

Stability of swimming performance and activity hierarchies among wild largemouth bass at multiple temporal scales: evidence for context-dependent shuffling between seasons

K.C. Hanson, C.T. Hasler, M.R. Donaldson, and S.J. Cooke

Abstract: Laboratory-based studies of locomotory performance in many taxa have noted that individuals form stable hierarchies of organismal performance. Though laboratory studies of teleost fishes have consistently demonstrated individual repeatability of swimming performance, this phenomenon has rarely been studied in the field and never across multiple years. Using a whole-lake acoustic telemetry array with submetre accuracy, we assessed the individual repeatability of two metrics of swimming performance (daily distance traveled and mean daily swimming speed) within four seasons during a year (fall, winter, spring, and summer), among these seasons, and between winters of 2 years. Largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) formed stable performance hierarchies within seasons except spring and no sex-specific differences in rankings were noted. Individual swimming performance was not repeatable among seasons during 1 year or across multiple winters. Seasonal changes in environmental and intrinsic biological conditions appear to result in a reshuffling of performance hierarchies, perhaps reflecting individual differences in organismal physiology.

Résumé : Les études en laboratoire de la performance locomotrice chez de nombreux taxons indiquent que les individus forment des hiérarchies stables de performances organismiques. Bien que les études de laboratoire chez les poissons téléostéens montrent de façon constante la répétabilité de la performance de nage, le phénomène a rarement été étudié en nature et jamais sur plusieurs années. À l'aide d'un réseau de télémétrie acoustique couvrant un lac entier et ayant une précision de moins de 1 m, nous avons évalué la répétabilité individuelle de deux métriques de la performance de nage (la distance du déplacement quotidien et la vitesse moyenne journalière de nage) durant les quatre saisons (automne, hiver, printemps et été) d'une année, ainsi qu'entre les saisons et entre les hivers de 2 années différentes. Les achigan à grande bouche (*Micropterus salmoides* (Lacepède, 1802)) forment des hiérarchies stables de performance au cours de chacune des saisons, à l'exception du printemps et il n'existe pas de différences spécifiques au sexe dans les classements. La performance individuelle de nage n'est pas répétable d'une saison à l'autre durant une même année, ni au cours de plusieurs hivers. Les changements saisonniers des conditions environnementales et biologiques intrinsèques semblent produire un remaniement des hiérarchies des performances, ce qui reflète peut-être des différences individuelles de physiologie organismique.

[Traduit par la Rédaction]

Introduction

Evolutionary biologists have long accepted that adaptive evolution of physiological and morphological traits occurs through the natural selection of whole organism performance (Bartholomew 1958; Huey and Stevenson 1979; Arnold 1983; Feder et al. 2000; Ghalambor et al. 2003). It has been recognized that organismal performance, particularly locomotory performance, is influenced by underlying physiological mechanisms (Prosser 1955; Feder et al. 2000;

Ghalambor et al. 2003). Individual variation in suborganismal traits is rooted in differences in genetics, development, and the interplay of these factors with current environmental conditions, and can have significant outcomes for overall organismal performance (Bennett 1987; Spicer and Gaston 1999). Additionally, research into the selection of traits on the suborganismal level generally includes empirical tests of whole organism performance as the mechanistic link between phenotypic traits and adaptive evolution (Irschick 2003; Cooke et al. 2006; Peterson and Husak 2006). Con-

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tinuing research seeks to further document individual variation in organismal performance, as well as the ramifications, of such variation on individual fitness.

Historically, individual variation has been considered to be statistical noise and has often been overlooked when examining performance indicators (Bennett 1987). However, considerable evidence exists that, for many species, individual variation is substantial and repeatable (Kolok 1999). Repeatability in locomotory ability has been examined for a number of species across multiple taxa, including mammals (Chappell et al. 1995), birds (Chappell et al. 1996), reptiles (Huey and Dunham 1987; Kolok 1999; Irschick 2003), amphibians (Austin and Shaffer 1992; Kolok 1999), and fish (Kolok 1992, 1999; Reidy et al. 2000). Increasingly, experiments are modeled after the methodology proposed in Arnold (1983) that sought to link laboratory-based assessments of suborganismal traits and whole organism performance with field-based assessments of fitness. For example, in a study of Eastern Collared Lizards (*Crotaphytus collaris* (Say in James, 1823)), sprint speed was shown to be under heavy sexual selection only in males because increased sprint speeds allowed individuals to defend larger home ranges that in turn granted access to more females with which to sire offspring (Peterson and Husak 2006). However, the validity of laboratory-based assessments of performance in relation to similar assessments made in the field has recently been called into question (Irschick 2003; Irschick et al. 2005). Because laboratory-based studies often operate under optimal conditions, these assessments may not reflect an individual's volitional performance (Irschick 2003). Consequently, there is a need to validate and calibrate laboratory-based measures of performance with field-based estimates (Hasler et al. 2009).

