

Boldness and intermittent locomotion in the bluegill sunfish, *Lepomis macrochirus*

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Intermittent locomotion, characterized by moves interspersed with pauses, is a common pattern of locomotion in animals, but its ecological and evolutionary significance relative to continuous locomotion remains poorly understood. Although many studies have examined individual differences in both intermittent locomotion and boldness separately, to our knowledge, no study to date has investigated the relationship between these 2 traits. Characterizing and understanding this relationship is important, as both locomotion and boldness are associated with several ecologically relevant behaviors such as foraging, mating, predator evasion, exploration, and dispersal. Here, we report on individual differences in boldness (risk-taking behavior) and intermittent locomotion in a novel laboratory environment in field-caught juvenile bluegill sunfish (*Lepomis macrochirus*). Our results show that juvenile bluegill sunfish exhibited individual-level variation in 2 modes of intermittent locomotion (undulatory and labriform swimming) and that this variation was correlated with differences in their boldness behavior. Generally, bolder individuals spent more time moving fast for longer durations and with shorter pauses than more timid individuals. Neither boldness nor locomotion was correlated with body size or body condition. This study provides the first empirical evidence for a link between an animal "personality" trait and intermittent locomotion. *Key words:* activity, exploration, labriform swimming, personality, risk taking, undulatory swimming. [*Behav Ecol* 21:57–62 (2010)]

Animals exhibit diverse patterns of locomotion, depending in part on habitat, ecological context, body form, and ontogenetic stage (e.g., McAdam and Kramer 1998; Kramer and McLaughlin 2001; Higham 2007). Understanding the nature of interindividual variation in animal locomotion is of considerable importance to evolutionary and behavioral ecologists as many important behaviors, including foraging, mating, predator evasion, exploration, and dispersal, all necessitate some level of movement. Until recently, most studies on animal locomotion have implicitly assumed that movement is steady state, involving long bouts of continuous movement at relatively slow speeds (reviewed in Kramer and McLaughlin 2001). However, most animals instead move by performing bursts of movement punctuated by stationary pauses of variable duration (Kramer and McLaughlin 2001). Such a pattern of locomotion is referred to as intermittent or saltatory locomotion (Kramer and McLaughlin 2001; McLaughlin and Grant 2001; Trouilloud et al. 2004).

Intermittent locomotion is widespread taxonomically and has been documented in numerous invertebrate and vertebrate species (reviewed in Kramer and McLaughlin 2001). Furthermore, this pattern of locomotion is strongly associated with individual differences in general activity, exploration, antipredator or vigilance behavior (Trouilloud et al. 2004), foraging (McLaughlin and Grant 2001), and other related behaviors (Kramer and McLaughlin 2001). However, although some studies have touched on the underlying perceptual and energetic bases for intermittent locomotion (Gleeson and Hancock 2001; McLaughlin and Grant 2001; Hancock and Gleeson 2005), to our knowledge, no study has yet examined this form of locomotion in the context of animal "personality" (*sensu* Réale et al. 2007) and what role personality may play in its underlying mechanistic basis.

Animal personality, or temperament, has broadly been defined as consistency in an individual's behavioral responses over time and/or situations (Réale et al. 2007). One axis of behavioral variation, which has potentially important implications for behavioral ecology and particularly the study of intermittent locomotion, is that of boldness. Boldness is a personality trait that is characterized by individual differences in willingness to explore and take risks in a variety of behavioral contexts (Wilson et al. 1994; Ward et al. 2004; Webster et al. 2007; Wilson and Godin 2009). Although variation in both intermittent locomotion and boldness has been separately observed in some species (e.g., Eastern chipmunk, *Tamias striatus*, Trouilloud et al. 2004; Martin and Réale 2008; brook charr, *Salvelinus fontinalis*, McLaughlin and Grant 2001; Farwell and McLaughlin 2009), surprisingly no attempt has been made to characterize and understand the relationship between these 2 behavioral traits at the individual level.

Boldness, like intermittent locomotion, is associated with individual differences in general activity (Wilson and McLaughlin 2007), exploration and antipredator behavior (Brown et al. 2005; Wilson and Godin 2009), mating (Godin and Dugatkin 1996), and dispersal (Fraser et al. 2001). Furthermore, several studies have posited that boldness is linked to fitness-related traits (Smith and Blumstein 2008), is heritable (Dingemanse et al. 2004; Sinn et al. 2006), and subject to selection (Réale and Festa-Bianchet 2003; van Oers et al. 2004). Thus, should boldness also be associated with intermittent locomotion, studying this relationship may offer further insights into the ecological and evolutionary implications of personality traits and animal movement, as well as their underlying mechanistic bases.

