## Original Article

# Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*)

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Although personality has been documented in numerous animals and characters, research into personality-dependent spatial ecology has focused on dispersal. Indeed, few authors have investigated the role of other important spatial traits such as home range, movement distance, vertical activity, and site fidelity, and it is not clear whether these behaviors are correlated with dispersal. In this study, we investigated individual differences in home range, dispersal from release, vertical activity, movement distance, and site fidelity of 44 wild burbot *Lota lota* over 2 years, using an acoustic telemetry array and a Bayesian mixed modeling framework. We tested whether the spatial behaviors met the following criteria for personality-dependent behavior: repeatability, cross-contextual consistency, and an absence of pseudo-repeatability associated with spatial context choice. We then tested for between-individual correlations among spatial behaviors, indicative of a behavioral syndrome. Our results documented repeatable, cross-contextually consistent, personality-dependent home range, movement, dispersal from release, and site fidelity. In contrast, behavioral differences in vertical activity were inconsistent across sampling years and may have been a product of habitat heterogeneity. Our data indicate a spatial behavioral syndrome occurred independently from dispersal from release, with behavioral types ranging from "resident" individuals with small home ranges, high site fidelity, and minimal movement to "mobile" individuals with large home ranges, high movement rates, and little site fidelity. Our findings suggest animal personality can play a key role in shaping the space use of individuals, and this diversity in spatial behaviors may be too complex to be captured by often used simple linear measures of dispersal.

*Key words*: **Bayesian mixed models burbot, home range, movement, site fidelity, telemetry, temperament.**

## INTRODUCTION

A significant proportion of the variance in many animal behaviors can be explained by consistent between-individual differences, known as animal personality (Gosling and John 1999; Bell 2007; Stamps and Groothuis 2010). However, although movement and space use have important consequences for animal populations including gene flow, spatial distribution, community structure and function, range expansion, colonization, and recolonization (Bowler and Benton 2005; Ronce 2007; Cote et al. 2010), few authors have investigated individual differences in spatial use behaviors, and the exceptions have focused almost entirely on dispersal (Cote et al. 2010).

Behavioral syndromes, defined as correlated suites of behavioral traits, have been documented for a wide range of taxa (Sih et al. 2004; Conrad et al. 2011) and behaviors (Sih et al. 2012). Although behavioral syndromes have often been identified by phenotypic correlations between behavioral traits, it is now recognized that only the between-individual correlations represent a true diagnostic of behavioral syndromes (Dingemanse et al. 2012; Brommer 2013a; Dingemanse and Dochtermann 2013). Dispersal behavioral syndromes, which link dispersal behavior with behavioral traits such as aggression, have been described by a few researchers (see Clobert et al. 2009; Cote et al. 2010 for reviews). However, it is unclear whether behavioral traits correlated with dispersal remain consistent throughout the lifetime of individuals or are more temporary (Cote et al. 2010), and many studies have relied on

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phenotypic correlation diagnostics. Further, in fishes, direct, long-term evidence of dispersal syndromes are rare, and the relationship between dispersal and other spatial behaviors such as home range (HR), site fidelity, and movement is untested.

Personality-dependent dispersal has been described in western bluebirds *Sialia mexicana* (Duckworth and Badyaev 2007; Duckworth 2008), great tits *Parus major* (Korsten et al. 2013), mosquitofish *Gambusia affinis* (Cote et al. 2011), and Trinidad killifish *Rivulus hartii* (Fraser et al. 2001). Nonetheless in both fish and other animal populations, evidence of temporally consistent, cross-contextual patterns of personality-dependent dispersal is rare (Miriam et al. 2013). Furthermore, only a few authors have investigated the role of personality in other important spatial ecology metrics including HR (Minderman et al. 2010), movement (Fraser et al. 2001; Chapman et al. 2011; Brodersen et al. 2012), and site fidelity (Brodersen et al. 2012). Indeed, individual differences in movement behaviors are a typical feature of spatial ecology data sets, particularly in fishes (Conrad et al. 2011; Taylor and Cooke 2012), which often feature "resident" and "mobile" contingent strategies (Skalski and Gilliam 2000; Fraser et al. 2001; Morrissey and Ferguson 2011; Radinger and Wolter 2013). Research on this heterogeneity has tended to focus on internal factors, such as body size and ontogeny, and external environmental cues, such as habitat-suitability, temperature, and light (Lucas and Baras 2001). However, few researchers have explicitly quantified the repeatability and contextual consistency of these spatial behavioral differences, particularly in fishes (see Taylor and Cooke 2014 for an exception).

Although dispersal can be defined as "movement from natal site to breeding site" (Cote et al. 2010), others argue for a more broad definition, that is, "the movement between habitat patches" (Bowler and Benton 2005). In this article, we choose the latter definition. For clarity, we identify the former as "natal dispersal" and the latter as "dispersal from release" to avoid the confusion which can occur as a result of the comparison between dispersal measured at differing scales and contexts (Bowler and Benton 2005). Indeed, we argue that for r-strategist animals, natal origin and breeding site criteria are hard to identify and, thus, rarely met. Accordingly, our "dispersal from release" definition allows for direct comparison with dispersal metrics used for fishes (e.g., Fraser et al. 2001; Cote et al. 2011; Radinger and Wolter 2013). Moreover, the dispersal from release metric may serve as a useful behavioral measure for managers investigating reintroduction programs or invasion events.

