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Repeatability of movement behaviour in a wild salmonid revealed by telemetry

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Movement estimates derived from sub-daily tracking of radio-tagged bull trout *Salvelinus confluentus* on the Columbia River, British Columbia, Canada, were used to test whether interindividual variation in behaviour was repeatable among contexts, both short- and long-term. Interindividual variation in *S. confluentus* behaviour was consistent across contexts. These findings emphasize the potential for telemetry as a tool in animal personality and temperament research.

Key words: behavioural syndrome; bull trout; personality; temperament.

Movement is a behaviour that enables fishes to respond to changing environmental conditions to maximize growth, survival and reproductive success (Kahler *et al.*, 2001). Movement is also important as it explains why and how fishes are distributed in both space and time (Lucas *et al.*, 2001). For example, knowledge of critical habitats and the movements among them is important for the protection of threatened species (Simpson & Mapleston, 2002; Ebner & Thiem, 2009). Movement and dispersal data can be used to refine stocking practices (Karam *et al.*, 2008) and control programmes for invasive fishes (DeGrandchamp *et al.*, 2008).

Recent reviews have provided examples of how behaviour influences animal fitness (Dingemanse & Réale, 2005; Smith & Blumstein, 2008). For example, the relationship between movement and growth is a modern subject in fish behaviour research (Conrad *et al.*, 2011). Mark–recapture studies have demonstrated a positive relationship between growth and movement in stream fish populations (Skalski & Gilliam, 2000; Fraser *et al.*, 2001; Kahler *et al.*, 2001; Petty & Grossman, 2004). The consistency of their movement patterns, however, was not addressed; these studies only used one to two movement estimates per fish. In fact, relatively little research has examined the repeatability of fish behaviour over time (Conrad *et al.*, 2011) which is

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problematic when making assumptions about the fitness consequences of behaviour. Mark–recapture studies with infrequent recaptures may not be useful for behaviour fitness research because one or two movement estimates may not be representative of individual behaviour as a whole, or across different contexts (*e.g.* temperature, ontogeny or prey densities). In addition, the repeatability of a given behaviour is a prerequisite to identifying a fish's temperament, the idea that interindividual differences in behaviours are intrinsic to the animal (*i.e.* repeatable over time and across situations; Réale *et al.*, 2007). Temperament traits have been shown to have implications for artificial propagation, habitat restoration and invasive species management (Conrad *et al.*, 2011).

Few have studied interindividual variation in behaviour of wild fishes using many location estimates over long periods of time (>1 month; Hanson *et al.*, 2010), perhaps because of the logistical constraints of estimating movements from free-ranging animals. Sophisticated radio and acoustic telemetry is now available to track fish movements (Cooke *et al.*, 2012), yet researchers have not yet begun to use this technology to examine the consistency of individual-level behaviours. Tracking the spontaneous movement of fishes in the wild, using telemetry, imposes no physical constraints on the range of fish movements other than natural barriers in the aquatic environment.

Distance travelled per time period (*i.e.* rate; average or maximum) is a common metric calculated from point locations of telemetered fishes (Cooke *et al.*, 2012) and used to describe their behaviour (Lucas & Baras, 2000). The purpose of this study was to test for the consistency of individual behaviour between different contexts, using data collected from telemetered bull trout *Salvelinus confluentus* (Suckley 1859) on the Columbia River, Canada. The objectives were to determine if interindividual variation in movement distances were repeatable among: (1) diel periods (am and pm) and (2) autumn and spring.

The study site was the hydropeaking reach of the Columbia River between Revelstoke Dam (REV) and the downstream Arrow Lakes Reservoir in British Columbia, Canada. Detailed site and species descriptions are found in the study of Taylor *et al.* (in press). *Salvelinus confluentus* movements were estimated from manually tracking their location during a companion study of *S. confluentus* swimming muscle activity using electromyogram (EMG) radio-transmitters (CEMG2-R16-25; dimensions: 16 mm × 62 mm, mass: 25 g in air; Lotek Wireless; www.lotek.com; mean tag:body mass = 1·4%, range = 0·4–2·6%). Details of *S. confluentus* capture and surgical methods are also found in the study of Taylor *et al.* (in press).