Here, we investigated the potential relationship between boldness behavior and aspects of intermittent locomotion in individual field-caught juvenile bluegill sunfish (*Lepomis macrochirus*). We characterized this relationship by exposing individual sunfish to an open arena test in the laboratory and quantifying their willingness to take risks and explore a novel environment. Our primary focus in this study was to ascertain how individuals moved while exploring and assessing

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Received 18 March 2009; revised 20 October 2009; accepted 20 October 2009.

potential risk. Sunfish are ideal candidates for studies of intermittent locomotion and boldness for a number of reasons. First, they exhibit 2 kinematically distinct modes of swimming: labriform swimming at lower speeds and undulatory swimming at higher speeds (Jones et al. 2007; Kendall et al. 2007). Labriform locomotion occurs when both lift and thrust are generated through the use of the pectoral fins without flexing the long body axis. In contrast, undulatory locomotion involves primarily the caudal fin and undulations of the long body axis to generate thrust. Second, sunfish exhibit distinct morphological and behavioral variation in relation to individual differences in habitat and resource use (Robinson et al. 1993; Skúlason and Smith 1995) and are commonly used to study fish locomotion (e.g., Jones et al. 2007; Kendall et al. 2007) and personality (e.g., Wilson et al. 1993; Coleman and Wilson 1998; Wilson and Godin 2009). Lastly, our recent mark-recapture study (Wilson and Godin 2009), on the same individuals as those used in the current study, demonstrated that aspects of boldness behavior are consistent in the field and the laboratory for individual juvenile sunfish and can be repeatable for at least 6–8 weeks in the wild.

MATERIALS AND METHODS

Field collection of subjects

Between 25 June and 7 August 2007, we collected 60 juvenile (year 1+) bluegill sunfish (fork length: 6.2–8.3 cm; weight: 3.55–9.17 g) from the littoral zone of a small bay in Patterson Lake, Ontario, Canada, using a 10-m beach seine. Captured individuals were placed in a cooler containing lake water (mean temperature = 23.1 °C) and transported to our laboratory at Carleton University (transit time ~1.5 h). Ten individuals were captured during each collection period, once per week. Patterson Lake is a small north temperate lake (<3 km² total area); it is a high-predation environment containing many piscivorous fishes (e.g., smallmouth and largemouth bass, northern pike, and pickerel) and birds (e.g., belted kingfisher, northern loon, and great blue heron).

Experimental holding conditions and general experimental apparatus

On arrival at the laboratory, each wild-caught fish was placed singly into the “refuge” area of 1 of 10 identical glass aquaria (82 l, 92 × 30 × 30 cm; Figure 1), similar to those used by Wilson and Godin (2009). Each aquarium contained aerated and filtered dechlorinated tap water maintained at 23 ± 1 °C and a gravel substratum. All aquaria were exposed to overhead fluorescent lighting on a 12:12 h light:dark cycle. Each aquarium was “divided” into thirds both horizontally and vertically with lines drawn on the front and back walls. In doing so, 9 distinct zones were delineated to facilitate the recording of fish water-column use. The refuge area was located at one end of the aquarium, contained a corner filter and a plastic aquarium plant for cover, and was separated from the remainder of the aquarium by an opaque white plastic partition equipped with a sliding door (9 × 12 cm; Figure 1). This gated partition was located 25 cm from the left side of the aquarium. All aquaria were covered externally with tan cardboard at both ends and the back wall to prevent interaction between subjects in other aquaria. To avoid any confounding effects associated with olfactory cues from conspecifics, the water in all experimental aquaria was replaced with new water between trials.