Animal personality research has traditionally been carried out under laboratory conditions, where environmental contexts can be easily controlled (Réale et al. 2007). However, the documentation of personality in a wild context can provide an important validation for animal personality based on captive contexts (Dingemanse et al. 2010). Moreover, laboratory-based studies of the spatial behavior of large-bodied animals are not practical. A key challenge associated with documenting personality in the wild has been the statistical disentangling of between-individual, residual, and context-driven variances (Brommer 2013a). Accordingly, many field-based investigations of animal personality have been criticized for a failure to consider the role of unmeasured context-driven differences, which can be amplified in animals free to choose their spatial context (Dingemanse et al. 2010). However, several mixed modeling method articles borrowing techniques developed for genetics have recently been published, which provide practical solutions for the partitioning of the contextual, between-individual, and residual variances (Nakagawa and Schielzeth 2010; Brommer 2013b; Dingemanse and Dochtermann 2013). These articles provide

methods for quantification of 2 key additional criteria for detecting personality in field data: 1) *cross-environmental correlation*, that is, a consistency in the ranking of individuals between categorical contexts defined as imparting plasticity (Brommer 2013b) and 2) *an absence of pseudo-repeatability*, that is, personality should not be a function of differing experience along an environmental gradient (Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013). Accordingly, these methods present an excellent opportunity for more field-based animal personality research.

Burbot, *Lota lota* provide an interesting model to test hypotheses regarding potential individual differences in spatial ecology, as a heterogeneity in spatial behaviors within burbot populations has been anecdotally noted (Dunnigan and Sinclair 2008; Paragamian and Wakkinen 2008), but the repeatability and consistency of these differences have not been tested. In this study, we monitor the spatial behavior of 44 wild, free-swimming burbot in Kinbasket Reservoir, British Columbia, over 2 years using acoustic telemetry. We test whether burbot's HR, horizontal movement, vertical activity, site fidelity, and dispersal from release meet the following personality-dependent behavior criteria: repeatability, cross-contextual correlation, and absence of pseudo-repeatability as a result of spatial context choice. Specifically, we test for repeatability in spatial behaviors, after accounting for possible sources of contextual variance defined by backward model selection, capture location, detection span, season, year, and body length. Next, we test for between-individual cross-contextual correlations across levels of variables previously defined as significant sources of contextual variance. We then investigate potential spatial context choice driven pseudo-repeatability by testing for between-individual correlations between our spatial behavior metrics and a reservoir distance variable. Finally, we investigate potential spatial behavioral syndromes by testing for between-individual correlations among spatial behaviors.

## MATERIALS AND METHODS
### Study species

Burbot, a large, benthic piscivore (Cott et al. 2011), are the only freshwater member of the gadoid family. Burbot have a northern circumpolar distribution (Stapanian et al. 2010) and are winter active, spawning in the late winter/early spring, with minimal summer movement (McPhail and Paragamian 2000). Long prespawning migrations have been reported by a number of authors (Breeser et al. 1988; Paragamian 2000) although burbot in general are considered fairly sedentary (Bergersen et al. 1993; Carl 1995). Burbot are also known to be night active (Müller 1973) and perform diel vertical migrations in lake habitats (Harrison et al. 2013).

### Study system

Kinbasket Reservoir, in southeastern British Columbia, Canada (52°08′N, 118°27′W; Figure 1), was formed by the construction of the Mica Dam in the upper reaches of the Columbia River in 1976. The reservoir is large (43 200 ha), deep (up to 190 m), glacial, and snowmelt-fed system (Bray 2011). Further detail on the reservoir can be found in Martins et al. (2013) and Nitychoruk et al. (2013).

### Telemetry array

Forty-two acoustic telemetry receivers (VR2W, VEMCO, Halifax, Nova Scotia, Canada) were deployed throughout the reservoir (Figure 1), in the spring of 2010 at minimum reservoir elevation and were downloaded and redeployed in the spring of 2011, and
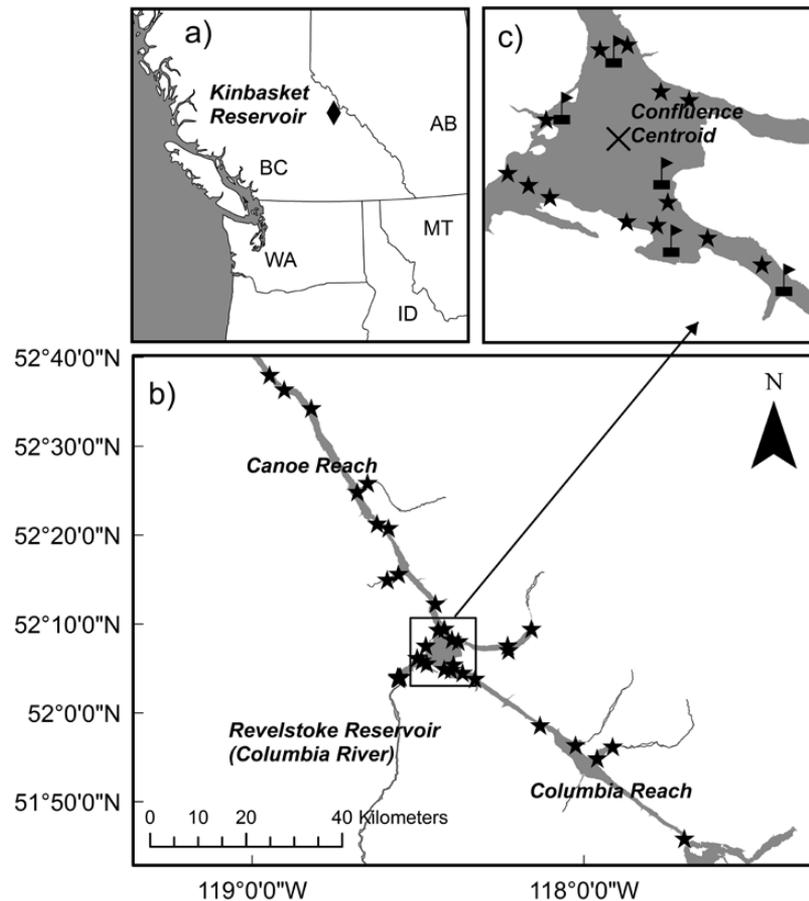
**Figure 1**
(a) Diamond indicates Kinbasket reservoir location. (b) Map of the study system, Kinbasket reservoir, British Columbia, Canada, with filled stars representing receiver locations. (c) Confluence region with an x indicating the centroid of the confluence region, filled stars representing receiver locations, and marker buoys representing capture locations.

downloaded and retrieved in the spring of 2012. All 42 receivers were retrieved and redeployed in 2011, and only 37 receivers were recovered in 2012. Array design allowed for a representative sample of habitat throughout the reservoir and accounted for ~8% of the reservoir surface area. Further details of mooring methods and array configuration can be found in Gutowsky et al. (2013).