Daily tracking sessions occurred at noon and midnight with the exception of some days (*c.* one session per week) to allow for rest and recovery of the trackers. Each session lasted *c.* 3 h and involved a scan of the entire study area. Tracking was conducted on shore, by foot, using a two-person team equipped with a three-element Yagi antenna (www.zx-yagi.com) and a Lotek SRX600 receiver. Successive gain reduction techniques (*i.e.* zero point tracking) were used whereby *S. confluentus* position was identified by successively reducing the gain until one was as close to the fish as possible on the adjacent shore.

Once directly adjacent to the *S. confluentus* (distance from the fish depended on the width of the river at each location), the longitudinal location was determined by standing on shore at 90° to the thalweg and recording a waypoint into the GPS (Garmin 60CS; Lotek). Tracker location error was estimated to range from 1 to 50 m, depending on water depth and safe access to shoreline. In order to ensure that movement estimates represented true movements and not location error, *S. confluentus* were only considered to have moved if re-locations were at least 100 m apart. The location error was considered too large to reliably detect lateral positions in river cross-section; therefore, movements were longitudinal only.

The differences in river distance between *S. confluentus* locations at time T_i and T_{i-1} were used as a movement estimate for each individual, for each 12 h period. All 12 h movement estimates were collapsed into one mean and one maximum value for each *S. confluentus* during each context. A Spearman rank correlation coefficient was used to test for a relationship between the ranked individual mean (and maximum) movement distances (*i.e.* one value per fish per context) in different contexts. The different contexts were season (autumn 2008 *v.* spring 2009) and diel period (am *v.* pm in both seasons). The physical conditions in the Columbia River were different between contexts. For example, water temperatures were 8·8° C in the autumn *v.* 5·5° C in the spring. Mean discharge was 636·0 $\text{m}^3\ \text{s}^{-1}$ in the autumn *v.* 576·0 $\text{m}^3\ \text{s}^{-1}$ in the spring. Mean water temperature was 7·1° C in the am *v.* 7·2° C in the pm. Mean discharges were 617·0 $\text{m}^3\ \text{s}^{-1}$ in the am *v.* 591·2 $\text{m}^3\ \text{s}^{-1}$ in the pm.

The effect of body size on movements was evaluated as swimming performance can scale with size (Brett, 1965). A significant correlation between fork length (L_F) and individual mean movement (y_mean) was found [GLM, $y_\text{mean} = -4{\cdot}036$ ($\pm 1{\cdot}740$ S.E.) $+ 0{\cdot}008$ ($\pm 0{\cdot}003$ S.E.) (L_F); $t = 3{\cdot}23$, $P = 0{\cdot}01$, $r^2 = 0{\cdot}14$]. A significant correlation was also found between *S. confluentus* L_F and individual maximum movement (linear range, y_max) [GLM, $y_\text{max} = -32{\cdot}631$ ($\pm 24{\cdot}930$) $+ 0{\cdot}110$ ($\pm 0{\cdot}037$) (L_F); $t = 2{\cdot}96$, $P = 0{\cdot}01$, $r^2 = 0{\cdot}12$]. Therefore, movements were size-adjusted by dividing the mean or maximum movement distance (one value per individual) by each respective body size before further analysis (Kolok, 1999). The same regressions were used to check for individual variation in movement that could be attributed to the number of times an *S. confluentus* was located; no adjustments for relocation success were needed.

Thirty-two *S. confluentus* were tagged and released, but only fish that were located in the study area during both seasons were included in the analysis ($n = 17$). Some *S. confluentus* overwintered in the downstream Arrow Lakes Reservoir and did not return to the hydropeaking reach below REV the following spring. Others moved to the reservoir following tagging, but then returned to the hydropeaking reach the following spring. *Salvelinus confluentus* were not tracked in the reservoir because of the attenuation of radio-signals in deep water, but mostly because of the main interest in relating swimming muscle activity to hydrologic conditions associated with hydropeaking (Taylor *et al.*, in press). Furthermore, because tracking occurred for 45 days in the spring (during the period 21 April to 15 June 2009), only the last 45 days of autumn tracking data (20 October to 8 December 2008) were used for this analysis to achieve a balanced comparison. Generally, *S. confluentus* were at-large in the river for at least 2 weeks before the data were used in this analysis to ensure that the tagging procedure itself did not affect their behaviour.