All aquaria were placed behind an observation blind to minimize external disturbance and to facilitate the recording of behavioral trials. All trials were recorded using a Digital8 video camera (Sony DCR-TRV280), and fish behaviors were quanti-

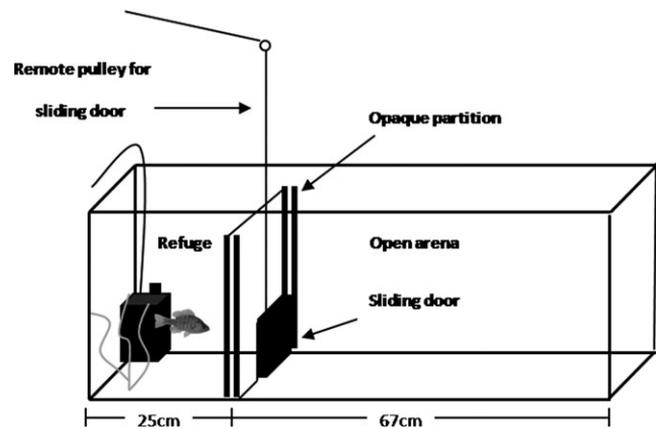


Figure 1
Schematic representation of the experimental aquarium used to quantify boldness and intermittent locomotion behaviors of individual juvenile bluegill sunfish in the laboratory.

fied from the tapes using the behavioral analysis software JWatcher (v1.0) (Blumstein and Daniel 2007).

Measures of boldness (risk taking) behavior in a novel environment

Approximately 24 h after arrival in the laboratory, individual sunfish were tested in their respective aquarium for their level of boldness in a novel environment (Figure 1). At the onset of each behavioral trial, the sliding door of the test aquarium was lifted manually via a remote pulley system operated from behind the blind. The test fish was then able to enter and swim freely throughout the remaining open area of the aquarium (hereafter the “arena”). Each fish was given a maximum of 60 min to exit the refuge area and explore the arena. On exiting the refuge, several measures of individual boldness were quantified for 10 min. These boldness measures were latency to emerge from the refuge area, general activity in the open arena, and total time spent in the upper third of the water column of the arena. Increased general activity, emergence from a refuge, and time spent near the water surface are behaviors that are inherently risky and that may increase the risk of predation in animals, particularly fishes (e.g., Lima and Dill 1990; Godin 1997; Sih 1997; Wilson and McLaughlin 2007). Here, we defined latency to exit the refuge as the total time elapsed from the moment the gated door was raised to the focal fish completely exiting the refuge area during the 60 min pretrial period. Those individuals that did not exit within 60 min ($n = 13$) were excluded from any further behavioral trials and analyses. Because we were primarily interested in measures of risk taking, behaviors were only quantified while the focal fish was in the presumably more risky open arena of the aquarium, not in the refuge. We quantified general activity as the total time the focal fish spent active (vs. being sedentary) outside the refuge in the open arena. Moreover, activity in the open arena was categorized by swimming mode and intermittent locomotion, as outlined below.

Measures of intermittent locomotion

The locomotor activity of individual test fish was quantified from trial videotapes using JWatcher (v1.0) as follows. For each individual fish, the number and duration of stationary pauses during the 10-min trial were recorded. A pause was defined as an interruption of self-propelled motion, wherein the

fish was either at rest on the substrate or maintaining a stationary position in the water column through use of only the pectoral and anal fins. Activity was quantified as time spent moving “fast” (>3 cm/s) and time spent moving “slow” (<3 cm/s). Based on our frame-by-frame analysis of the videotapes, we note that this threshold swimming speed (3 cm/s) corresponds to the transition between labriform and undulatory modes of locomotion in juvenile bluegill sunfish in our experimental aquaria. Fast movement, or undulatory swimming, typically incorporated the caudal fin as the main means of propulsion, with comparatively minimal contribution to forward motion from other fins. In contrast, slow movement, or labriform swimming, generally involved a gentle sculling movement of the pectoral fins, with little input from the caudal fin. For all forms of activity, the number of bouts of activity, the duration of each bout, and the mean duration of bouts overall were quantified. Any movement of the body forward or backward, irrespective of fin use, was recorded as activity. It was not possible to consistently assess speeds of movement accurately beyond the conservative measure provided here, and therefore, we do not provide an estimate of distance travelled within the arena during trials. All videotape analyses were performed blind with respect to individual fish identity to minimize risk of observer bias.

At the end of an experimental trial, the standard length (SL) and wet weight (W) of the focal individual were recorded and its body condition calculated as $[W \text{ (g)}/SL^3 \text{ (cm)}] \times 100$ (Bolger and Connolly 1989).