## Burbot capture and tagging

Trapping and decompression procedures followed the recommendations of Neufeld and Spence (2004). Burbot were anesthetized in a clove oil bath and total length measured to the nearest centimeter and weight to the nearest gram. Only fish meeting the <2% tag weight in water to body weight in air ratios were selected for surgery (Brown et al. 1999). Seventy-five burbot (50 in 2010 and 25 in 2011) were implanted with temperature and depth-sensing acoustic telemetry transmitters (VEMCO V13TP, 45 mm × 13 mm, 6 g in water, signal transmission rate 60–180 s, average 120 s, expected battery life 1028 days, VEMCO) following the surgical procedure described in Wagner et al. (2009). Details of capture and release locations are provided in Figure 1. Sex determination was not possible due to postspawning capture timing. Following full recovery, all burbot were released from the surgery boat, as close as possible to capture location (<500 m), and the geographic coordinates were recorded. Further details on capture and tagging procedures are given in Harrison et al. (2013).

## Preanalysis filtration

Depth time series plots were used to identify and remove from the data set all fish that appeared to have died or shed their tag postsurgery ($n = 17$, 22%). Code collisions and false detections that can occur as a result of overlapping detections at a single receiver were eliminated by the use of a minimum of 2 detections per 24-h period filter (Heupel et al. 2006). Detection span was calculated as the time between first and last detections in a given month, and a minimum span of 20 (not necessarily consecutive) days was applied. Fourteen (18.6%) burbot did not have a sufficient detection span in any month and were subsequently removed from the data set. The filtration span of 20 days was designed as a compromise between ensuring sufficient data in a given month were available to realistically estimate spatial behavior and ensuring we were not artificially excluding individuals not frequently within receiver range. Detections within 2 weeks of the surgical procedure were not included in the analysis to remove potential short-term bias in behaviors (Rogers and White 2007).

## Spatial behavioral metric calculations

Daily (24 h) center of activity (COA) locations were calculated following methods described by Simpfendorfer et al. (2002). HR estimation requires 2 spatially distinct detections, so for individuals

detected at only one receiver in a given month that met the 20-day span filtration criteria, HR was estimated. HR was estimated as the area of a circle (20.42 ha) with a radius of 255 m, with the radius equaling the standard deviation (255 m) of a fish normally distributed within receiver range (i.e., 0–750 m). We consider that our 20-day filtration criteria ensured fish assigned the estimated HR value were likely exhibiting minimal movement. Further, where overlapping receiver ranges allowed greater COA precision, our detection of 20 monthly HR values smaller than the estimate indicates that our value is unlikely to be a large underestimate. The estimated HR value was assigned to 27 fish in a total of 37 months (12.25% of the total number of monthly measures) with 9 individuals accounting for 65% of the estimated HR values. We considered the estimation option to be favorable to the alternative, that is, discarding the data points, as removal would likely inhibit abilities to detect infrequently moving behavioral types. Monthly HRs were then computed based on daily COA locations using the biased random bridge (BRB) method outlined in Benhamou (2011). The method involved casting our COA data into a trajectory format, applying an uncertainty of locational standard deviation of accuracy measure (255 m), and an estimation of a diffusion parameter $D$ (calculated using maximum likelihood methods for each fish). We then used the BRB function to estimate utilization distributions (UDs) for each fish (Benhamou 2011). HR sizes were estimated at 95% UD and recorded in hectares. All HR analyses were calculated using the adehabitatHR package for R. HRs were exported to arcGIS and clipped to a shape file of the reservoir before areas were recalculated.

Horizontal movement metrics were calculated based on our COA data set and calculated as the sum of all movements in a given month.

Vertical activity was calculated by the sum of absolute changes in depth in a given month divided by the detection span (h) within a given month and recorded in meters per hour.

Monthly site fidelity was calculated as the Euclidian distance (m) between the current COA and the most recent COA divided by the time in months elapsed between the 2 locations.

Monthly dispersal from release site was calculated as the Euclidian distance between the release site coordinates and the monthly COA.

## Statistical analysis

All models were fitted using the Bayesian modeling package MCMCglmm for R (Hadfield 2010). Bayesian models necessitate the use of priors, but when prior knowledge of relationships is minimal, flat uninformative proper priors are deemed the most appropriate (Hadfield 2010). Consequently, all models below were fitted using flat uninformative inverse Gamma priors (Hadfield 2010), using the univariate or multivariate forms appropriately. Each model was also alternatively fitted with the inverse Wishart prior using univariate or multivariate forms appropriately. Insensitivity to prior type was then confirmed for all models by comparison of the posterior distributions. Autocorrelation of the fixed effects and variance Markov Chain Monte Carlo chains for all models were assessed using autocorr function from the coda package, following the methods described in Hadfield (2010), to ensure autocorrelation between chains was <0.1. Conservatively, long iteration chains were applied to all models consisting of 1 300 000 iterations, a thinning length of 1000, and a burn-in of 300 000. Convergence was visually confirmed using the plot function for MCMCglmm. All confidence intervals (CIs) were estimated without multiple comparison

adjustment, as adjustment are not necessary in Bayesian mixed-effects models (Gelman et al. 2012).

## Contextual variance estimation

Bayesian univariate mixed-effects models were fitted with response variables of monthly HR, horizontal movement, vertical activity, site fidelity, and dispersal from release site. Individual fish were used as the random effects. Each model was first fitted with the following fixed effects: season, composed of winter (November–April) and summer (May–October); sampling year, year 1 (May 2010–April 2011) and year 2 (May 2011–April 2012); mean centered (Zuur et al. 2009) burbot total length (cm), and capture location (a factor variable consisting of 5 locations, Figure 1). For the HR and movement models, detection span (in days, mean centered) was also included in the models. All pairwise interactions were considered. Backward selection was performed using nonzero overlapping CIs and $P$ values (<0.05) to determine fixed effects significance. Variables remaining after backward selection were deemed sources of contextual variance and used as confounding factors in the repeatability estimation below and then checked for cross-contextual consistency.

