



Original Article

Individual differences exceed species differences in the movements of a river fish community

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Repeatable individual differences often account for large proportions of intraspecific variation in animal movements. However, meta-population models have continued to rely on single species-level and season-specific species-level means for movement prediction. Here, we test the hypothesis that repeatable individual differences can account for a similar proportion of movement distance variation as species differences. We used radio telemetry to generate repeated measures of movement from 504 hetero-specific fish. We tracked 5 large bodied fish species (*Salvelinus confluentus*, *Oncorhynchus mykiss*, *Prosopium williamsoni*, *Thymallus arcticus*, and *Sander vitreus*) in the upper reaches of the Peace River, British Columbia, Canada, over 8 years. We applied a hierarchical framework to partition repeatability of movement distances at the intra- and interspecific biological levels, and among short-term (within-season) and long-term (across seasons and years) temporal levels. Our results show that long-term movement distance repeatability was higher at the intraspecific level than at the interspecific level, demonstrating that animal personality can account for more variation in movement than species differences. These findings provide a novel, community level demonstration of the importance of individual variation, highlighting the predictive gains associated with a shift in the focus of spatial ecology, away from species mean and seasonal species-level mean predictive approaches, towards a spatial behavioral types-based predictive approach.

Key words: animal personality, community ecology, dispersal, fish ecology, interspecific variation, intraspecific variation, spatial ecology, telemetry.

INTRODUCTION

Movement allows animals to avoid predators, competitors, and unfavorable environmental conditions, and facilitates foraging and reproduction (Nathan et al. 2008; Clobert et al. 2009). All animal movements, irrespective of their underlying causes, carry costs and benefits for fitness (Fahrig 2007; Holyoak et al. 2008; Bonte et al. 2012). This high potential for fitness effects means that variation in animal movement influences a wide range of eco-evolutionary processes including the spatial flow of genes (dispersal), mortality and fecundity (Biro and Stamps 2008), foraging and resource use (Harrison, Gutowsky, Martins, Ward, et al. 2017), range extents

(Dingle and Drake 2007; Nathan et al. 2008), and responses to environmental change (Sih et al. 2011; Lowe and McPeck 2014; Bestion et al. 2015). Movement distance, that is the distance between successive animal locations, is perhaps the best studied animal movement metric (Ronce 2007) and a key metric for dispersal research (Clobert et al. 2009). Movement distance metrics are simple to understand and provide the raw material for many more complicated spatial ecology metrics. Movement distance variation is closely linked to gene flow (Clobert et al. 2009), and to a wide range of behavioral, ecological and life-history traits (Stevens et al. 2014; Comte and Olden 2018). Accordingly, a better understanding of the determinants of movement distance variation represents a major goal for ecology and evolution.

Individuals of the same species often differ in their behavior at the within population level, and these differences are often repeatable

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across environmental or temporal contexts (Wolf and Weissing 2012). This phenomenon, known as animal personality, has been documented in taxa spanning the animal kingdom and the effect size of this individual variation is often large. In a meta-analysis of animal personality research, Bell et al. (2009) showed that on average personality can explain 37% of within-species behavioral variation. Individual differences are also often observed in the movement behavior of wild animals (reviewed in Spiegel et al. 2017), where they also often account for large proportions (>30%) of variation (e.g., Harrison et al. 2015 and Villegas-Ríos et al. 2017). Consequently, potential exists for these individual differences in movement distances to meet or even exceed the variation explained by interspecific differences. For example, intraspecific variation in dispersal distance has been shown to equal interspecific variation in European butterflies (Stevens et al. 2010). Among-population intraspecific variation has been shown to meet or exceed interspecific trait variation in plant communities (Messier et al. 2010; Violle et al. 2012; Siefert et al. 2015), the ecological effects of individual variation have been shown to exceed species effects in animal communities (Des Roches et al. 2018; Raffard et al. 2017), and high levels of among-population intraspecific variation have been recorded in meta-analyses of fish movement (Radinger and Wolter 2014; Comte and Olden 2018). However, investigations into individual differences in movement, like investigations into animal personality in general, have focused largely on isolated species- and population-specific demonstrations of repeatability (but see Pruitt et al. 2012; Pruitt and Modlmeier 2015 for examples of community personality work). Thus, within-community comparisons of repeatable individual and interspecific variation have not previously been performed.

Investigations into intraspecific variation in movements and dispersal have often relied on single or mean estimates of movement from individuals, to identify dispersal/movement phenotypes and to assess intraspecific variation (e.g., Stevens et al. 2010; Radinger and Wolter 2014; Comte and Olden 2018). However, for labile traits, repeated measures of movement are necessary to characterize an individual's behavioral phenotype (Dingemans and Dochtermann 2013). Thus, the general importance of individual variation in movement distance and in comparison to species variation are not well resolved. Here, we attempt to fill this knowledge gap by partitioning variation in repeated measures of a riverine fish community movement, at the species and individual level.