The concept of stability in performance hierarchies has been put forward as a measure of individual consistency, where the same individual measured multiple times will show consistent performance even under variable environmental conditions (Kolok 1992; Martínez et al. 2002). Individual consistency and repeatability of performance has important implications for studies aimed at relating differences in performance to fitness differentials among individuals. Typically, these studies rely on quantifying performance using very few trials that often take place within controlled environmental parameters and assume that the techniques used to quantify performance are accurate and precise and work well across a range of organismal performance capacities (Adolph and Hardin 2007; Adolph and Pickering 2008). Furthermore, these studies presume that differences among individuals reflect phenotypic variation, establishing a fitness differential among individuals and providing the raw material upon which natural selection can act (Adolph and Hardin 2007; Adolph and Pickering 2008). Paradoxically, at present no studies have assessed the temporal stability of performance hierarchies on a scale exceeding a few months, let alone across multiple seasons and years, in the wild, thereby leaving these assumptions in question. Such information is essential for determining if and how organismal physiology and performance influence individual fitness and population demography (Ricklefs and Wikelski 2002).

Multiple studies of fish swimming performance have noted that stable hierarchies exist among individuals sub-

jected to swimming trials in the laboratory setting (Kolok 1992; Martínez et al. 2002). Additionally, these performance hierarchies tend to be conserved in the face of changing environmental factors, such as water temperature (Kolok 1992) and food availability (Martínez et al. 2002), indicating a relationship between performance and genetics (Marras et al. 2010). Recent studies have also begun to demonstrate that performance hierarchies exist among free-ranging individuals in the field. Daily swimming performance (critical swimming speed) of blacknose dace (*Rhinichthys atratulus* (Hermann, 1804)) in small streams was noted to be repeatable across multiple samplings during 6 months in a laboratory setting (Nelson et al. 2008). During the spawning migration of sockeye salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)), individuals maintained an ordered hierarchy of swimming speed that was stable across the length of the in-river portion of the migration (Hanson et al. 2008). Within largemouth bass (*Micropterus salmoides* (Lacépède, 1802)), the model species of this study, Hanson et al. (2007b) noted that individual swimming performance (maximum daily swimming speed) across the parental-care period was conserved as the brood developed towards independence. As locomotion in many taxa is required for prey capture, predator avoidance, migration, and successful reproduction (Irschick 2003; Irschick et al. 2008), differences in swimming performance are a readily testable whole organismal trait related to fitness differentials between individuals (Irschick 2003; Marras et al. 2010). Stable hierarchies of swimming performance can lead to fitness differentials between individuals and form the raw material upon which natural selection can act (Irschick et al. 2008).

The goal of this study was to determine the prevalence and repeatability of stable swimming performance hierarchies across a calendar year in a population of temperate fishes that would be exposed to a range of environmental factors corresponding to seasonality (fluctuating temperature, dissolved oxygen, habitat, resource availability). Additionally, we sought to determine if these performance hierarchies were stable between years when fish were exposed to similar environmental conditions. First, because of the prevalence of repeatability of locomotory performance hierarchies noted in laboratory studies, we predicted that stable performance hierarchies would be found within each season during the annual cycle. Second, we predicted that performance hierarchies would be correlated between seasons as previous work has demonstrated that these hierarchies are generally conserved in the face of changing biotic and abiotic factors in the laboratory (Martínez et al. 2002). Third, we predicted that performance hierarchies among individuals would be conserved across multiple years within seasons with similar abiotic conditions.