Data analyses

First, comparisons of individual boldness and locomotory traits within the context of exploration and risk taking in a novel environment were made using the nonparametric Spearman rank correlation test. Second, to test for any relationships between boldness and modes of intermittent locomotion more directly, boldness and locomotory traits (fast/undulatory and slow/labriform) were collapsed into first principal component (PC1) scores for each axis using principal components analysis (PCA) (Table 1). Correlations between PC1 scores for boldness and locomotion traits were then calculated using the Spearman rank correlation test as above. To minimize Type I errors in our statistical analyses, the alpha level ($\alpha = 0.05$) was adjusted to be more conservative using the sequential Bonferroni correction (Rice 1989).

Table 1
PCA loadings of behavioral and locomotory variables used to generate a PC1 score to assess correlations between boldness and modes of intermittent locomotion in individual juvenile bluegill sunfish

Trait	Behaviors within each context	Loadings for PC1	% Variation explained
Boldness	Latency to emerge from refuge	-0.7071	72.7
	Time spent near water surface	0.7071	
Intermittent locomotion (undulatory/fast swimming)	Time spent swimming fast	0.7071	77.6
	Mean duration of sedentary pause	-0.7071	
Intermittent locomotion (labriform/slow swimming)	Time spent swimming slow	0.7071	64.4
	Mean duration of sedentary pause	0.7071	

RESULTS

Correlations across behavioral and locomotion traits

These correlations are pairwise Spearman rank correlations ($n = 47$ fish). In general, individual fish that spent more time moving fast (>3 cm/s) exhibited shorter latencies to emerge from the refuge ($r_s = -0.77$, $P < 0.0001$; Figure 2a), shorter sedentary pauses ($r_s = -0.80$, $P < 0.0001$; Figure 2b), and longer bouts of activity ($r_s = 0.72$, $P < 0.0001$) than individuals that moved more slowly (<3 cm/s). Faster individuals also spent more time near the water surface (upper third of water column; $r_s = 0.44$, $P = 0.002$; Figure 2c).

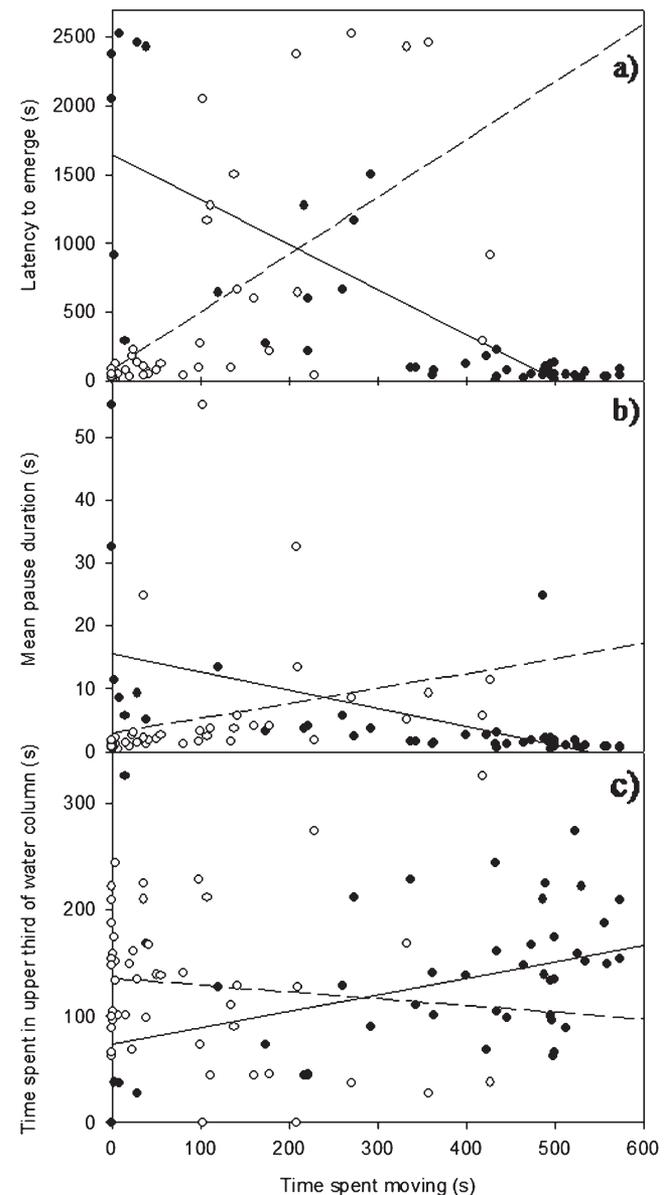


Figure 2
Individual differences in latency to emergence from a refuge (a), sedentary pause duration (b), and time spent near the water surface (c) in relation to undulatory (fast) and labriform (slow) swimming behavior in juvenile bluegill sunfish. Each data point represents an individual ($n = 47$). Open circles and dashed lines represent values for time spent moving slowly (<3 cm/s). Closed circles and solid lines represent time spent moving fast (>3 cm/s). Each line represents a line-of-best-fit through the relevant data obtained from a least-square regression.