While contemporary spatial ecology studies often statistically account for individual variation, the effect size and the implications of individual variation in movement are still largely overlooked (Holyoak et al. 2008). Consequently, meta-population models continue to rely on species-level and season-specific-species-level mean estimates for movement prediction (Stevens et al. 2010). However, if individual variation meets or exceeds among-species variation, then movement and dispersal models based on species as the unit of prediction, will fail to explain large proportions of movement variation, and thus provide potentially erroneous predictions. Accordingly, an increased understanding of the partitioning of intra- and interspecific variation in movement distance has the potential to significantly improve movement and dispersal predictions.

The timescale over which repeatability is measured has implications for interpretation (Wilson 2018). Repeatability in movement over shorter periods may occur as a conditional response to among-individual variation in experience of temporally correlated environmental factors (Boulton et al. 2014; Araya-Ajoy et al. 2015; Biro and Stamps 2015). Repeatability in the behavior of wild animals over longer time frames, and over variable environmental conditions, suggest that individual differences occur as

a function of more permanent “intrinsic” behavioral traits (Wilson 2018). Long-term repeatability has different implications for ecological and evolutionary processes, in particular the quantity of variation that is available for selection, than short-term transient consistency (Wolf and Weissing 2012). If short-term and long-term repeatabilities are not partitioned, then short-term consistency can artificially inflate measures of trait repeatability (Araya-Ajoy et al. 2015). This temporal partitioning of repeatability is of particular importance in field based studies where the environmental experience of individuals cannot be standardized (Biro and Stamps 2015). In this manuscript, we treat movement as a continuous behavioural trait and take a repeated measures approach to assess intraspecific trait variation. Furthermore, we partition intra- and interspecific movement repeatability at short-term (within seasons) and long-term levels (across seasons and years).

The underlying causes of movement can be difficult to determine in aquatic environments, because direct observation of reproduction, foraging, exploration, or predation avoidance are rarely possible (Cooke et al. 2004; Burgess et al. 2016). In iteroparous and potadromous fish, multiple spawning locations, reproductive site residency phenotypes, and missed spawning years, complicate attempts to identify spawning migrations (Chapman et al. 2012; Hirsch et al. 2017). Following the precedent of Nathan et al. 2008; Harrison et al. 2015; Nakayama et al. 2016; Villegas-Ríos et al. 2017, we do not attempt to categorize movements as migratory or otherwise, and we do not attempt to assign underlying causes to each movement step. Instead, we simply analyze all movements together. Nonetheless, we design our short-term temporal seasonal categories around the key reproductive movement periods of our focal species. Thus, much of the variation in movement associated with seasonal movement and migratory patterns, can be captured by our within and among season-repeatability estimates.

In this study, we used 2 radio-tracking datasets spanning a total of 8 years, featuring 5 behaviorally, and ecologically, diverse riverine fish species (Table 1), sampled in the Peace River in British Columbia, Canada. We used a mixed-effects modeling framework to decompose variation in movement distance at a series of hierarchical and multilevel levels. Specifically, we test the hypothesis that repeatable intraspecific differences account for as much variance in movement distance as interspecific differences. We test this hypothesis at both the short-term (within-seasons) and long-term (across seasons and years) levels.

METHODS

Study system and sampling overview

This study was completed in the upper reaches of the Peace River in Northeastern British Columbia, Canada (Supplementary Figure S1). The Peace River is a major tributary of the Mackenzie River, and flows from the Rocky Mountains in British Columbia northeast towards its confluence with the Slave River (Supplementary Figure S2). The Peace Canyon Dam, on the main-stem of the Peace River (55°58'55"N 121°59'40"W) formed the upper boundary of the study site; and the town of Peace River, Alberta (56°14'02"N 117°17'23"W), approximately 370 km downstream, formed the lower boundary of sampling (Supplementary Figure S1).

Two discrete radio-tag tracking datasets were merged and analyzed for this paper. The first dataset from study (a), tracked fish from 1996 to 1999 (Burrows et al. 2001; AMEC Earth and Environmental & LGL Ltd 2010). The second dataset from study (b), tracked fish between 2005 and 2009 (AMEC Earth and Environmental & LGL Ltd 2008a, b, 2009). Although the 2 studies

Table 1
Sample sizes, biometrics, seasonal reproductive phenology, and foraging strategy of radio-tracked Peace River fish species

Species	<i>n</i>	Mean fork length (cm) (Min, Max)	Spawning season	Spawning location	Seasonal migrations	Adult diet
Bull trout ^{1,2,3}	165	56.6 (26.6, 88.5)	Fall	Tributary	Early fall spawning migration	Piscivore
Rainbow trout ^{1,2,3}	56	35.1 (22.8, 45.2)	Spring	Tributary	Spring spawning migration to tributaries	Generalist (insectivore/piscivore)
Walleye ^{1,6}	54	43.2 (27.5, 57.4)	Spring	Main river	Not well known in rivers	Piscivore
Mountain whitefish ^{1,4}	110	33.6 (25.2, 48)	Fall	Tributary	Fall spawning migration	Benthivore
Arctic grayling ^{1,5}	119	34.0 (25, 40.5)	Spring	Tributary	Spring spawning migration and overwinter migration	Drift feeding insectivore

¹(Scott & Crossman 1973); ²(Behnke 1992, 2010); ³(Quinn 2005); ⁴(Northcote & Ennis 1994); ⁵(Northcote 1995); ⁶(Paul 2013).

had different goals, they were largely compatible for our purposes, having used similar fish-tracking methods in broadly the same geographic location.