## Repeatability estimation

Repeatability estimates ($r$) and associated 95% CIs for each response variable were calculated based on the posterior distribution from our most parsimonious univariate Bayesian mixed models (Dingemanse and Dochtermann 2013). For models where significant fixed effects were identified, adjusted repeatability (adj. $r$) values that included fixed effect structure in the model were calculated. $r$ values with CIs not overlapping 0 were deemed repeatable (Nakagawa and Schielzeth 2010). Following the recommendations of Nakagawa and Schielzeth (2010) and Dingemanse and Dochtermann (2013), individuals with only one sampling point ($n = 5$) were not removed from the data set.

## Cross-contextual correlation analysis

Variables previously identified as confounding factors were then assessed for cross-contextual correlations using the univariate Bayesian character state approach described by Brommer (2013b). The method allows for the computation of between-individual correlations statistics, which represent the consistency in behavioral rankings between levels of categorical fixed effects. The variables found to be significantly influencing movement data were both categorical binary variables (season and year), with 2 levels or contexts each (winter and summer, and year 1 vs. year 2). We chose the character state approach over the Bayesian random regression approach for its ability to work with the smaller sample sizes (Brommer 2013b). Separate models were fitted for each relevant trait, with fixed effects comprising the appropriate context (character state) variable ($E$), with a random effect composed of the interaction between $E$ and individual fish (ID). Covariance terms for the random effects were determined by the MCMCglmm function us, which allows for cross-character state covariance estimation (Hadfield 2010; Brommer 2013b).

Only individuals sampled multiple times in both contexts were included in the analysis (Dingemanse and Dochtermann 2013). Between-individual correlations among environments and associated CIs were calculated using covariance estimates from the posterior distribution following the standard definitions of correlations with the coding provided in Brommer (2013b).

## Spatial pseudo-repeatability analysis

Reservoir distance was computed as the Euclidian distance in meters from the centroid of the confluence region to the monthly COA location (Figure 1). Kinbasket reservoir consists of a large deep (up to 190 m) confluence region formed by a dam to the south. The confluence is fed by 2 main arms, the Canoe arm and the Columbia arm. As such the reservoir generally becomes increasingly shallower and narrower with increasing distance from the confluence region (Figure 1). The reservoir distance metric, therefore, was designed to capture some of the changes in habitat between the lacustrine confluence region and upper reaches of the reservoir. Given that the location of burbot within the reservoir is a behavioral choice, spatial context was not included as a fixed effect in our confounding effect models. Instead, the influence of spatial context choice on each of our traits identified as repeatable was assessed using the spatial context variable as a Poisson-distributed trait $y$, in the bivariate mixed modeling approach detailed below. In this case, the detection of significant between-individual correlation between a behavioral trait and the confluence distance would indicate that behaviors vary predictably along the spatial gradient and, thus, would indicate possible spatial context–driven pseudo-repeatability.

## Between-individual correlations among traits

Individual-level correlations among traits were assessed using Bayesian bivariate mixed models (Dingemanse and Dochtermann 2013). Only fish with repeated measures and simultaneous assays for both traits were included in the models (Dingemanse and Dochtermann 2013). As our primary interest was in the random effects structure, all fixed effects and pairwise interaction terms used in our univariate analysis were included in the bivariate models, regardless of significance. Between-individual, residual, and phenotypic correlations, within-trait repeatability values, and all relevant CIs were calculated from the posterior modes of the models (Dingemanse and Dochtermann 2013). For models with Gaussian distributions for both response variables, the correlation significance was confirmed by comparing deviance information criterion (DIC) values from the unconstrained model against DIC values from models where between-individual covariance or residual covariance was constrained to 0. Significance was assigned with a DIC reduction of >2. A pairwise bivariate framework was chosen over a single multivariate model, because of its ability to compare against zero constrained covariance component models, which would not be possible within a single multivariate model

(Dingemanse and Dochtermann 2013). Given the reduced power associated with our sample sizes ($n = 39$) to detect weak correlations, the use of the Bayesian equivalent of a log-likelihood ratio test (Dingemanse and Dochtermann 2013) was deemed important as it provided us further confirmation of the significance of correlation in addition to the use of nonzero overlapping CI tests. As DIC is not an appropriate test for Poisson-based models (Hadfield 2010), only CIs were used to assess significance in models containing Poisson-distributed responses.

## RESULTS

Burbot detections (930 282) were recorded over 2 years. Monthly spatial measures were recorded on 302 occasions for 44 burbot, with a mean of 6.86 (range 1–22) not necessarily consecutive replicates per individual. Burbot ranged in length from 44.8 to 74.1 cm. Individual burbot HR averages varied from 20.42 ha per month to 1471.88 ha with a median of 145.07 ha. HR was significantly repeatable ($r = 0.33$, Table 1). TL, sampling year, capture location, season, detection span, and all possible 2-way interactions had no significant influence on HR (all $P < 0.05$, Table 1). The random effect only model was the most parsimonious model, and, therefore, no cross-contextual correlation analysis was performed. Between-individual-level correlation between HR and the reservoir distance metric was not observed, indicating that individuals located farther from the confluence did not have larger HRs and suggesting that the confluence distance variable was not imparting pseudo-repeatability (Table 3 and Figure 2).