Materials and methods

Study site

This study was carried out on data collected during the 2004–2005 calendar years in Warner Lake (8.3 ha surface area; 44°31'N, 76°20'W), eastern Ontario, Canada. Warner Lake is equipped with the only whole-lake acoustic telemetry system in the world and can position fish with submetre accuracy at fine temporal scales (seconds) year-round, in-

cluding under the ice (Hanson et al. 2007a). Detailed activity of individually tagged largemouth bass could therefore be monitored across multiple time scales, providing a unique opportunity to evaluate performance hierarchies in the wild. To do so, four time periods were chosen to represent various temperature regimes common during the annual cycle. To represent stable temperature regimes during winter and summer, data collected during 27–31 December 2004 (4.1 ± 0.4 °C; mean \pm SD) and 20–24 June 2005 (21.5 ± 1.1 °C) were analyzed. To represent changing temperature regimes during the transitional fall and spring time periods, data collected during 2–6 November 2004 (8.8 ± 0.4 °C) and 14–18 April 2005 (10.1 ± 1.4 °C) were analyzed. These dates corresponded with changes in water temperature associated with winter cooling (before ice on) and spring warming (after ice off). Additionally, to determine if performance hierarchies are stable across multiple years, data were collected on the same six individuals experiencing similar seasonal temperature regimes in 16–20 December 2005 (3.8 ± 0.6 °C) and 16–20 December 2006 (3.6 ± 0.4 °C). Further details on the lake structure and community can be found in Suski (2000) and Hanson et al. (2007a). Briefly, Warner Lake is a small, shallow (maximum depth of 8 m) eutrophic lake consisting of two basins characterized by emergent and submergent aquatic vegetation and coarse woody debris. Other documented fish species include white sucker (*Catostomus commersonii* (Lacépède, 1803)), pumpkinseed (*Lepomis gibbosus* (L., 1758)), yellow perch (*Perca flavescens* (Mitchill, 1814)), brown bullhead (*Ameiurus nebulosus* (Lesueur, 1819)), and golden shiner (*Notemigonus crysoleucas* (Mitchill, 1814)) in addition to a population of ~700 adult largemouth bass (total length >250 mm).

Study animals

Largemouth bass were collected by angling in Warner Lake between 14 and 16 October 2004. In total, 11 males and 9 females (male total length: 391 ± 23 mm (mean \pm SD); female total length: 408 ± 30 mm) were implanted with code division multiple access (CDMA) temperature–pressure sensing acoustic transmitters (Lotek CTP-M16-25, 16 mm \times 25 mm, signal transmission rate 10 s, depth resolution ± 0.7 m, temperature resolution ± 0.5 °C, life expectancy of 1 year, weighing 10.0 g in air). A second collection and implantation event took place between 5 and 6 October 2005, during which 4 males and 6 females (male total length: 398 ± 20 mm; female total length: 396 ± 18 mm) were implanted with longer life expectancy CDMA transmitters (Lotek MA-TP16-25, 16 mm \times 25 mm, signal transmission rate 60 s, depth resolution ± 0.7 m, temperature resolution ± 0.5 °C, life expectancy of 3 years, weighing 23.9 g in air). Implanted transmitters weighed less than 2%–3% of the body mass to avoid an effect of the tag on individual behaviour (Winter 1983; Brown et al. 1999), and transmitters were implanted into the intraperitoneal cavity. Indeed, previous research on adult largemouth bass in Warner Lake has validated that acoustic transmitters used in the current study had negligible impacts on organismal health or condition relative to untagged individuals (Caputo et al. 2009). In both surgery sessions, all surgeries followed methods described in Cooke et al. (2003) and Hanson et al. (2007a) and were conducted by the same experienced indi-

vidual to eliminate variance associated with multiple surgeons (Cooke et al. 2003). Briefly, prior to surgery, individual fish were anesthetized in a 60 ppm induction bath of clove oil (emulsified in ethanol, a clove oil to ethanol ratio of 1:9) and ethanol (Anderson et al. 1997). Upon equilibrium loss, fish were measured (total length to the nearest millimetre) before being moved to a foam-lined surgery table where a recirculating maintenance dose of anesthetic (20 ppm of clove oil) in lake water was used to irrigate the gills. During transmitter implantation, the sex of individuals was determined. The surgical incision was closed by two simple interrupted sutures (3/0 PDS II, absorbable monofilament sutures; Ethicon Inc.). Additionally, all individuals were marked with a passive integrated transponder (PIT) placed within the surgical incision to allow for future identification. Following surgery, fish were placed in a recovery tank containing fresh lake water until equilibrium was regained (usually within 5 min). Fish were then released into the lake at a central location.