Study species

Study (b) featured 5 iteroparous species of fish including 4 salmonids: bull trout *Salvelinus confluentus*, rainbow trout *Oncorhynchus mykiss*, Arctic grayling *Thymallus arcticus*, and mountain whitefish *Prosopium williamsoni* and the percid walleye *Sander vitreus*. Study (a) included only bull trout and Arctic grayling. More details concerning body sizes, sample sizes, and general migratory and foraging ecology are given in Table 1. While 39 species of fish have been documented in the Peace River, the upper Peace river, is a salmonid dominated, somewhat species poor system (Taylor et al. 2014). The 5 tagged species represent the majority of taggable sized species at our study site. AMEC Earth and Environmental & LGL Ltd (2008c) reported that longnose suckers *Catostomus catostomus*, were also abundant in our study site. Large bodied species (large enough to tag) which are present but rare (<1% of abundance) include: burbot *Lota lota*, Northern pikeminnow *Ptychocheilus oregonensis*, largescale sucker *Catostomus macrocheilus*, white sucker *Catostomus commersonii*, Northern pike *Esox lucius*, and goldeneye *Hidon alosoides*. Small bodied fish species (too small to tag) present in our study site include: longnose dace *Rhinichthys cataractae*, reddsider shiner *Richardsonius balteatus*, spottail shiner *Notropis hudsonius*, slimy sculpin *Cottus cognatus* and trout-perch *Percopsis omniscomaycus* (AMEC Earth and Environmental & LGL Ltd 2008b).

Capture and tagging

Study (a) focused on the capture and release of bull trout in the Halfway River watershed, and Arctic grayling in the Halfway and Sukunka river watersheds. Fish tagged in study (b) were captured and released in the Peace River main-stem, with the exception of bull trout, which were tagged and released almost exclusively in the Pine River and its tributaries (Supplementary Figure S1). Fish were captured by boat electrofishing, trapping, or angling. All captured fish were anesthetized using a clove oil solution, and were weighed and measured (fork length) before surgery. Minimum fish sizes for tagging were established using the 2% wet weight rule (Brown et al. 1999). Pulse-coded microprocessor radio transmitters (5-s transmission rate, 3 V battery, 400 mm antenna, Lotek wireless) were surgically implanted into the peritoneal cavity, with the antenna extruding through the body wall and trailing posteriorly behind the fish. In both studies fish <400 mm were fitted with Lotek model MCFT-3FM transmitters (10 g in air, 4.6 g in water, 11 × 59 mm, 378 day expected battery life), and larger fish with model

MCFT-3A transmitters (16 g in air, 6.7 g in water, 16 × 46 mm, 761-day battery life). For additional information on the tagging including delayed transmitter activation in some years (depending on timing of tagging of some species), refer to AMEC Earth and Environmental & LGL Ltd (2008a, 2008b, 2009).

Tracking

Tracking was performed by a combination of helicopter and fixed-wing aircraft in both studies. In Study (a), tracking was concentrated on the Halfway River, the Peace River between Sneddon Creek and the Peace Canyon Dam, Moberly River, and the Pine River with an emphasis on the Sukunka River tributary (Supplementary Figure S1). Mobile-tracking in study (a) was performed using a single Lotek SRX400 receiver. 72 tracking flights occurred between September 1996 and March 1999. With the exception of March 1997, November 1998, and February 1999, tracking occurred at least once in every month of each year, with an average of 2.5 flights per month, and a maximum of 5 flights per month.

Study (b) initially tracked fish using fixed-wing aircraft equipped with 2 Lotek SRX400 receivers, but added an additional receiver in April 2007. Typically, mobile surveys included the Pine River and its major tributaries, the Peace River main-stem from the Peace Canyon Dam to the Alberta border (often continuing to the town of Peace River), and occasionally portions of the Halfway, Moberly or Beaton rivers. Forty-one mobile-tracking surveys (many spanning several days) were performed between February 2006 and October 2009, including 7 between February and October 2006, 12 between March and November 2007, 12 between March and October 2008, and 10 between March and October 2009.

In addition to mobile tracking, fixed-station receivers were also used in both studies. For study (b), 9 receivers (Lotek SRX400 or SRX600) were deployed in 2006, 10 in 2007, 7 in 2008, and 6 in 2009. For study (a), one fixed station SRX400 was operated at Chowade River from August 1997 through July 1998 (Supplementary Figure S1).