Individual movement distance averages ranged from 0 (km/month) to 162.08 (km/month), with a median of 15.57 (km/month). Movement was significantly repeatable (adj. $r = 0.32$, Table 1). TL had no influence on movement, and no significant difference in movement was found between sampling years (all $P > 0.05$). No significant interaction effects were observed (all $P > 0.05$). Capture location and detection span also had no influence on movement (Table 1). Behavioral plasticity was observed between seasons, with increased winter movement (back transformed model estimates ($x + SE$, $x − SE$): winter 43.99 (44.04, 43.95) km/month and summer 25.13 (41.02, 15.40) km/month). Cross-context correlation analysis, however, revealed consistent behavioral rankings between seasons ($R = 0.98$, Table 2), with individuals moving the farthest during the winter also moving the furthest during summer. Between-individual correlations between movement and the reservoir distance were not observed, indicating that individuals that were located farthest from the confluence

## Table 1

**Repeatability of burbot spatial behavioral traits**

| Trait | $r$ | Lower | Upper | Significant contexts ($P < 0.05$) | Nonconfounding effects ($P > 0.05$) |
|---|---|---|---|---|---|
| HR | **0.33** | 0.20 | 0.48 | None | Season, year, capture location, detection span, total length, and all 2-way interactions |
| Movement | **0.32*** | 0.21 | 0.50 | Season | Year, capture location, detection span, total length, and all 2-way interactions |
| Vertical activity | **0.42*** | 0.28 | 0.58 | Season + year | Capture location, total length, and all 2-way interactions |
| Dispersal | **0.55*** | 0.46 | 0.63 | Season × year | Capture location, total length, and all other 2-way interactions |
| Site fidelity | **0.21** | 0.12 | 0.37 | None | Season, year, capture location, total length, and all 2-way interactions |

Significant repeatability ($r$) values are shown in bold, with associated 95% CIs. All traits were cube root transformed and fitted with a Gaussian distribution. For all models, 302 replicates were used in total, from 44 individual fish with mean number of replicates per individual of 6.86 and ranging from a minimum of 1 to a maximum of 22.
*Adjusted repeatability value in the presence of significant fixed effects.

did not necessarily exhibit the most movement and suggesting an absence of spatial context–driven pseudo-repeatability (Table 3).

Individual vertical activity averages ranged from 1.0 to 14.3 m/h, with a median 5.01 m/h. Vertical activity was deemed significantly repeatable (adj. $r = 0.42$, Table 1). Behavioral contextual plasticity was observed between seasons and between sampling years with significantly increased activity in winter and in sampling year 1 (back transformed model estimates ($x - SE$, $x + SE$): year 1 summer 4.7 (4.3, 5.1) m/h, year 1 winter 5.6 (5.2, 6.0) m/h, year 2 summer 3.5 (3.1, 3.9), and year 2 winter 4.3 (3.8, 4.7)). Total length and capture location had no influence on burbot vertical activity, and no interaction effects were observed (all $P > 0.05$). Cross-contextual correlations were observed at the between season level (Table 2); however, cross-contextual correlation between years was not observed, indicating that the ranking of behaviors was not consistent between sampling years. Individual-level correlation between vertical activity and reservoir distance indicative of context-driven pseudo-repeatability was observed, with individuals situated farther from the confluence exhibiting decreased vertical activity (Table 3).

Individual dispersal from release averages ranged from 143 to 26 179 m with a median of 2938 m. Dispersal distance was significantly repeatable (adj. $r = 0.55$, Table 1). TL and capture location had no influence on dispersal distances (Table 1). Contextual plasticity was observed in the season and sampling year interaction. Back transformed model estimates in m($x + SE$, $x - SE$) were as follows: year 1 summer 1977 (1540, 2489), year 1 winter 3804 (3110, 4594), year 2 summer 3050 (2428, 3769), and year 2 winter 3266 (2597, 4041). Cross-contextual analysis was not performed due to the small number of individuals repeatedly measured in all season × year levels ($n = 8$). Dispersal distance was found to be correlated at the between-individual level with our spatial context variable (Table 3).

Individual mean site fidelity distances ranged from 51.2 to 9648.2 (m/month), with a median of 1632.7 (m/month). Burbot

displayed significant repeatable individual differences in site fidelity ($r = 0.22$, Table 1), with a random effects only model found to be the best predictor of site fidelity (all $P > 0.05$, Table 1), and therefore, cross-context analysis was not performed. Site fidelity was not correlated with reservoir distance at the between-individual level (Table 3).

Strong between-individual correlations (all $R > 0.5$, Table 4 and Figure 2) were found among all combinations of HR, horizontal movement, and decreasing site fidelity. No significant between-individual correlations were observed between vertical activity or dispersal and any other trait (Table 4 and Figure 2). Strong residual correlations ($R \geq 0.4$) were observed between all combinations of HR, dispersal from release, site fidelity reduction, and movement, with weaker positive correlations ($R \leq 0.25$) observed among all other combinations of traits (Table 4 and Figure 2).

## DISCUSSION

Our results provide empirical documentation of repeatable, cross-contextually consistent, personality-dependent HR, horizontal movement, dispersal, and site fidelity in a free-swimming wild fish. Although repeatability was detected in burbot vertical activity, inconsistency across sampling years and a correlation with reservoir distance suggest that contextual differences are likely responsible for the heterogeneity observed. Our trait correlation analysis suggests the existence of a spatial behavioral syndrome where behavioral types range from "resident," with small HRs, minimal movement, and high site fidelity, to "mobile," with large HRs, high rates of movement, and continuously shifting HR locations. The data also suggest that the spatial behavioral syndrome observed occurs independently from dispersal from release site at the between-individual level.

