, and density effects were calculated as a change in 100 individuals.

that had been classified as explorers in our assay, medium-sized individuals were 4.5 times as likely to have been recaptured outside of the original 25-m target segments compared to small-sized individuals, and 11 times as likely as large individuals.

Significant differences among density manipulations were also detected. Individuals were 8.7 (3.5–21.9) times as likely to be captured outside of their original capture location when southern leatherside chub density was reduced in the 50 m immediately upstream of the 25-m target segment (Adjacent manipulation) compared to individuals in control sites. In contrast, density manipulations where southern leatherside chubs were removed > 50 m upstream (Skip manipulation) produced no significant differences in the odds of recapture outside of the original 25-m target segment (odds ratio = 1.9 [0.8 – 5.0]) relative to individuals at control sites.

3 Discussion

The utility of being able to assess short-term behavioral phenotypes and subsequently link this with long-term patterns provides a unique and powerful tool to understand evolutionary and ecological dynamics. In their seminal review on behavioral syndromes Sih et al. (2004) noted that correlated behaviors within individuals consistently occur for activity, boldness, and exploration, any of which may be related to the process of dispersal. Our results clearly indicate that variation in exploration personality exists within the population of southern leatherside chub we studied and that this variation can be assessed sufficiently well to provide information on the prevalence and expression of the phenotype within a population, even using somewhat coarse techniques. More importantly, our very brief assessment of exploration personality is useful to explain naturally occurring dispersal patterns within this population.

In a study similar to ours, Fraser et al. (2001) used a simple assessment of the time it took for individual Trinidad killifish to cross a gap within a laboratory setting. They subsequently found that such assessments were able to predict the distances moved over a short-period of time (24 h) by these fish once they were returned to a natural environment. Although in their study they termed the personality axis measured to be "boldness," it is also related to the exploration axis. Boldness is defined as the reaction of an individual in the presence of perceived danger; whereas, exploration involves an individual's tendency to investigate novel objects or environments (Conrad et al., 2011; Réale et al., 2007). Similarly, Cote et al. (2010) reported that

mosquito fish sociability was associated with dispersal distance given that individuals measured as more asocial dispersed greater distances in an artificial stream over a 24 h period. They concluded that this personality-based dispersal paradigm may enable better understanding of invasion of new habitats by this species. However, these authors did not find a relationship between exploration personality and dispersal distance.

Each of these studies involved laboratory periods for the fish and the period of time over which individuals were permitted to express their behaviors was very brief. As such, the authors were left to suggest that such differences would in fact operate in the natural environments and be maintained over time. In contrast, our study included minimal handling time and spanned a significantly longer period of time (1 yr). By allowing fish to express behavior over a year we were able to actually document that individuals that are more prone to explore a novel environment are also more prone to undertake dispersal-like movements. We say dispersal-like because we recognize that many researchers define dispersal as movement between breeding areas and must include the potential for gene flow (Ronce, 2007), while others may simply define it as movement among patches (Stenseth and Lidicker, 1992).

Interestingly, the proportion of explorer individuals measured in our personality assay progressively decreased moving upstream. One may ask if explorer individuals tend to disperse more often and dispersal is predominantly in an upstream direction than why does this pattern occur? It may be an artifact of small sample sizes due to lower densities upstream, or possibly some underlying relationship with habitat that our data are unable to clarify. For example, personality assays with relatively high sample sizes upstream of our study reach in the same system yielded proportions similar to the lowest sites (J. Rasmussen, *unpublished data*). The physical habitat of this area was more similar to the downstream sites than the nearby upstream sites used in the study, but because of the presence of predatory trout in the area this site was not included in the study due to a potential confounding variable. The relative rank of individual behavior among a group can be consistent across a variety of contexts (e.g. feeding, courting, or predator avoidance) even when the actual level of expression of the behavior may change depending on the context (Conrad et al., 2011; Dingemanse and Réale, 2005; Sih et al., 2004). For example, a group of feeding individuals may be less aggressive than if they were courting, but if they were to be ranked in either context

the order would be similar. We may therefore explain this pattern of declining proportions of explorer individuals as one moves upstream in the system as a context-dependent shift in the expression level of the behavior. In this case, the context is varying habitat conditions (see Table 1) instead of activities the organism is engaged in. Nevertheless, further research is necessary to provide a better test of this potential interaction between personality and habitat.