Data processing and variable definitions

Raw radio telemetry data were filtered to remove potentially false records. Detections were removed if power levels were less than 50 (on a 1–232 level), if tags were not recorded multiple times within a fixed-station zone within a short period (i.e., 20 min), or if fish appeared to make impossible movements (e.g., fish could not be detected at 2 places at once). Positional error was estimated as ±350 m. Further, radio-tagged fish confirmed dead or presumed to be dead (moved less than positional error distance over entire study period) and those that were never detected were filtered from the

dataset and excluded from further analysis. The first week of data following surgery was excluded from analyses. For additional information on data filtering, and the minimum movement thresholds to determine mortality, refer to AMEC Earth and Environmental & LGL Ltd (2008a, 2008b, 2009). For mobile detections, the position of the fish was assumed to be that of the aircraft (downloaded from the GPS unit) at the time of the most powerful detection event. Fish detections recorded by the fixed-station receiver were assigned the coordinates of the receiver. Study (a) recorded a total of 2339 positions from 199 tags during mobile surveys and 85,302 detection events at fixed receivers, resulting in a database containing 1989 movement steps from 115 fish. In study b, 5458 positions were recorded from 442 tags during mobile surveys, and 11,391,045 detections were recorded at fixed stations. These detections resulted in a database containing 4649 movement steps from 389 fish.

In total 6,638 movement observations were recorded from a total of 504 individual fish from 5 species (see Table 1 for sample sizes and fork lengths by species), yielding an average of 13.2 replicates per fish, and an average of 100.8 individuals per species. At the short-term level, individuals recorded a mean of 2.9 replicates per (season \times year \times individual) group (2271 levels), and species recorded a mean of 96.2 replicates per $V_{spec \times series}$ group (69 levels). Of the 567 winter movement observations, 431 occurred in study (a), where winter tracking occurred more frequently than in the study (b) data set. The mean *time-elapsd* was 20.44 (Min 0.5, Max 61) days.

Our response variable, movement distance (m) was estimated as the distance along river centerlines between successive detections, using ArcGIS. Movement data were filtered to exclude any movement steps which exceeded 2 months duration, thereby excluding erroneous movement rates which can occur as a result of large temporal gaps in detection histories.

A continuous variable time-elapsd, calculated as the time in days (24 h) between the 2 successive detections and used to estimate a movement step, was fitted as a fixed effect. This variable was designed to capture any potentially confounding variation in movement distance that might occur due to differences in time elapsed between the 2 detections that comprise a sampling event. This variable was standardized to 2 standard deviations (SD) to allow for direct comparison with other fixed effects, and to facilitate mode convergence. While we acknowledge that among-individual and among-species differences in slopes are possible, data were not sufficient to fit these parameters as random slopes.

Season was defined based on physical conditions (e.g., water temperature, discharge) at our study site, which has a climate typical of Northern British Columbia, characterized by long cold winters with large amounts of snowfall volumes, late spring periods featuring high flow events during spring run-off due to large volumes of melting snow, and short relatively hot summers. Our seasonal categorization allowed us to capture the seasonal movement patterns of both fall and spring spawning species, which fall into our fall and spring categories. Seasons featured 4 categorical levels: winter, December 1st to March 31st captured the coldest water temperatures (<4 °C), low flow conditions and partial ice cover in some parts of the study area.; spring, April 1st to June 30th captured spring spawning period for both rainbow trout and Arctic grayling (Table 1), and included spring run-off period where due to large volumes of melting snow, water levels are highest; summer, July 1st to August 31st, captured the period between spring and fall spawning and generally included periods with water temperature >15 °C fall, September 1st to November 30th, captured declining water temperatures and fall spawning period for bull trout,

and mountain whitefish. Seasonal categorization of a movement event was based on the median date between detections.

River zone consisted of 6 categorical levels which were defined as major tributary (Halfway River, Pine River, Beatton River, or Moberly River) and main river (Lower and Upper) occupation (Supplementary Figure S1). River zone occupation was determined by the location of the initial detection in a movement step. River zones were designed to capture broad level ecological difference between differing regions of the study site.

Two zero mean continuous variables were defined to quantify variation in movement associated with heterogeneity in body size (fork length); body size relative to the community mean *bodysizeAll*, and body size relative to the species mean, *bodysizeWithin*, where fork length was standardized (to 2 SD) across all fish, and within-species groups, respectively.

A binary variable *Study*, was fitted to capture any potential variation in movement that might occur due to differences in sampling methods between study (a) and (b). This variable was coded as 0 and 1, then mean centered and divided by 2 standard deviations to ensure a zero mean in a perfectly balanced dataset (Gelman and Hill 2007; Araya-Ajoy et al. 2015).