Although the detection of personality-dependent spatial behaviors is relatively rare, our detection of personality-dependent HR, movement, dispersal, and site fidelity complements personality-dependent spatial ecology noted in other studies and for other taxa, including HR in feral cats *Felis catus* (Barratt 1997), and starlings *Sturnus vulgaris* (Minderman et al. 2010), migratory movements and site fidelity in roach *Rutilus rutilus* (Chapman et al. 2011; Brodersen et al. 2012), and dispersal in invasive mosquitofish G. affinis (Cote et al. 2010 2011). Furthermore, our repeatability values are similar to the average values ($R = \sim 0.37$) reported for most behaviors in a meta-analysis by Bell et al. (2009). Our detection of seasonal plasticity in behavior, with increased winter movement and dispersal, corresponds with the winter active life-history patterns of burbot described in the literature (McPhail and Paragamian 2000;
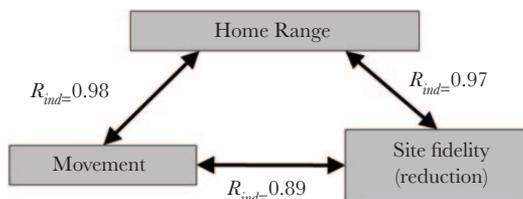


**Figure 2**
Between-individual correlations indicative of a spatial behavioral syndrome in wild *Lota lota* in Kinbasket Reservoir, Canada. Arrows used to indicate significant between-individual correlations among traits, with associated correlation statistic provided alongside.

**Table 2**
**Between-individual cross-context correlation ($R_{12}$) and within-context repeatability ($r_1$ and $r_2$) of burbot spatial behavioral traits previously identified as contextually plastic**

| Trait | Context | $r_1$ [CI$_{lower}$, CI$_{upper}$] | $r_2$ [CI$_{lower}$, CI$_{upper}$] | $R_{12}$ [CI$_{lower}$, CI$_{upper}$] | $\Delta$DIC$_{ind0}$ | $n$ | Rep |
|---|---|---|---|---|---|---|---|
| Movement | Summer$_1$ Winter$_2$ | **0.13** [0.05, 0.40] | **0.28** [0.17, 0.53] | **0.98** [0.51, 0.99] | **−5.02** | 24 | 244 |
| Vertical activity | Summer$_1$ Winter$_2$ | **0.56** [0.42, 0.74] | **0.53** [0.41, 0.74] | **0.43** [0.04, 0.75] | **−2.58** | 24 | 244 |
| Vertical activity | Year 1$_1$ Year 2$_2$ | **0.69** [0.47, 0.90] | **0.69** [0.45, 0.90] | 0.26 [−0.51, 0.78] | −0.01 | 8 | 117 |

$r$ values in bold represent statistical significance $P < 0.05$ based on DIC. $\Delta$DIC$_{ind0}$ represents the change in DIC between the unconstrained model, and a model with the individual covariance set to 0. DIC reduction >2 was considered "significant" support for the unconstrained model. $n$ is the number of individuals found in both contexts, and Rep is the total number of paired observations. All traits were cube root transformed and fitted with a Gaussian distribution.

**Table 3**

**Between-individual ($R_{ind}$), residual ($R_{error}$), and phenotypic correlations ($R_p$) between monthly burbot spatial behavioral traits and our spatial location variable (Poisson-distributed distance from the monthly COA to the centroid of the confluence region rounded to the meter)**

| Trait$_x$ | $R_{ind}$ [CI$_{lower}$, CI$_{upper}$] | $R_{error}$ [CI$_{lower}$, CI$_{upper}$] | $R_p$ [CI$_{lower}$, CI$_{upper}$] | $n$ | Rep |
|---|---|---|---|---|---|
| HR | −0.08 [−0.67, 0.51] | **0.27** [0.14, 0.37] | 0.01 [−0.19, 0.23] | 39 | 297 |
| Movement | −0.38 [−0.28, 0.80] | **0.28** [0.14, 0.38] | 0.17 [−0.02, 0.29] | 39 | 297 |
| Vertical activity | **-0.99** [−0.99, −0.85] | 0.05 [−0.04, 0.19] | **-0.77** [−0.85, −0.50] | 39 | 297 |
| Site fidelity | 0.18 [−0.29, 0.50] | **0.36** [0.26, 0.46] | **0.14** [0.06, 0.22] | 39 | 297 |
| Dispersal | **0.75** [0.44, 0.89] | **0.71** [0.64, 0.76] | **0.36** [0.26, 0.44] | 39 | 297 |

Correlations featuring CIs not overlapping were deemed significant (bold values represent $P < 0.05$). All spatial traits were cube root transformed and fitted with a Gaussian distribution.

**Table 4**

**Between-individual ($R_{ind}$), residual ($R_{error}$), and phenotypic correlations ($R_p$) among monthly burbot spatial behavioral traits**

| Trait$_x$ | Trait$_y$ | $R_{ind}$ [CI$_{lower}$, CI$_{upper}$] | $R_{error}$ [CI$_{lower}$, CI$_{upper}$] | $R_p$ [CI$_{lower}$, CI$_{upper}$] | ΔDIC$_{ind0}$ | ΔDIC$_{error0}$ |
|---|---|---|---|---|---|---|
| HR | Movement | **0.98** [0.95, 0.99] | **0.85** [0.82, 0.89] | **0.47** [0.44, 0.51] | **−10.77** | **−331.84** |
| HR | Vertical activity | 0.25 [−0.55, 0.86] | **0.14** [0.04, 0.27] | 0.12 [−0.13, 0.30] | 0.32 | **−4.74** |
| HR | Site fidelity | **0.97** [0.80, 0.99] | **0.51** [0.42, 0.61] | **0.36** [0.29, 0.41] | **−11.77** | **−65.91** |
| HR | Dispersal | 0.86 [−0.09, 0.97] | **0.51** [0.41, 0.60] | **0.30** [0.05, 0.45] | 1.12 | **−69.10** |
| Movement | Vertical activity | 0.70 [−0.17, 0.89] | **0.24** [0.11, 0.35] | 0.20 [−0.02, 0.41] | −0.73 | **−12.49** |
| Movement | Site fidelity | **0.89** [0.76, 0.99] | **0.41** [0.33, 0.54] | **0.37** [0.31, 0.43] | **−22.32** | **−46.47** |
| Movement | Dispersal | 0.53 [−0.12, 0.85] | **0.51** [0.41, 0.61] | **0.26** [0.16, 0.35] | −0.07 | **−71.45** |
| Vertical activity | Site fidelity | 0.53 [−0.37, 0.84] | **0.22** [0.05, 0.30] | 0.19 [−0.10, 0.35] | −0.13 | **−6.17** |
| Vertical activity | Dispersal | −0.39 [−0.83, 0.62] | **0.10** [0.01, 0.25] | −0.17 [−0.40, 0.31] | 0.30 | **−2.55** |
| Site fidelity | Dispersal | 0.26 [−0.18, 0.78] | **0.54** [0.46, 0.62] | **0.18** [0.09, 0.32] | −0.01 | **−86.16** |