Information about surrounding areas can greatly decrease costs and risks of dispersal (Dall et al., 2005), and may also be important input affecting the expression of behaviors and personality. This information can be "personal", i.e. gathered through direct experience of the individual, such as during exploratory excursions, or the information may be acquired from other individuals through social interactions (Brown and Laland, 2003; Dall et al., 2005; Danchin et al., 2004). The area about and from which an individual may reasonably gather and process information, known as neighborhood size, may be an important variable dependent on the species and the environment. It makes sense that upstream dispersal is more prevalent in fish since the directional nature of flowing water creates a bias in available information. However, the area of available information appears to be somewhere less the 50 m for southern leatherside chub. Open habitat > 50 m upstream apparently prompted relatively little dispersal behavior. This density manipulation produced similar movement probabilities as the control. Individuals were either unaware that this habitat was available or unwillingly to undertake such a long dispersal. However, rare instances of long-distance dispersal (> 1 km) have been observed in this species (J. Rasmussen, unpublished data). In contrast, when open habitat was nearer (< 50 m), fish were much more likely to disperse. This indicates that the southern leatherside chub are able to assess at least this much territory, whether by exploratory expeditions or some form of public information (Danchin et al., 2001; Gowan and Fausch, 2002). Our data suggest that it is via exploratory behavior that these individuals are gathering information since it was those individuals that were categorized with an explorer personality that were most often moving into these areas. If the information was of a more public nature then we suspect that the probability of being captured in these "opened" areas would have been more evenly spread across the personality categories.

Individual body size has often been found to be correlated with dispersal (Bowler and Benton, 2005;

Clobert et al., 2001); however, these measurements are likely confounded with other, more difficult to measure, traits that may be correlated with both size and dispersal. Size, in reality, may be a surrogate for many other factors such as age, ontogenetic stage, reproductive status or possibly segment quality. Size might also correlate with dispersal in the short-term, as in the case of *Brachyrhaphis episcopi* juveniles that were quicker to move from refuge than adults, attributed to higher metabolisms and energy needs (Brown and Braithwaite, 2004). However, when viewed over longer intervals, differences in size more likely reflect ontogenetic shifts, but may also be affected by size-preferences of predators. We found no differences among the size classes in the proportions of exploration phenotypes in this system, but our data showed a significant propensity to disperse by medium-sized individuals that were classified as explorers relative to all other size and personality combinations. This might explain discrepancies in annual mortality estimates among size classes of this species. Small and large size classes of southern leatherside chub in this stream were estimated to have apparent annual mortality of approximately 40%, but estimates of mortality for the medium size class were approximately 50 % (M. Belk, unpublished data). Our data suggest that mortality estimates among the size classes are more similar than they appear with a portion of the difference being attributable to a segment of the medium-sized individuals in the population that are more prone to exploration and subsequent emigration from the study area.

This research provides further clarification of the factors influencing the dispersal of stream fish. Individuals may have unique probabilities of expressing dispersal behavior based on underlying personalities. Such variation will influence the evolutionary and ecological dynamics of the population or group to which they belong as well as surrounding groups (Cote et al., 2011). This knowledge can be useful on many levels, such as evaluation of management options given population and environmental characteristics, and illumination of evolutionary pressures within diverse habitats or species. Likewise, understanding how dispersal behavior correlates with other behavioral traits will extend our ability to assess the development of and the social pressures that influence behavioral syndromes.

References

Andreu J, Barba E, 2006. Breeding dispersal of great tits *Parus major* in a homogeneous habitat: Effects of sex, age, and mating status. Ardea 94: 45–58.

Aragon P, Meylan S, Clobert J, 2006. Dispersal status-dependent response to the social environment in the common lizard *Lacerta vivipara*. Funct. Ecol. 20: 900–907.

Belanger G, Rodriguez MA, 2002. Local movement as a measure of habitat quality in stream salmonids. Environ. Biol. Fishes 64: 155–164.

Bell AM, Stamps JA, 2004. Development of behavioural differences between individuals and populations of sticklebacks *Gasterosteus aculeatus*. Anim. Behav. 68: 1339–1348.

Bohonak AJ, 1999. Dispersal, gene flow, and population structure. The Quarterly Review of Biology 74: 21–45.

Bowler DE, Benton TG, 2005. Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. Biol. Rev. (Camb) 80: 205–225.

Brown C, Laland KN, 2003. Social learning in fish: A review. Fish Fish 4: 280–288.

Brown C, Braithwaite VA, 2004. Size matters: A test of boldness in eight populations of the poeciliid *Brachyrhaphis episcopi*. Anim. Behav. 68: 1325–1329.

Budaev SA, 1997. "Personality" in the guppy *Poecilia reticulata*: A correlational study of exploratory behavior and social tendency. J. Comp. Psychol. 111: 399–411.