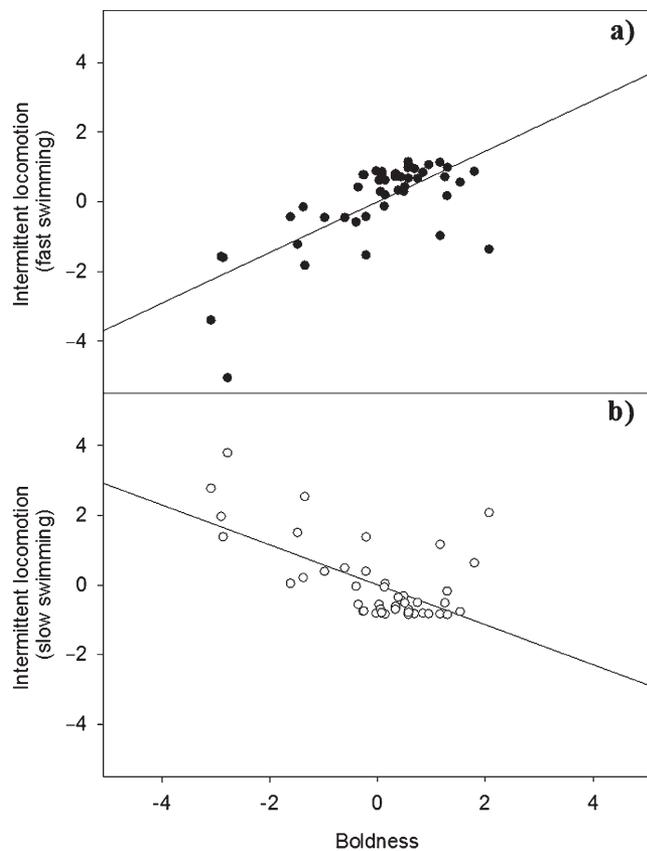


Figure 3
Individual differences in modes of intermittent locomotion (undulatory/fast, a; labriform/slow, b) relative to boldness in juvenile bluegill sunfish ($n = 47$) in a novel environment. Each data point represents an individual's PC1 score for each trait shown. For each panel, the line shown represents a line-of-best-fit through the data obtained from a least-square regression.

In contrast, those individuals that spent more time moving slowly tended to prefer the lowest third ($r_s = 0.42$, $P = 0.0032$) over the upper third of the water column ($r_s = -0.21$, $P = 0.1617$; Figure 2c) and, as expected, took longer to emerge from refuge ($r_s = 0.75$, $P < 0.0001$; Figure 2a) and had longer sedentary pauses ($r_s = 0.77$, $P < 0.0001$; Figure 2b) while in the open arena. Body size (SL and weight) and body condition were not significantly correlated with any boldness or locomotory traits (all $P > 0.05$, Bonferroni corrected).

PCA of boldness and intermittent locomotion traits

The PC1 scores for boldness and intermittent locomotion behavior of sunfish in a novel environment (Table 1) were significantly correlated with each other. More specifically, boldness was strongly positively correlated with undulatory or fast swimming ($r_s = 0.58$, $P < 0.0001$; Figure 3a) but conversely negatively correlated with labriform or slow swimming ($r_s = -0.46$, $P = 0.001$; Figure 3b). Neither boldness nor locomotion PC1 scores were correlated with body size or body condition (all $P > 0.05$, Bonferroni corrected).

DISCUSSION

We found that juvenile bluegill sunfish exhibited interindividual differences in modes of intermittent locomotion, which in turn were correlated with differences in their boldness (risk

taking) behavior. Although bold and timid individuals may have utilized both undulatory and labriform modes of locomotion, the amount of time spent in each mode and their associated pauses differed between behavioral types. Generally, bolder individuals spent more time moving fast (undulatory swimming) for longer durations and with shorter pauses than more timid, slower moving (labriform swimming) individuals. Correspondingly, as revealed by our PCA, bolder individuals had higher intermittent locomotion scores when moving fast and conversely lower intermittent locomotion scores when moving slowly and vice versa for timid individuals. To our knowledge, the current study is the first to have characterized the relationship between intermittent locomotion and boldness in any species.