ΔDIC$_{ind0}$ represents the change in DIC between the unconstrained model and a model with the individual covariance set to 0. ΔDIC$_{error0}$ represents the change in DIC between the unconstrained model and a model with the residual covariance restrained to 0. ΔDIC > −2 was considered as significant support for the unconstrained model. Correlations deemed significant based on DIC ($P < 0.05$) are in bold. All traits were cube root transformed and fitted with Gaussian distributions.

Paragamian and Wakkinen 2008; Harrison et al. 2013). Our detection of cross-contextual correlations between seasons for movement distance suggests that although burbot tended to move more in the winter, individuals that moved the most during the winter also moved the most during the summer period, a pattern consistent with personality-dependent behavior. For dispersal, small sample sizes of individuals found in all combinations of season and year ($n = 8$) prevented cross-context analysis. Our finding that HR, movement, and site fidelity are not correlated at the between-individual level with the spatial context variable suggests that measured spatial contextual differences are not responsible for the individual differences in observed behavior and lend support to our personality-dependent behavior hypothesis. We suspect that correlations between dispersal distance and reservoir distance are likely an artifact of the proximity of our release sites to the confluence region (Figure 1), which in turn resulted in those individuals that dispersed the furthest also being located furthest from the confluence.

For vertical activity, while adjusted $r$ values suggest personality-dependent behavior, cross-contextual correlation analysis between sampling years suggest inconsistent ranking between years and indicate we should reject a personality-dependent hypothesis (Brommer 2013b; Dingemanse and Dochtermann 2013). Furthermore, between-individual correlations between vertical activity and reservoir distance suggest context-driven behavioral differences and provide further evidence to reject our personality-dependent vertical activity hypothesis. We suspect reservoir bathymetry, which is deepest in the confluence (~190 m max) and shallower in the more riverine upper reaches (~30 m in the bush arm, Figure 1), may have constrained vertical activity. Although our linear reservoir distance variable could not account for all possible finer scale nonlinear

habitat heterogeneity, we consider that the scale of our analysis was appropriate, given the large size of observed HRs. Indeed our detection of context-driven behavioral differences in vertical activity validates our method of assessing the influence of spatial location on personality measures in the wild. Only a few authors have considered the influence of spatial or habitat context in animal personality field studies to date (Martin and Réale 2008), and we hope our study will encourage future researchers to explicitly consider and test for the presence of spatial contextual plasticity.

Our documentation of an absence of body size effect for all spatial behaviors tested contrasts with the observations of increasing space use with increasing fish size (e.g., HR; Minns 1995) and increasing dispersal distance (Radinger and Wolter 2013). However, body size relationships were not reported for burbot in Dunnigan and Sinclair (2008) or in Paragamian and Wakkinen (2008), and we consider that our results are likely a consequence of the mature size of our tagged fish, in comparison with size ranges of fish in Radinger and Wolter (2013) and Minns (1995), which likely span ontogeny. The lack of a capture location effect in any of our models supports our argument that spatial context was not responsible for the heterogeneity in behavior observed. Likewise, our lack of detection span effects suggests that our filtering process resulted in an adequate within-month sampling period to capture burbot spatial behaviors. We cannot exclude the possibility that a proportion of the variance in spatial behavior could be explained by sex differences, which we were unable to determine due to the postspawning capture timing. Indeed, sex-biased dispersal has been noted in other fishes, for example, brook charr *Salvelinus fluviatilus* (Hutchings and Gerber 2002). Nonetheless, although the spatial ecology of burbot has rarely been investigated, neither Dunnigan and Sinclair (2008)

nor Paragamian and Wakkinen (2008) reported sex differences in the HR or spatial ecology of burbot located in locations similar to our study site. Further, no sex-related differences in burbot swimming speed or endurance were reported by either Jones et al. (1974) or Vokoun and Watrous (2009). Nonetheless, we suggest that ruling out this potential source of pseudo-repeatability would potentially be a valuable exercise for future research. However, burbot's sensitivity to barotrauma represents a tagging challenge and although a prespawning (fall) capture might allow for easier sex determination, increased water temperature and increased gonad development would likely increase surgery stress/mortality and reduce catch rates.

We found no evidence for a dispersal syndrome, with the lack of correlation between dispersal from release and other behavioral traits at the between-individual level, indicating that individuals that dispersed further from the release site did not have consistently larger HRs, higher vertical activity and movement rates, or reduced site fidelity on a long-term basis. Although our data are not directly comparable to other authors who found dispersal correlated with other behavioral traits (Fraser et al. 2001; Edelsparre et al. 2013), our data suggest that simple linear dispersal from release measures, which are quite frequently used to interpret the spatial ecology of fishes, may be too simple to capture much of the within-population diversity in spatial behaviors. Our detection of significant phenotypic correlations (Table 4) between dispersal and movement, dispersal and HR, and dispersal and site fidelity reduction might historically have been interpreted as evidence of behavioral syndrome. However, our modeling framework allowed us to detect that phenotypic correlation was driven largely by residual correlations. In a simulation study using a study design similar to our research ($n = 25–50$, with 6 replicates per individual and a repeatability value of 0.5), Dingemanse and Dochtermann (2013) show that the power to detect between-individual differences was high (>0.8) where correlations were strong($R \geq 0.5$) and much lower (power < 0.6) with weaker correlations ($R \leq 0.5$). Accordingly, we acknowledge that our sample size ($n = 39$) may have reduced our power to detect more subtle between-individual correlations. However, our high number of replicates per individual (7), and good repeatability values (0.55 for dispersal and an average of 0.36 for all traits), likely allowed us to maintain good power to detect strong correlations and provide support for the hypothesis that dispersal from release was not strongly correlated with other behavioral traits. Indeed, parallels can be drawn between the lack of a correlation between HR and dispersal observed in our study, and other studies suggest that dispersal is not always correlated with exploratory behavior (e.g., great tit; Quinn et al. 2011). Nonetheless, the differing scales and definitions used to describe and measure dispersal throughout the literature complicate comparisons between studies (Bowler and Benton 2005).