On average, *S. confluentus* moved at least 100 m once every second 12 h time period between tracking sessions in the autumn, and once every fourth period between tracking session in the spring. When they did move, individual mean 12 h movements ranged from 8 to 1153 m in the autumn and 24 to 279 m in the spring. Individual maximum 12 h movements ranged from 183 to 7777 m in the autumn and 285 to 5838 m in the spring.

Mean 12 h movement distances in the autumn were significantly correlated with mean 12 h movement distances of the same individuals in the spring [$r_S = 0{\cdot}78$, P (one-tailed) $< 0{\cdot}001$; Fig. 1(a)]. Maximum 12 h movement distances in the autumn were also significantly correlated with maximum 12 h movement distances of the same individuals in the spring [$r_S = 0{\cdot}49$, P (one-tailed) $= 0{\cdot}05$; Fig. 1(b)].

On average, *S. confluentus* moved at least 100 m once every third 12 h time period between tracking sessions during the am and once every third period between tracking sessions in the pm. When they did move, individual mean 12 h movements ranged from 24 to 725 m during the am and 28 to 590 m during the pm. Individual maximum 12 h movements ranged from 402 to 5247 m during the am and 482 to 1296 m in the pm.

Mean 12 h movement distances in the am (midnight to noon) were significantly correlated with mean 12 h movement distances of the same individuals in the pm [noon to midnight; $r_S = 0{\cdot}81$, P (one-tailed) $< 0{\cdot}001$; Fig. 2(a)]. Maximum 12 h movement distances in the am (midnight to noon) were significantly correlated with maximum 12 h movement distances of the same individuals in the pm [noon to midnight; $r_S = 0{\cdot}62$, P (one-tailed) $< 0{\cdot}001$; Fig. 2(b)].

It was revealed that interindividual variation in *S. confluentus* movement behaviour was repeatable across two contexts (diel period and season). This may suggest that relatively fewer movement estimates are needed to classify individuals with different behaviours within a population, *e.g.* classifying individuals as belonging to a mobile or static population. Individual differences in movement may be a behavioural manifestation of individual variation in resting metabolic rate (Nespolo & Franco, 2007; Careau *et al.*, 2008). Animals with relatively large growth rates have higher resting metabolic rates (Książek *et al.*, 2004) and this increased metabolic demand may result in relatively higher activity rates. Indeed, this relationship has been shown in Atlantic salmon *Salmo salar* L. 1758 (Cutts *et al.*, 1998) and Arctic charr *Salvelinus alpinus* (L. 1758) (Cutts *et al.*, 2001).

The repeatability of movement behaviour in fishes has received little attention outside of laboratory studies that examined behavioural traits such as boldness and exploration (Coleman & Wilson, 1998) and swimming capacity (Kolok, 1992; Claireaux *et al.*, 2007). Considering the disparity between animal behaviour in laboratory and field assessments (Irschick, 2003; Irschick *et al.*, 2005), volitional

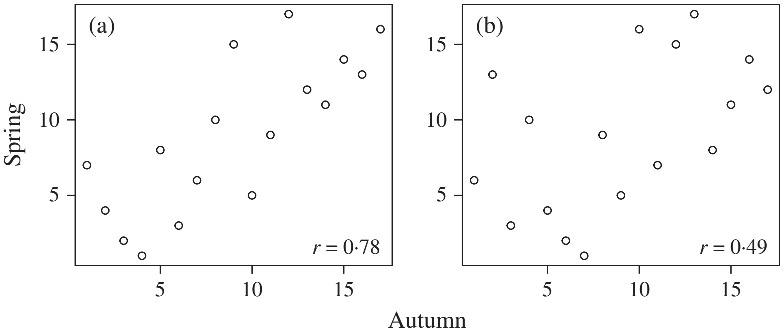

FIG. 1. Ranked movements of individual *Salvelinus confluentus* (one value per individual) in spring relative to autumn (a) mean movement distance and (b) maximum movement distance.