Statistical analysis

Comparison of inter- versus intraspecific variation

Data were analyzed using a hierarchical multilevel random intercept modeling approach (Gelman and Hill 2007; Zuur et al. 2009). Data from all 5 species were included in our full data model. By fitting random intercepts for species (*spec*) and individuals (*ind*), we estimated and compared the proportions of total variation in movements that were accounted for by among-individual differences, with the proportions of total movement variation explained by among-species differences. These proportions of total variation provide estimates of long-term repeatability, that is, repeatability across seasons and years. Furthermore, by fitting further nested random intercepts of *ind* \times *season* \times *year* and *spec* \times *season* \times *year*, we compared the proportions of variation accounted for by individual by season interactions and species by season interactions. These proportions represent short-term repeatability, that is the within-group level consistency within a season (Araya-Ajoy et al. 2015). We also fitted a number of other fixed and random factors, to control for any confounding factors that could potentially inflate individual repeatability estimates if not accounted for. The variable *river zone* was also fitted as a potentially partially crossed random intercept to account for potentially confounding river zone location variation in our unbalanced design. Data were not sufficient to allow for the fitting of interactions between zone and individuals or species, moreover the categorical nature of the river zone variable mean that random slopes, that is, behavioral reaction norm approaches were not possible. The variables *bodysizeAll*, *bodysizeWithin*, *Study*, and *Time elapsed*, were fitted as fixed effects, and standardized to 2 SD ensuring each effect had a zero mean and an SD of 0.5 (Nakagawa and Schielzeth 2010).

We applied an inverse hyperbolic sine (IHS) transformation to normalize our response variable, movement distance. IHS transformation was chosen for its ability to provide a relatively strong transformation of data which included zeros (Burbidge et al. 1988). While alternative distributions can be fitted using rptR (Stoffel et al. 2017), with the size of our data set, excessively long computational time for bootstrapping convergence, meant such an approach was not feasible.

Models assumptions (including homogeneity of variance among fixed effects levels, and normality, were initially validated using the package lme4 (Bates et al. 2015) for R (R Core Team 2017), which allows for combinations of nested, crossed, and partially crossed designs, and fits the design based on the data, rather than by a priori design selection. A complete depiction of the hierarchical and multilevel structure of our design is given in Supplementary Figure S3. Given that our aims were to partition variance, not to produce parsimonious models, we fitted full fixed effects and random effects structures without backwards selection (Whittingham et al. 2006; Zuur et al. 2009). Log-likelihood ratios for random effects, and repeatabilities and confidence intervals were estimated using the rptR package for R using 1000 parametric bootstrap iterations (Nakagawa and Schielzeth 2010). Following Villemereuil et al. (2018), repeatabilities were calculated as proportions of total variability (the sum of all fixed and random effects variance). Computation methods for estimates of long-term and short-term repeatabilities are detailed in the supplementary material. R code and model descriptions can be found in the supplementary material.

Comparison of repeatability among-species

Species-specific movement repeatabilities were also estimated using a hierarchical multilevel mixed-effects modeling approach. Separate models were fitted for each species. All models featured the same response variable, fixed effects and random effects as the full model, with the exception of the omission of:species and $spec \times season \times year$ random effects, and across species body size fixed effects. Model design, packages and variance partitioning were identical to our full data method. Confidence intervals around repeatability were again calculated using bootstrap simulated posterior distributions, thus facilitating comparison across species (Hadfield et al. 2010; Dingemanse and Dochtermann 2013).

RESULTS

Long-term individual differences, which accounted for 12% of overall movement variation, explained more variation in movement than among-species differences (2%) (Table 2; Figure 1). Overall patterns of variation found in the raw data can be seen in Figure 2. Short-term repeatability of movements, that is, repeatability within season \times year levels, was higher at the among-individual level (24% of total variation) than the among-species

level (20%), but the difference between the proportions was not significant (Table 2; Figure 1). River zones also explained a significant proportion of overall movement variation (16% of total variation, Table 2). The combination of our fixed effects (*bodysizeAll*, *bodysizeWithin*, *Method*, and *time-elapased*) accounted for 2% of total movement variation (Table 1). Coefficients for all fixed effects can be seen in Table 3. Body size had minimal influence (Table 3, Figure 2). Residual variances at the among-species scale were broadly homoscedastic (Supplementary Figure S1).

While a degree of variation in species-specific long-term repeatability was observed, all fish species demonstrated significant repeatability and no differences in short-term or residual variation were observed (Figure 3, Supplementary Table S1). Differences among species-specific repeatabilities were not significant, with the exception of Arctic grayling and Walleye, which represented the lowest and highest mean species-specific repeatability values respectively (0.4 and 0.19) (Figure 3 and Supplementary Table S1). In Figure 2, we can see that while bull trout have the highest among-individual variance, they also exhibit the highest within-individual differences (error bars), supporting our finding that no one species is having a undue influence on long-term repeatability in our full model. Likewise, while we can see in Figure 2, that bull trout likely account for a high proportion of among-species variance in our full model, bull trout's higher levels of within-individual variance (error bars) suggest that bull trout are not having an outsized influence on species repeatability. Fixed effects coefficients for species-specific models can be seen in Supplementary Table S2.