Telemetry array

Fish movements were recorded by a fixed station acoustic telemetry array originally installed in Warner Lake in November of 2003. The physical structure of the array consists of two multi-port MAP_600 receivers (Lotek Wireless, Inc., Newmarket, Ontario, Canada) connected by cabling to 13 hydrophones configured in an optimal geometry to provide coverage throughout the entire lake. Details on system performance and accuracy can be found in Niezgodá et al. (2002) and Hanson et al. (2007a). Briefly, the system relies upon CDMA technology that encodes transmissions from each telemetered individual on the same frequency eliminating issues associated with signal collision and data loss associated with monitoring multiple transmitters on the same frequency in a discrete area. Submetre accuracy of positioning of instrumented fish results from the geometry of the implemented hydrophone array, which was surveyed by differential GPS (± 0.2 m) (Niezgodá et al. 2002). Error decreases significantly as more hydrophones receive the transmissions and are added to triangulation calculations, and triangulation by as few as four hydrophones have sub-metre precision within the footprint of the array and precision greater than 1 m outside the footprint of the array (Niezgodá et al. 2002). All received data are immediately logged on flash storage cards prior to transfer to a personal computer for data processing.

Data processing and analysis

Data processing details may be found in Niezgodá et al. (2002) and Hanson et al. (2007a). Initially, raw data were loaded into the software program BioMAP version 2.1.12.1 (Lotek Wireless, Inc.) and subjected to a two-dimensional positioning engine to form raw position solutions. To remove outliers, multiple filtering procedures within BioMAP (as detailed in Niezgodá et al. 2002) assess the numerical stability of each transmission event and remove all nonstable positions. Additionally, any transmission events that did not exhibit a sub-metre geometric dilution of precision were removed. Additional filtering processes are employed to prepare data for further analysis. The first statistical outlier removal treatment separates samples on the basis of signifi-

cance with respect to the underlying trend and removes any position solution determined to be an outlier (Coifman and Wickerhauser 1995). The second treatment employs an adaptive trend filter to smooth the trajectory of position estimates (Wakeling et al. 2002). Measures of mean daily swim speed and daily distance traveled were calculated for each individual during each day (day defined as starting with the point closest to 00:00:00 h and ending with the closest signal to 23:59:59 h, both typically within 1 min). Mean daily swimming speed was included as a metric of voluntary swimming performance of the individual, as mean daily swimming speed is less likely to be influenced by outliers than maximum swimming speed. Daily distance traveled was included as a measure of volitional activity and has been noted to be positively correlated with burst swimming (commonly employed during foraging and prey avoidance) capacity in fish (McDonald et al. 2007). In general, fewer fish were included in analyses of summer months because of extensive movements by some individuals outside of the footprint of the array (e.g., in shallow backwater areas choked with vegetation), which results in a lack of reliable position estimates after filtering of the data.

Statistical analysis

To determine the repeatability of rank within performance hierarchies in both daily mean swim speed and daily distance traveled within each season, nonparametric Spearman's ρ coefficient of rank correlation tests were conducted on sequential days (Kolok 1992; Zar 1999). Additionally, differences between the rankings of male and female individuals within the hierarchies in each season were assessed by the Wilcoxon rank-sum test (Zar 1999). Spearman's ρ coefficient of rank correlation tests were also conducted to determine if there were correlations between the rank order of individuals with respect to both of the swimming performance variables averaged across the 5-day sampling periods and total body length (Kolok 1992; Zar 1999). To determine between-season repeatability of performance hierarchies, mean daily distance traveled and mean daily swimming speed were determined by individual during each season. Correlations between the rank order of individuals with respect to both of these variables averaged across the 5-day sampling periods was assessed between all four seasons (Kolok 1992; Zar 1999). Last, to test the stability of performance hierarchies for the same individuals across multiple years, correlations between the rank order of individuals with respect to both daily mean swim speed and daily distance traveled averaged across the 5-day sampling periods were assessed between time periods with similar temperature and photoperiod regimes (December 2005: 3.8 ± 0.6 °C; December 2006: 3.6 ± 0.4 °C) across 2 years. All analyses were conducted within the statistical package JMP version 7.0.1 (SAS Institute Inc., Cary, North Carolina, USA). The level of significance for all tests (α) was assessed at 0.05 (Zar 1999). Values reported in the Results are means \pm SE unless otherwise noted.