Our findings are novel and important to behavioral ecologists, as both boldness and intermittent locomotion are associated with foraging, mating, exploration, dispersal, and antipredator behaviors in animals (Kramer and McLaughlin 2001; Sih et al. 2004; Dingemanse and Réale 2005; Réale et al. 2007). Indeed, in a related study (Wilson and Godin 2009) on the same individual sunfish that were used in the current study, we found that boldness variables (i.e., refuge emergence and distance from refuge) were highly correlated with individual differences in exploration and general activity in multiple behavioral contexts, forming a behavioral syndrome. Furthermore, we demonstrated that these interindividual differences in behavior were both consistent and repeatable in the field as part of a mark-recapture study over a period of 2 months (Wilson and Godin 2009).

To date, intermittent locomotion has typically been considered only in the contexts of foraging and vigilance or antipredator behavior (e.g., McAdam and Kramer 1998; Kramer and McLaughlin 2001; Trouilloud et al. 2004). We suggest that this type of locomotion may also play an important role in general exploration and risk assessment in novel environments and/or situations. Intermittent locomotion may therefore offer a novel paradigm to evaluate animal personality (i.e., boldness) and, more specifically, to predict behaviors of important ecological interest, such as dispersal tendency and invasiveness. For example, previous studies have suggested that bolder individuals are not just more active but also tend to disperse further than more timid individuals (e.g., Fraser et al. 2001; Dingemanse et al. 2003). Because boldness is both heritable and subject to selection (e.g., Dingemanse et al. 2002; Réale and Festa-Bianchet 2003; Sinn et al. 2006), the relationship between boldness and intermittent locomotion, described herein, may offer new insight into the origin of these individual-level differences in behavior and how they are maintained in natural populations.

Previous studies on intermittent locomotion have focused primarily on energetic explanations for individual-level differences or on morphological correlates of such movement (e.g., Brana 2003; Trouilloud et al. 2004). Comparatively few studies have considered possible perceptual or behavioral (functional) explanations for intermittent locomotion. Kramer and McLaughlin (2001) suggested that self-motion can interfere with visual perception or visual acuity. Though sensory systems are inherently designed to reduce such interference, animals commonly exhibit bursts of movement interspersed with short stationary pauses while foraging (McLaughlin and Grant 2001; Trouilloud et al. 2004) or when exhibiting antipredator behavior (e.g., predator inspection; Dugatkin and Godin 1992). It is therefore possible that such pauses facilitate the visual assessment of environmental cues within the animal's visual field (cf., Kramer and McLaughlin 2001). However, this hypothesis remains untested and does not exclude metabolic or energetic factors determining such interindividual differences in locomotion.

Fishes exhibit considerable variation in swimming speeds (i.e., undulatory/labriform swimming), which, in addition to energetic considerations (e.g., muscle type ratios; metabolic rate), may reflect adaptive processes allowing for more effective sensory processing and risk assessment. For example, the likelihood of detecting a potential threat (e.g., predator) or food item generally increases with the duration of visual scanning-type behavior (though detection is also influenced by head/eye movement and interscan intervals; Hart and Lendrem 1984; Bednekoff and Lima 2002) in animals. However, such a relationship may be constrained by the higher levels of activity (Barros et al. 2004) commonly exhibited by bold individuals (Kortet and Hedrick 2007; Webster et al. 2007; Wilson and Godin 2009), irrespective of locomotory pause frequency and duration.

In the current study, we found no differences in body size or body condition between timid and bold sunfish, suggesting that these fish had similar energetic states. Recent work on juvenile bluegill sunfish (Binder TR, Wilson ADM, unpublished data) has revealed that individual differences in boldness (as measured by latency to exit a refuge) do not appear to be related to underlying individual differences in standard metabolic rate. The above proposition is also supported by similar findings in other fishes testing for individual differences in body size or metabolic rate relative to boldness or locomotory behavior (e.g., Sundström et al. 2004; Farwell and McLaughlin 2009). Furthermore, because interindividual variation in boldness can be influenced by experience (Wilson et al. 1993; Frost et al. 2007; Martin and Réale 2008), it is likely that individual differences in perceptual ability and experience represent important correlates of boldness and intermittent locomotion irrespective of the possible involvement of energetic factors.