Clobert J, Danchin E, Dhondt AA, Nichols JD, 2001. Dispersal. New York: Oxford University Press.

Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M, 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol. Lett. 12: 197–209.

Coleman K, Wilson DS, 1998. Shyness and boldness in pumpkinseed sunfish: Individual differences are context-specific. Anim. Behav. 56: 927–936.

Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A, 2011. Behavioural syndromes in fishes: A review with implications for ecology and fisheries management. J. Fish. Biol. 78: 395–435.

Cote J, Clobert J, 2007a. Social personalities influence natal dispersal in a lizard. Proc. R. Soc. Biol. Sci. Ser. B 274: 383–390.

Cote J, Clobert J, 2007b. Social information and emigration: Lessons from immigrants. Ecol. Lett. 10: 411–417.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A, 2010. Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. Phil. Trans. R. Soc.

B 365: 4065–4076.

Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A, 2010. Personaltiy traits and dispersal tendency in the invasive mosquitofish *Gambusia affinis*. Proc. R. Soc. B 277: 1571–1579.

Cote J, Fogarty S, Brodin T, Weinersmith K, Sih A, 2011. Personality-dependen dispersal in the invasive mosquitofish: group composition matters. Proceedings of the Royal Society B 278: 1670–1678.

Croft DP, Albanese B, Arrowsmith BJ, Botham M, Webster M et al., 2003. Sex-biased movement in the guppy *Poecilia reticulata*. Oecologia 137: 62–68.

Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW, 2005. Information and it use by animals in evolutionary ecology. Trends Ecol. Evolut. 20: 187–193.

Danchin E, Hemg D, Doligez B, 2001. Public information and breeding habitat selection. In: Clobert J, Danchin E, Dhondt AA, Nichols JD ed. Dispersal. Oxford: Oxford University press, pp. 243–260.

Danchin E, Giraldeau L-A, Valone TJ, Wagner RH, 2004. Public information: From nosy neighbors to cultural evolution. Science 305: 487–490.

Diekmann U, O'Hara B, Weisser W, 1999. The evolutionary ecology of dispersal. Trends Ecol. Evolut. 14: 88–90.

Dingemanse NJ, Réale D, 2005. Natural selection and animal personality. Behaviour 142: 1159–1184.

Dodson, JJ, 1997. Fish migration: An evolutionary perspective. In: Godin JJ ed. Behavioural Ecology of Teleost Fishes. Oxford: Oxford University Press, 10–36.

Downs CC, Horan D, Morgan-Harris E, Jakubowski R, 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. N. Am. J. Fish. Manage. 26: 190–200.

Duckworth RA, Badyaev AV, 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proc. Natl. Acad. Sci. USA 104: 15017–15022.

Eikenaar C, Richardson DS, Brouwer L, Komdeur J, 2008. Sex biased natal dispersal in a closed, saturated population of Seychelles warblers *Acrocephalus sechellensis*. J. Avian Biol. 39: 73–80.

Ekman J, 2007. Delayed dispersal: Youth costs carry lifetime gains. Curr. Biol. 17: R417–R418.

Fausch KD, Gowan C, Richmond AD, Riley SC, 1995. The role of dispersal in trout population response to habitat formed by large woody debris in Colorado mountain streams. Bull. Fr. Peche Piscic. 179–190.

Fausch KD, Young MK, 1995. Evolutionary significant units and movement of resident stream fishes: A cautionary tale. In: Nielsen JL ed. Evolution and the Aquatic Ecosystem: Defining unique units in population conservation. American Fisheries Society Symposium 17. Bethesda: American Fisheries Society, 360–370.

Fraser DF, Gilliam JF, MacGowan MP, Arcaro CM, Guillozet PH, 1999. Habitat quality in a hostile river corridor. Ecology 80: 597–607.

Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalski GT, 2001. Explaining leptokurtic movement distributions: Intra-population variation in boldness and exploration. Am. Nat. 158: 124–135.

Godinho AL, Kynard B, Godinho HP, 2007. Migration and spawning of female surubim (*Pseudoplatystoma corruscans*, Pimelodidae) in the Sao Francisco river, Brazil. Environ. Biol. Fishes 80: 421–433.

Gowan C, Fausch KD, 2002. Why do foraging stream salmonids move during summer? Environ. Biol. Fishes 64: 139–153.

Gresswell RE, Hendricks SR, 2007. Population-scale movement of coastal cutthroat trout in a naturally isolated stream network. Trans. Am. Fish. Soc. 136: 238–253.