Results

Within the 2004–2005 year, repeatable performance hierarchies for both daily distance traveled and mean daily

swimming speed were noted during most seasonal sampling periods (Table 1, Figs. 1–4). In particular, swimming performance as expressed in two ways (i.e., daily mean swim speed and daily distance traveled) was highly correlated between individual days during both winter and summer (Table 1, Figs. 2A–2B, 4A–4B). During the fall period, individual performance in relation to daily distance traveled was stable between the majority of days (Table 1, Figs. 1A–1B). Neither daily distance traveled nor mean daily swimming speed performance hierarchies were repeatable between multiple days during the spring sampling session (Table 1, Figs. 3A–3B). During each season, there was no difference between the rankings of male and female fish within the performance hierarchies for both metrics (Table 2). Additionally, there were no consistent correlations between either metric of swimming performance and individual total length (Table 3). Between each season, there were no correlations between the rank order of individual performance in daily distance traveled and mean daily swimming speed averaged across the 5-day sampling period, indicating that performance hierarchies were not stable between seasons (Table 4, Figs. 5A–5B). Repeatability of performance was also noted in both metrics during the winter of two separate years (2005 and 2006) (Table 5). However, performance hierarchies were not repeatable when sampling period means were compared between the 2 years (Table 5, Figs. 6A–6B).

Discussion

Although the existence of stable performance hierarchies in relation to various swimming performance metrics has been repeatedly demonstrated in the laboratory setting for fish (Kolok 1992; Kolok and Farrell 1994; Martínez et al. 2002; Claireaux et al. 2007; Nelson et al. 2008), very few studies have empirically tested this phenomenon in the wild (Hanson et al. 2007b; Hanson et al. 2008), and none have done so across multiple months or years. In general, repeatability of swimming performance is postulated to originate from multiple phenotypic differences between individuals that affect whole organism performance (Ghalambor et al. 2003; Claireaux et al. 2007). Additionally, multiple studies have shown that swimming performance is a heritable trait in fish derived from genetic predispositions of individuals (Nicoletto 1995; Garenc et al. 1998; Martínez et al. 2002). As such, stable performance hierarchies can provide a link to variation in individual fitness and influence the evolution of organismal performance and morphology within a population. The existence and maintenance of stable performance hierarchies in the wild supports the findings of earlier laboratory studies. Specifically, within every season and every year tested in the current study, largemouth bass assorted in performance hierarchies that were stable across 5-day time periods even though environmental conditions varied drastically among sampling periods (Table 1). Largemouth bass did not form stable performance hierarchies in only one season sampled (spring of 2004; Table 1), which was most likely due to behavioural alterations among male fish prior to spawning (Hanson et al. 2007a). During this time period, male fish occupy a small spatial area, as they construct a nest, spawn with females, and provide parental care to the brood for up to a month (Kramer and Smith 1962). The prevalence of stable swimming performance hierarchies

Table 1. Within-season repeatability of largemouth bass (*Micropterus salmoides*) swimming performance hierarchies for daily distance traveled and mean daily swimming speed in Warner Lake, Ontario.