DISCUSSION

Our results show that long-term repeatable intraspecific differences, accounted for more variation in movement distances than species differences in a riverine fish community. At the within-season level, individual differences accounted for a similar proportion of variation in movement as species differences. These findings, obtained from 5 ecologically diverse fish species, tracked over long periods in their natural environment, have important implications for our understanding of animal movements. Descriptions of individual differences in the spatial ecology of animals are common at the within-species level (reviewed in Spiegel et al. 2017). Our study provides a novel location-specific within-community demonstration that these repeatable, nonspecies-specific, movement specializations can explain more variation in movement than species differences.

Table 2

Variance partitioning estimates for movement repeatability (R_p) and associated 95% confidence intervals (CI) were estimated as proportions of total variation. Significance was determined from log-likelihood ratio tests ($Log-L$). Fixed effects captured the sum of the variation explained by body-size standardized within and across species, sampling methods, and movement step sample length. Asterisks identify short-term repeatability estimates that are calculated as the sum of among- and within group among season by year variance, and thus do not have log-likelihoods

Parameter	R_p (CI)	Log-L	n
Among-individual (long term)	0.12 (0.09, 0.15)	$D = 241, P < 0.001$	504
Within-individual among season \times year	0.12 (0.08, 0.15)	$D = 199, P < 0.001$	2281
Among-individual (short term)*	0.24 (0.17, 0.30)	na	na
Among-species (long term)	0.02 (0, 0.08)	$D = 1.85, P = 0.09$	5
Within-species among season \times year	0.08 (0.05, 0.12)	$D = 316, P < 0.001$	72
Among-species (short term)*	0.10 (0.05, 0.20)	na	na
Among-river zone	0.16 (0.02, 0.34)	$D = 102, P < 0.001$	6
Fixed effects	0.02 (0.01, 0.05)	na	na
Residual	0.48 (0.37, 0.57)	na	na

Movement distance variation is known to facilitate species coexistence, ecological and evolutionary responses to environmental change, dispersal, invasion, and colonization (Spiegel et al. 2017). Our findings suggest that intraspecific variation may play an equal, if not larger role than interspecific variation in facilitating these ecological and evolutionary processes. Our findings indicate that community dispersal models that rely on species as the unit of prediction, will fail to account for the large proportions of variation in the dispersal of an animal community that occur as a consequence of individual variation, and thus may be fundamentally flawed. Similarly, our findings suggest that community movement models that rely on species-level seasonal predictions, may fail to account for the large proportion of variation that occurs at the among-individual within-season level. Consequently, conservation policy

based on species mean dispersal models, or species-season mean movement models, may be ineffective.

Our demonstration that intraspecific variation in movement distance was repeatable across varying seasons and years, indicate that these movement specializations represent permanent intrinsic behavioral traits (Wilson 2018). The ecologically relevant time scale over which trait repeatability occurred, suggest that repeatability was not an artifact of short-term correlation in environmental variables (Araya-Ajoy et al. 2015). Accordingly, these movement distance specializations occurred as a consequence of unmeasured permanent environmental differences, or genetic variation. Long-term repeatability (0.10–0.15) was lower than the mean of 0.37 described by Bell et al. (2009), in their meta-analysis of individual variation in a variety of behaviors. Our repeatability estimates were, however, within the range of reported data in the Bell et al. (2009) dataset. Repeatability was lower than estimates of movement activity in other fishes including cod, *Gadus morhua*, 0.34 and 0.23 (Villegas-Ríos et al. 2017), and perch *Perca fluviatilis* 0.21–0.33 (Nakayama et al. 2016) and burbot *Lota lota* 0.32 (Harrison et al. 2015). Our more modest repeatability metrics may have occurred because we excluded short-term repeatability from our estimates, which may have inflated repeatability in previous field studies (Biro and Stamps 2015). Unlike many previous studies, we presented repeatability as a proportion of total variation including all fixed and random effects variation (Villemereuil et al. 2018). While our estimates of repeatability are modest, our method has allowed us to make strong inferences about the intrinsic nature of these movement behavioral traits. Correspondingly, the movement specializations observed in this study have high potential for ecological and evolutionary consequences.

We showed that repeatable within-season intraspecific differences can account for a similar proportion of variation in movement as interspecific differences, even in a putatively phenologically diverse community. These findings indicate that individual movement distance traits continue to exert an influence over seasonally structured movements. Given that seasons were based on the reproductive periods of our focal species, intraspecific variation may be partially attributed to intraspecific variation in seasonal movement