Nonetheless, the energetic basis of individual variation in boldness, as with intermittent locomotion, and its relationship to fitness correlates is a subject of current interest (Réale et al. 2007; Careau et al. 2008; Smith and Blumstein 2008). The relationship between the shy–bold axis of personality and intermittent locomotion, which we characterized here for the first time using the bluegill sunfish, offers an opportunity to investigate such interindividual variation in behavior from a physiological perspective, incorporating both genetic and condition-dependent factors (e.g., red:white muscle index, liver glycogen, and fat stores). Furthermore, much as boldness varies between behavioral contexts (e.g., Coleman and Wilson 1998; Wilson and Stevens 2005; Webster et al. 2007), so does the behavior of individuals exhibiting intermittent locomotion (current study). Patterns of intermittent movement vary with changes in the type of behavior exhibited by individual animals (e.g., changes in habitat, foraging, and vigilance; Kramer and McLaughlin 2001). However, the inherent trade-offs associated with changes in exploratory, foraging, and antipredator behaviors remain largely unknown in the context of intermittent locomotion and represent a subject for further investigation.

FUNDING

The Natural Sciences and Engineering Research Council of Canada (Discovery research grant to J.-G.J.G., postgraduate scholarship to A.D.M.W.).

We thank S. Lee-Jenkins for assistance in collecting fish in the field, R. Bell for permission to access Patterson Lake, the Ministry of Natural Resources of Ontario for the necessary fish collection permit, and 2 anonymous reviewers for comments on the manuscript. This study was approved by the Institutional Animal Care Committee at Carleton University (protocol B06-7) and thus adheres to the guidelines of the Canadian Council on Animal Care and the laws of Canada.

REFERENCES

- Barros M, Alencar C, Tomaz C. 2004. Differences in aerial and terrestrial visual scanning in captive black tufted-ear marmosets (*Callithrix penicillata*) exposed to a novel environment. *Folia Primatol.* 75:85–92.
- Bednekoff PA, Lima SL. 2002. Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance. *J Avian Biol.* 33:143–149.
- Blumstein DT, Daniel JC. 2007. Quantifying behavior the JWatcher way. Sunderland (MA): Sinauer Associates, Inc.
- Bolger T, Connolly PL. 1989. The selection of suitable indices for the measurement and analysis of fish condition. *J Fish Biol.* 34:171–182.
- Brana F. 2003. Morphological correlates of burst speed and field movement patterns: the behavioural adjustment of locomotion in wall lizards (*Podarcis muralis*). *Biol J Linn Soc.* 80:135–146.
- Brown C, Jones F, Braithwaite V. 2005. In situ examination of boldness-shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Anim Behav.* 70:1003–1009.
- Careau V, Thomas D, Humphries MM, Réale D. 2008. Energy metabolism and animal personality. *Oikos.* 117:641–653.
- Coleman K, Wilson DS. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim Behav.* 56:927–936.
- Dingemans NJ, Both C, Drent PJ, Tinbergen JM. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proc R Soc Lond B Biol Sci.* 271:847–852.
- Dingemans NJ, Both C, Drent PJ, Van Oers K, Van Noordwijk AJ. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim Behav.* 64:929–938.
- Dingemans NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proc R Soc Lond B Biol Sci.* 270:741–747.
- Dingemans NJ, Réale D. 2005. Natural selection and animal personality. *Behaviour.* 142:1159–1184.
- Dugatkin LA, Godin J-GJ. 1992. Prey approaching predators: a cost-benefit perspective. *Ann Zool Fenn.* 29:233–252.
- Farwell M, McLaughlin RL. 2009. Alternative foraging tactics and risk taking in brook charr (*Salvelinus fontinalis*). *Behav Ecol.* doi: 10.1093/beheco/arp059.
- Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalski GT. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *Am Nat.* 158:124–135.
- Frost AJ, Winrow-Giffen A, Ashley PJ, Sneddon LU. 2007. Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proc R Soc Lond B Biol Sci.* 274:333–339.
- Gleeson TT, Hancock TV. 2001. Modeling the metabolic energetics of brief and intermittent locomotion in lizards and rodents. *Am Zool.* 41:211–218.
- Godin J-GJ. 1997. Evading predators. In: Godin J-GJ, editor. *Behavioural ecology of teleost fishes*. Oxford: Oxford University Press. p. 191–236.
- Godin J-GJ, Dugatkin LA. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proc Natl Acad Sci USA.* 93:10262–10267.
- Hancock TV, Gleeson TT. 2005. Intermittent locomotor activity that increases endurance also increases metabolic costs in the desert iguana (*Dipsosaurus dorsalis*). *Physiol Biochem Zool.* 78:163–172.
- Hart A, Lendrem DW. 1984. Vigilance and scanning patterns in birds. *Anim Behav.* 32:1216–1224.
- Higham TE. 2007. The integration of locomotion and prey capture in vertebrates: morphology, behavior, and performance. *Integr Comp Biol.* 47:82–95.
- Jones EA, Lucey KS, Ellerby DJ. 2007. Efficiency of labriform swimming in the bluegill sunfish (*Lepomis macrochirus*). *J Exp Biol.* 210:3422–3429.
- Kendall JL, Lucey KS, Jones EA, Wang J, Ellerby DJ. 2007. Mechanical and energetic factors underlying gait transitions in bluegill sunfish (*Lepomis macrochirus*). *J Exp Biol.* 210:4265–4271.
- Kortet R, Hedrick A. 2007. A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. *Biol J Linn Soc.* 91:475–482.
- Kramer DL, McLaughlin RL. 2001. The behavioral ecology of intermittent locomotion. *Am Zool.* 41:137–153.
- Lima SL, Dill LM. 1990. Behavioral decisions under the risk of predation: a review and prospectus. *Can J Zool.* 68:619–640.