Season	Day comparison	N	Daily distance traveled		Mean daily swimming speed	
			Spearman's ρ	P	Spearman's ρ	P
Fall	2 vs. 3 November	20	0.61	0.005*	0.43	0.06*
	3 vs. 4 November	20	0.56	0.01*	0.23	0.32
	4 vs. 5 November	20	0.31	0.12	0.09	0.71
	5 vs. 6 November	20	0.76	<0.001*	0.62	0.004*
Winter	27 vs. 28 December	20	0.56	0.01*	0.70	<0.001*
	28 vs. 29 December	20	0.72	<0.001*	0.65	0.002*
	29 vs. 30 December	20	0.62	0.004*	0.68	0.001*
	30 vs. 31 December	20	0.51	0.02*	0.67	0.001*
Spring	14 vs. 15 April	20	0.28	0.23	0.36	0.12
	15 vs. 16 April	20	0.45	0.048*	0.52	0.019*
	16 vs. 17 April	20	0.19	0.43	0.25	0.28
Summer	17 vs. 18 April	20	0.51	0.02*	0.43	0.06
	20 vs. 21 June	12	0.75	0.002*	0.63	0.016*
	21 vs. 22 June	12	0.81	<0.001*	0.55	0.052
	22 vs. 23 June	12	0.94	<0.001*	0.68	0.014*
	23 vs. 24 June	12	0.92	<0.001*	0.91	<0.001*

Note: *, $P < 0.05$.

Fig. 1. Repeatability of individual largemouth bass (*Micropterus salmoides*): (A) daily distance traveled (m) and (B) mean daily swimming speed (m/s) during fall (2–6 November 2004) in Warner Lake, Ontario.

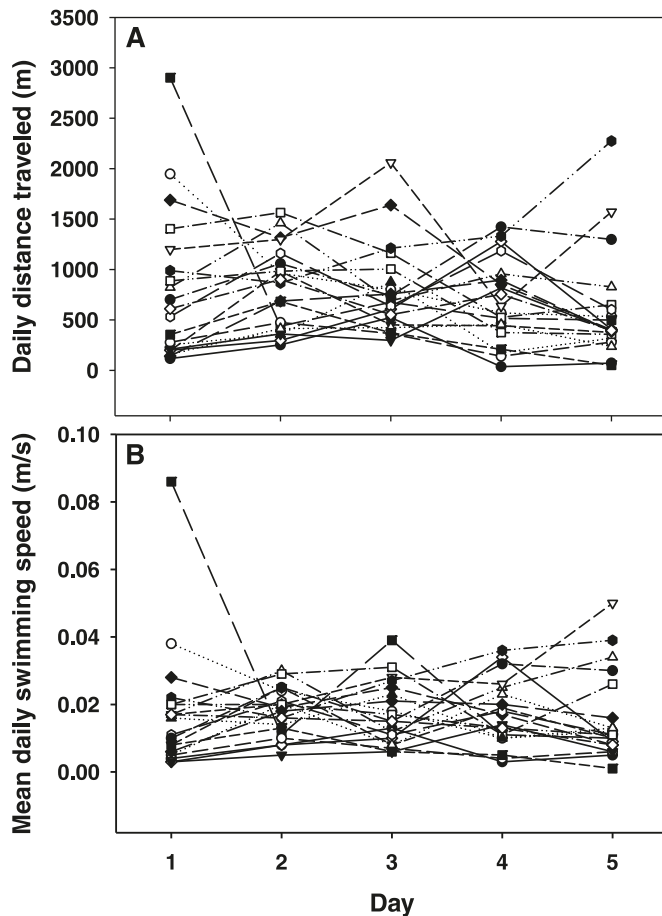


Fig. 2. Repeatability of individual largemouth bass (*Micropterus salmoides*): (A) daily distance traveled (m) and (B) mean daily swimming speed (m/s) during winter (27–31 December 2004) in Warner Lake, Ontario.