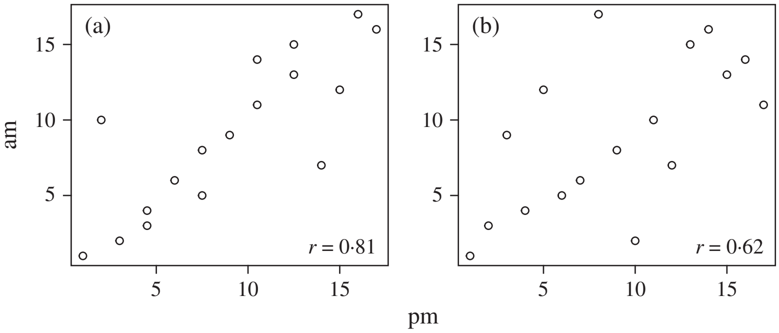

Fig. 2. Ranked movements of individual *Salvelinus confluentus* (one value per individual) in the am relative to the pm (a) mean movement distance and (b) maximum movement distance.

behaviour of free-swimming fishes may be a more relevant metric to test theories about individual behaviour in these animals.

Significant heterogeneity in behaviour of fishes has been identified using mark–recapture studies in the field (Skalski & Gilliam, 2000; Fraser *et al.*, 2001; Kahler *et al.*, 2001; Petty & Grossman, 2004). The stabilities of these interindividual variations were tested using relatively low temporal resolution; often such analyses used only one to two location estimates per fish over the period of 6 months to 2 years. Significant long-term repeatability of interindividual variation in behaviour of free-ranging fishes could not be found in the literature and can probably only be derived from telemetered fishes. This study used individual *S. confluentus* movement estimates that were established using multiple relocations per context (mean ± s.d. = 67·5 ± 12·5 relocations per individual across all contexts). Despite the fact that telemetry can be used to generate movement estimates with relatively higher temporal resolution than mark–recapture estimates, researchers have not exploited this technology in fundamental studies of fish behaviour.

A notable exception is the work by Hanson *et al.* (2007, 2010) using acoustic telemetry technology. For example, Hanson *et al.* (2007) found that maximum daily swimming speed of free-swimming largemouth bass *Micropterus salmoides* (Lacépède 1802) was repeatable across the parental care period (1 month). Hanson *et al.* (2010) found that wild *M. salmoides* formed consistent individual movement hierarchies within seasons, but not between seasons. In contrast, the results presented here demonstrate that interindividual movements of *S. confluentus* were consistent across at least two seasons.

Perhaps, the most important implication for the repeatability of interindividual fish movements is that it demonstrates the potential for movement behaviour to be classified as temperament (Réale *et al.*, 2007) or a behavioural syndrome (Conrad *et al.*, 2011) with implications for evolutionary ecology. Conrad *et al.* (2011) defined ‘activity syndrome’ as ‘individual consistency in activity’. Interindividual consistency in movement behaviour cannot be considered a ‘syndrome’, as behavioural syndromes are usually a correlated suite of variables (*e.g.* boldness and aggression). Although the present data may suggest that *S. confluentus* exhibit a ‘temperament’ according to some definitions, the strictest meaning of the term is reserved for behavioural ‘traits’ which, by definition, are heritable. Nevertheless, repeatability provides initial evidence that interindividual variation in behaviour is intrinsic to the individual, but does not necessarily prove genetic heritance. Indeed, for natural selection to occur a trait must possess repeatable variation among individuals, be determinant of an individual's fitness and be heritable (Falconer & McKay, 1996). Research has shown that fishes exhibit considerable interindividual variation in movement behaviour; it is the norm in fish telemetry studies (Taylor & Cooke, 2012). Published reviews on behavioural syndromes in fishes have demonstrated links between behaviour and fitness (Conrad *et al.*, 2011). Only a limited amount of research has been conducted on the heritability of behaviour, *e.g.* the heritability of activity in three-spined sticklebacks *Gasterosteus aculeatus* L. 1758 (Bell, 2005). This study should encourage researchers to examine heritability of movement behaviour in order to determine if it is a relevant selection trait.

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