Our findings that movement, HR, and site fidelity are all correlated at the between-individual level suggest a spatial behavioral syndrome with a diversity of behavioral types, ranging from philopatric, "resident" individuals with high site fidelity, minimal movement, and small HRs, to "mobile" individuals that occupy large HRs and continuously shift the location of these HRs. Heterogeneity in fish movement has been documented elsewhere (Crook 2004; Alldredge et al. 2011; Radinger and Wolter 2013). Our results, however, are among the first to document a spatially and temporally consistent spatial behavioral syndrome. Although the documentation of this "mobile" behavioral type that continuously shift HR location is somewhat at odds with the traditional concept of restricted movement and fixed HR location (Gerking 1959), shifting HRs have been recorded in lowland river fish (Crook 2004). Furthermore, our data support the work of others who question the validity of the restricted movement paradigm (Gowan et al. 1994; Rodríguez 2002).

Although individual-level correlations remain the most important diagnostic of behavioral syndromes (Dingemanse and Dochtermann 2013), our detection of positive residual correlation for most combinations of traits is also of interest (Table 4 and Figure 3). Residual correlations may indicate a missing covariate and are sometimes known as "within individual correlations," which in part represent the simultaneous short-term correlations within an individual (Dingemanse and Dochtermann 2013). Indeed the positive residual correlations we observed seem intuitive for our closely related spatial behavioral traits and perhaps occur as a result of a physiological or hormonal covariate. Nonetheless, it is important to note that residual correlation can also be a function of correlated measurement errors (Brommer 2013a) and, in our case, could perhaps be a function of the array design and coverage, differing receiver detection ranges (Mathies et al. 2014), and may in part be suggestive of an unmeasured spatial covariate or unmodeled temporal autocorrelation.

Our detection of a mobile behavioral type, independently from dispersal from release, may have important consequences for population dynamics and species' management programs. Our data show that mobile behavioral types utilize much larger habitat areas than the average member of the population. These larger HRs hold consequences for the design and size of conservation areas and reintroduction programs, the carrying capacity of occupied habitats, gene flow, and the selection of behavioral types suitable for captive programs. Dispersive traits have been shown to be important for range expansion, colonization, recolonization, and invasion (Rehage and Sih 2004; Duckworth and Badyaev 2007), and we suspect that the mobile trait observed here may also have an important role in range expansion. Indeed, in freshwater systems that are becoming increasingly fragmented, range expansion opportunities are likely restricted by connectivity bottlenecks (Ricketts 2001), and range expansion opportunity does not necessarily follow a linear pattern of increasing opportunity with distance from natal origin (Van Dyck and Baguette 2005). Therefore, a mobile exploratory behavioral type, which traverses large areas throughout its lifetime, may have an increased likelihood of encountering and passing important connectivity bottlenecks.
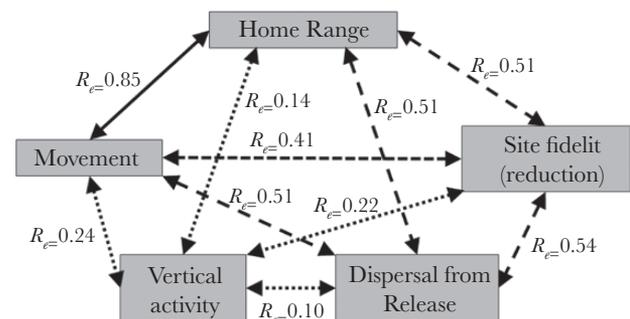


**Figure 3**

Residual correlations between spatial behavioral traits of wild *Lota lota* in Kinbasket Reservoir, Canada. Arrows indicate significant residual correlations between traits, with associated correlation statistic alongside. Line weights indicate the strength of the relationship.

The recognition that behavioral type diversity may be important for the resilience of a species to environmental change is gaining momentum (Réale et al. 2007; Sih et al. 2012; Wolf and Weissing 2012), and it seems likely that the maintenance of the kind of spatial behavioral type diversity we observed will be important for the conservation of fish and other animal populations. Nonetheless, further work is required to understand the proximate and ultimate causes and the evolutionary and ecological consequences of these behavioral types and to better account for spatial behavioral diversity in conservation and management policy. At a species-specific scale, the diversity in spatial behavioral types observed may help explain the apparent contradiction between the generally sedentary behavior reported for burbot (Bergersen et al. 1993; Carl 1995), and their extremely wide northern circumpolar distribution (Stapanian et al. 2010) and has implications for the selection of individuals for planned burbot reintroduction programs (Worthington et al. 2010).

## CONCLUSION

Our study is among the first to document spatially and temporally consistent personality-dependent space use among wild animals, in a wild setting. Our results show that personality can play a significant role in determining how animals utilize space and that personality-dependent spatial behavior may be more complex than the often used linear measures of dispersal would imply. Study findings suggest that heterogeneity in fish movement is a product of a diversity of spatial behavioral types ranging from "resident" individuals, who exhibit high site fidelity, minimal movement, and small HRs, to highly exploratory individuals, who continuously shift HR location, show high rates of movement, and exploit much larger HR areas. This within-population spatial behavioral type diversity will likely have important implications for spatial conservation and management policy based on mean measures of space use. Identification and preservation of the type of diversity we observed may prove important for maintaining the resilience of fish and animal populations to environmental change.

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