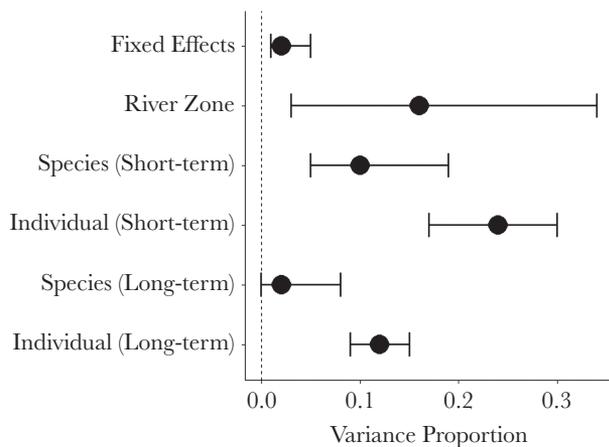


Figure 1

Variance partitioning of movements from a hetero-specific fish community in the upper Peace River, Canada. Long-term estimates represent repeatability across seasons and years, and short-term estimates represent repeatability within seasons. Error bars represent 95% confidence intervals. Fixed effects estimates include variation explained by body-size standardized within and across species, sampling methods, and movement step sample length.

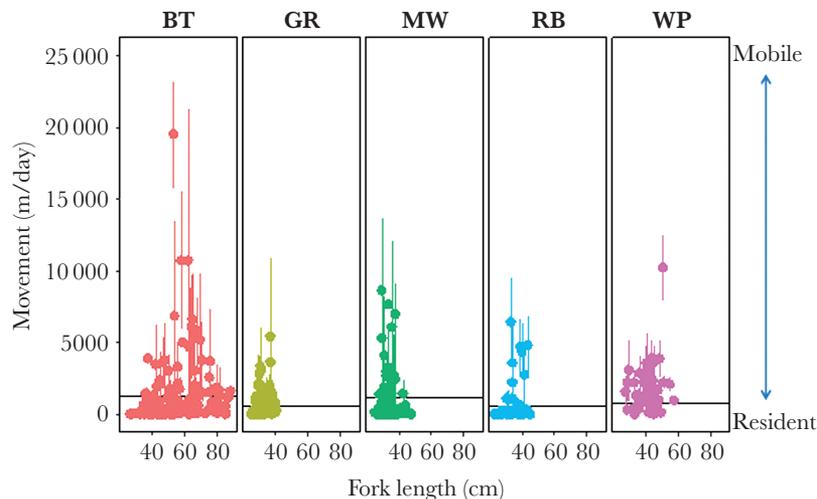


Figure 2

Mean movement distance (m/day) of individual fish derived by telemetry in the upper Peace River, Canada, demonstrating resident to mobile behavioral specializations and providing a visual comparison of intra- and interspecific variation. Error bars represent individual specific standard errors, horizontal black lines represent species-level means. Species codes: BT, bull trout, GR Arctic grayling, MW mountain whitefish, RB rainbow trout, and WP walleye.

and migratory behavior (Chapman et al. 2011; Dodson et al. 2013; Harrison, Gutowsky LFG, Martins EG, Patterson, et al. 2017). These seasonal level repeatabilities demonstrate that among-season plasticity in movement, was apparent at both the within-individual and within-species levels. Such among-season variation in movement patterns are common in temperate animals (Dingle and Drake 2007). Nonetheless, the existence of plasticity at the individual level, provides a validation for our continuous approach to estimations of movement.

Our finding that long-term repeatabilities were similar among species and significant within each species, indicate that estimates were not inflated by a single species with unusually high repeatability in comparison to other species. Nonetheless, our finding that walleye had greater long-term individual variation than Arctic grayling, indicates that a degree of among-species variation in repeatability did occur. Our data show that Arctic grayling and Mountain whitefish had slightly lower mean repeatabilities, than the more piscivorous salmonids and walleye. This may be because Arctic grayling and Mountain whitefish have a lower trophic status and thus a greater propensity to exhibit antipredation shoaling behavior (Pitcher and Parrish 1993), than the more piscivorous salmonids

and walleye. Further research is now required to identify the causes and consequences of this among-species variation in repeatability.

By relying on a large sample size (504) and a good average number of replicates per fish (13), power to detect repeatability at the individual level was high. While our sample size for species ($n = 5$) was lower than for individuals, it met minimum requirements for random effects levels (5, Gelman and Hill 2007). Our bootstrapping approach also meant that any uncertainty in estimates associated with small sample sizes was accurately reflected by our confidence interval estimates, which were used exclusively for hypothesis testing.

Given that we were unable to tag several members of the fish community due to site, rarity, or small body sizes, we may not have captured the entire interspecific movement variation present in the community. By sampling only a proportion of individuals from the population, we may also have underestimated the total intraspecific variation present within the community. Nonetheless, given that we sampled large numbers of individuals in 5 of the 6 most abundant species in our study site, we hypothesize that the increase in variability explained by individuals in comparison to species seen in our study, is likely be reflected in the community.

By including a river-zone main effect, we demonstrated that general habitat effects were not confounding our estimation of repeatability at a species or individual level. Our finding that river zone accounted for a similar proportion of variation as individual variation suggests that among-individual plasticity in movement in response to environment/geographic location, may provide an interesting future research topic. By including *time-elapsed*, *study*, and *body-size* fixed effects in our estimates of total variation, we demonstrated that repeatability estimates were not confounded by body size, or sampling regime variation. Our mobile air-borne tracking method meant that positional errors were not likely to be correlated at the individual or species level (White and Garrott 1990), and thus also unlikely to inflate repeatability.