- Martin JGA, Réale D. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Anim Behav.* 75:309–318.
- McAdam AG, Kramer DL. 1998. Vigilance as a benefit of intermittent locomotion in small mammals. *Anim Behav.* 55:109–117.
- McLaughlin RL, Grant JWA. 2001. Field examination of perceptual and energetic bases for intermittent locomotion by recently-emerged brook charr in still-water pools. *Behaviour.* 138:559–574.
- Réale D, Festa-Bianchet M. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Anim Behav.* 65:463–470.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemans NJ. 2007. Integrating animal temperament within ecology and evolution. *Biol Rev.* 82:291–318.
- Rice WR. 1989. Analyzing tables of statistical tests. *Evolution.* 43:223–225.
- Robinson BW, Wilson DS, Margosian AS, Lotito PT. 1993. Ecological and morphological-differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. *Evol Ecol.* 7:451–464.
- Sih A. 1997. To hide or not to hide? Refuge use in a fluctuating environment. *Trends Ecol Evol.* 12:375–376.
- Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an integrative overview. *Q Rev Biol.* 79:241–277.
- Sinn DL, Apiolaza LA, Molschanivskyj NA. 2006. Heritability and fitness-related consequences of squid personality traits. *J Evol Biol.* 19:1437–1447.
- Skúlason S, Smith TB. 1995. Resource polymorphisms in vertebrates. *Trends Ecol Evol.* 10:366–370.
- Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. *Behav Ecol.* 19:448–455.
- Sundström LF, Petersson E, Hojesjo J, Johnsson JI, Jarvi T. 2004. Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behav Ecol.* 15:192–198.
- Trouilloud W, Delisle A, Kramer DL. 2004. Head raising during foraging and pausing during intermittent locomotion as components of antipredator vigilance in chipmunks. *Anim Behav.* 67:789–797.
- van Oers K, de Jong G, Drent PJ, van Noordwijk AJ. 2004. A genetic analysis of avian personality traits: correlated, response to artificial selection. *Behav Genet.* 34:611–619.
- Ward AJW, Thomas P, Hart PJB, Krause J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav Ecol Sociobiol.* 55:561–568.
- Webster MM, Ward AJW, Hart PJB. 2007. Boldness is influenced by social context in threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour.* 144:351–371.
- Wilson ADM, Godin J-GJ. 2009. Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behav Ecol.* 20:231–237.
- Wilson ADM, McLaughlin RL. 2007. Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Anim Behav.* 74:689–698.
- Wilson ADM, Stevens ED. 2005. Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. *Ethology.* 111:849–862.
- Wilson DS, Clark AB, Coleman K, Dearstyne T. 1994. Shyness and boldness in humans and other animals. *Trends Ecol Evol.* 9:442–446.
- Wilson DS, Coleman K, Clark AB, Biederman L. 1993. Shy bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *J Comp Psychol.* 107:250–260.