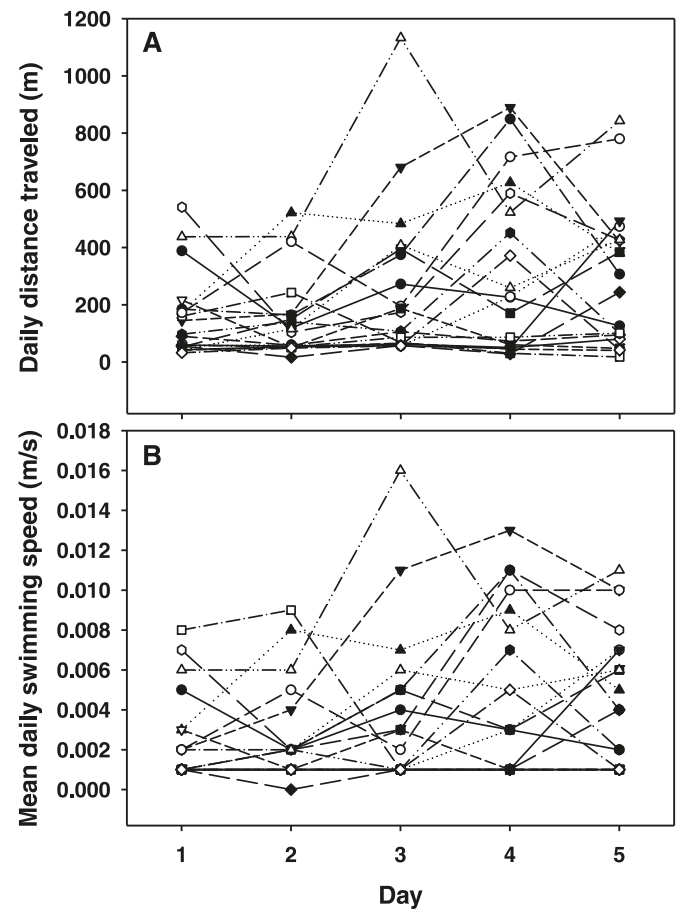


Fig. 3. Repeatability of individual largemouth bass (*Micropterus salmoides*): (A) daily distance traveled (m) and (B) mean daily swimming speed (m/s) during spring (14–18 April 2005) in Warner Lake, Ontario.

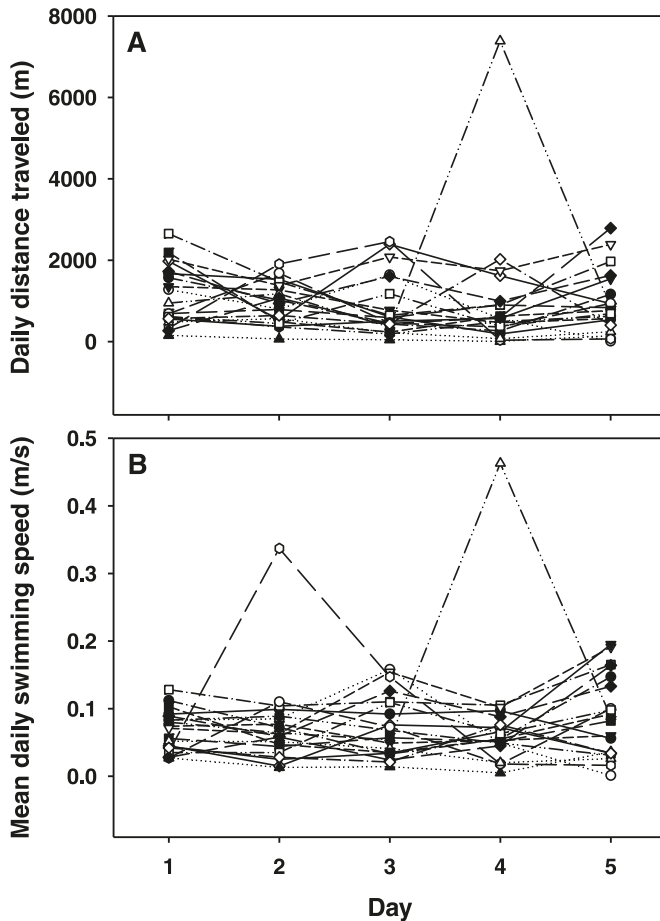
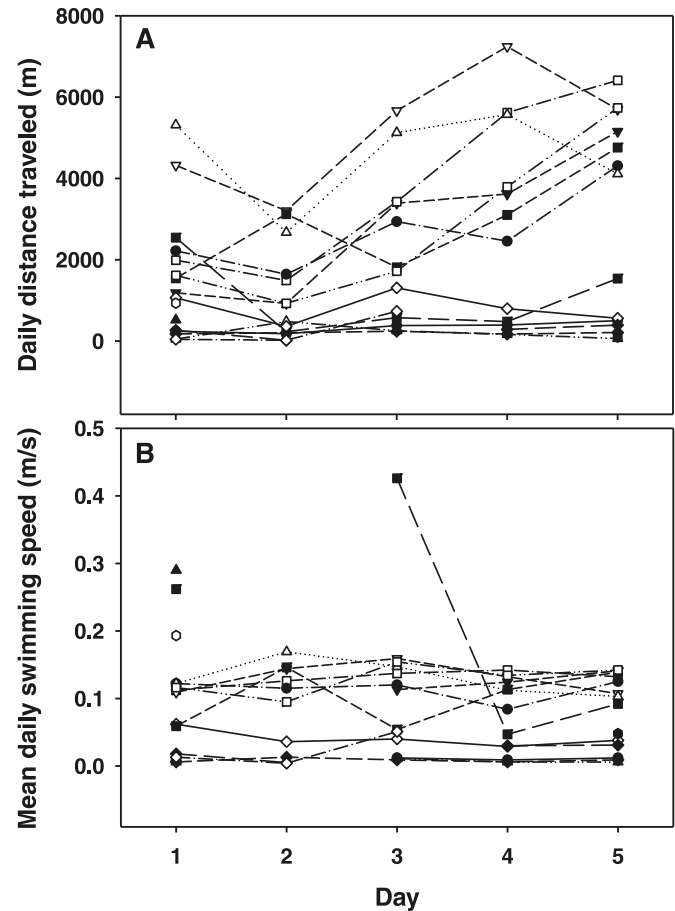