Hanski I, Gaggiotti OE, 2004. Metapopulation biology: Past, present, future. In: Hanski I, Gaggiotti OE ed. Ecology, Genetics, and Evolution of Metapopulations. Amsterdam: Elsevier Academic Press, 3–22.

Harrell FE, Jr., 2001. Regression Modeling Strategies: With Applications to Linear Models, Logistic Regression, and Survival Analysis. New York: Springer.

Harrell FE, Jr., 2007. Design package, R version 2.1-1. Available at ttp:/biostat.mc.vanderbily.edu/twiki/bin/view/Main/Design.

Hassel MP, Nay RM, 1985. From individual behaviour to population dynamics. In: Sibly RM, Smith RH ed. Behavioral Ecology: Ecologcial Consequences of Adaptive Behavior. Oxford: Blackwell Scientific Publications, 3–32.

Hosmer DW, Lemeshow S, 2000. Applied logistic regression. New York: John Wiley and Sons, Inc.

Johnson JB, Belk MC, Shiozawa DK, 1995. Age, growth, and reporductions of leatherside chub. Great Basin Nat. 55: 183–187.

Knaepkens G, Baekelandt K, Eens M, 2005. Assessment of the movement behaviour of the bullhead *Cottus gobio*, an endangered European freshwater fish. Anim. Biol. 55: 219–226.

Lawrence WS, 1987. Dispersal: An alternative mating tactic conditional on sex ratio and body size. Behav. Ecol. Sociobiol. 21: 367–373.

McMahon TE, Matter WJ, 2006. Linking habitat selection, emigration and population dynamics of freshwater fishes: A synthesis of ideas and approaches. Ecol. Fresh Fish. 15: 200–210.

Mikheev VN, 2005. Individual and cooperative food searching tactics in young fish. Zoologichesky Zhurnal 84: 70–79.

Neely DA, George AL, 2006. Range extensions and rapid dispersal of Etheostoma blennioides (Teleostei : Percidae) in the Susquehanna River drainage. Northeast Nat. 13: 391–402.

O'Rian MJ, Jarvis JUM, Faulkes C, 1996. A dispersive morph in

the naked-mole rat. Nature 380: 619–621.

Pollock KH, Otto MC, 1983. Robust estimation of population size in closed animal population from capture-recapture experiments. Biometrics 39: 1035–1049.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. Vienna. Available at http://www.R–project.org.

Réale D, Gallant BY, Leblanc M, Festa-Bianchet M, 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. Anim. Behav. 60: 589–597.

Réale D, Festa-Bianchet M, 2003. Predator-induced natural selection on temperament in bighorn ewes. Anim. Behav. 65: 463–470.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ, 2007. Integrating animal temperament within ecology and evolution. Biological Reviews 82: 291–318.

Ronce O, 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annu. Rev. Ecol. Evol. Syst. 38: 231–253.

Schürch R, Heg D, 2010. Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. Behav. Ecol. 21: 588–598.

Sigler WF, Sigler JW, 1996. Fishes of Utah: A Natural History. Salt Lake City: University of Utah Press.

Sih A, Bell AM, Johnson JC, Ziemba RE, 2004. Behavioral syndromes: An integrative overview. Q. Rev.Biol. 79: 241–277.

Stenseth NC, Lidicker WZ, 1992. Animal dispersal: Small mammals as a model. New York: Chapman & Hall, 365.

Tallmon DA, Luikart G, Waples RS, 2004. The alluring simplicity and complex reality of genetic rescue. Trends Ecol. Evolut. 19: 489–496.

Valone TJ, Templeton JJ, 2002. Public information for the assessment of quality: A widespread social phenomenon. Philos. Trans. R. Soc. London B 357: 1549–1557.

Walser CA, Belk MC, Shiozawa DK, 1999. Habitat use of leatherside chub *Gila copei* in the presence of predatory brown trout *Salmo trutta*. Great Basin Nat. 59: 272–277.

White GC, Burnham KP, Otis DL, Anderson DR, 1978. User's Manual for Program CAPTURE. Logan: Utah State University.

Wilson ADM, Godin JJ, 2009. Boldness and behavioral syndromes in the bluegill sunfish *Lepomis machorchirus*. Behav. Ecol. 20: 231–237.

Wilson ADM, Godin JJ, 2010. Boldness and intermittent locomotion in the bluegill sunfish *Lepomis macrochirus*. Behav. Ecol. 21: 57–62.

Wilson KW, Belk MC, 2001. Habitat characteristics of leatherside chub *Gila copei* at two spatial scales. West N. Am. Nat. 61: 36–42.