Table 3
Fixed effects estimates for Peace river fish community movement model. All fixed effects are standardized to 2 standard deviations

Parameter	Estimate	SE	t value
Intercept	8.23	0.37	22.46
Body size across species	0.62	0.27	2.30
Body size within species	0.07	0.16	0.42
Study	0.38	0.22	1.78
Time elapsed	0.01	0.04	0.17

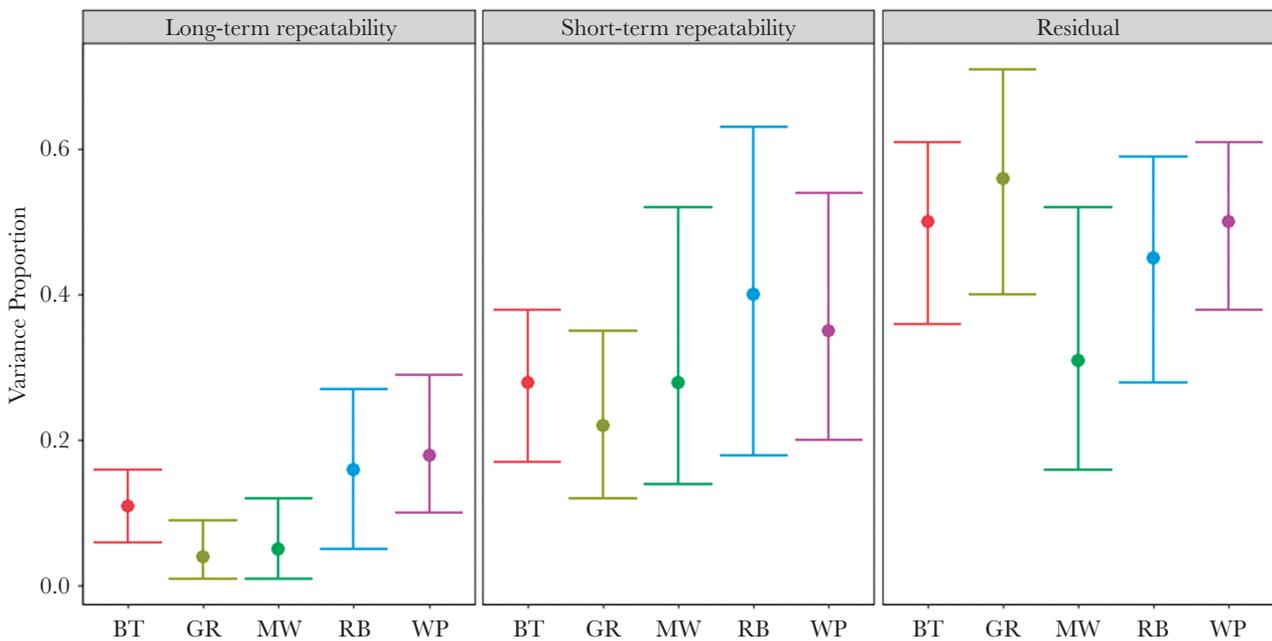


Figure 3
Comparison of long-term and short-term repeatability, and residual (within-individual within-season x year) variation of movement among 5 species in the upper Peace River, Canada. Error bars represent 95% confidence intervals. Species codes: BT, bull trout, GR Arctic grayling, MW mountain whitefish, RB rainbow trout, and WP walleye.

Within-species individual variation is known to support population resilience and stability (Wolf and Weissing 2012; Spiegel et al. 2017). Our findings suggest that these population level resilience effects may extend to the community and the ecosystem levels. Further research is now required to determine whether the importance of repeatable individual variation in comparison to interspecific variation seen here is reflected in differing animal communities, different behavioral traits and wider levels of biological organization. While individual variation is beginning to be recognized in conservation and management policy (Killen et al. 2016; Ward et al. 2016), spatial management policy largely continues to be guided by mean species-level estimates of dispersal and movement (Holyoak et al. 2008). Our data show that our ability to accurately predict animal movements in a community could be greatly improved by prior knowledge of individual movement behavioral types. Accordingly, research into methods to quickly identify movement behavioral types should be prioritized. As habitats become increasingly fragmented (Fahrig 2003), there is a pressing need to understand and mitigate the impacts of barriers to migration on individual variation in movement distances (Hirsch et al. 2017). Given the importance of variation in animal movements in facilitating an adaptive response to environmental change (Sih et al. 2011; Bestion et al. 2015), conservation of the type of intraspecific diversity in movement documented here, may prove important for the conservation of animal communities in the Anthropocene.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Data (Harrison et al. 2019) are archived and freely, publicly, and permanently available in the MacOdrum Library Data Repository, Carleton University Dataverse. <https://doi.org/10.5683/SP2/AP28O3>.

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