Fig. 4. Repeatability of individual largemouth bass (*Micropterus salmoides*): (A) daily distance traveled (m) and (B) mean daily swimming speed (m/s) during summer (20–24 June 2005) in Warner Lake, Ontario.



throughout a single year and across multiple years suggests that this is a common occurrence resulting from individual variation in locomotory performance.

While swimming performance hierarchies were stable within each season, there were no correlations between the rank orders of individual swimming performance between seasons (Table 4). In concert with this idea, current studies have noted that swimming performance, as well as performance hierarchies, may be a very plastic response in fishes. Nelson et al. (2008) noted that when riverine blacknose dace were placed in a novel environment (i.e., no-flow water conditions), sprint performance swimming hierarchies tended to break down because the fastest fish performed poorly and the slowest fish performed better. Similarly, in our study, when individuals encountered two distinct sets of environmental conditions (i.e., winter abiotic conditions vs. summer abiotic conditions), swimming performance hierarchies among largemouth bass changed (Table 4). Of particular importance, water temperature has often been noted as being the “master factor” controlling fish performance and behaviour through moderation of biochemical reactions within the body (Brett 1971; Fry 1971). As such, certain individuals may be adapted to perform maximally at certain temperatures because of differences in many physiological

variables among individuals. Consistent with this idea, intra-specific differences in swimming performance and scope for activity have been shown to vary with temperature in adult migrating Pacific salmonids in the laboratory (Lee et al. 2003) and have been validated in the field (Farrell et al. 2008). These data suggest that certain individuals are genetically predisposed to perform better than others under certain sets of abiotic conditions. In essence, a given level of performance may be context-specific (or seasonally specific) for a given individual. Fish of a given size, age, behavioural personality (e.g., shy, bold), sex, or energetic condition may operate at a different optimal activity level in different seasons. For example, in the winter, a male with high levels of energy may be less active than a female with low levels of energy, but this hierarchy may flip in the spring. We did not investigate the role of sex on hierarchy formation in the current study, but we found no differences between the rankings of males and females in each season (Table 2). Additionally, we did not note consistent correlations between swimming performance rank and total length of individuals (Table 3). Finally, as all individuals were sampled by angling, which is selective for either aggressive or actively feeding bass at the time of capture, the fish included in this study potentially represent a subset of individuals within the

Table 2. Comparison of male and female rankings within largemouth bass (*Micropterus salmoides*) swimming performance hierarchies for daily distance traveled and mean daily swimming speed in Warner Lake, Ontario.

Seasonal comparison	N	Daily distance traveled		Mean daily swimming speed	
		Wilcoxon Z	P	Wilcoxon Z	P
Fall	20	-0.21	0.84	-0.70	0.48
Winter	20	0.04	0.97	0.12	0.90
Spring	20	1.20	0.23	0.54	0.59
Summer	19	0.32	0.75	1.30	0.19

Table 3. Correlations between-season swimming performance hierarchies and body size (total length, mm) for daily distance traveled and mean daily swimming speed of largemouth bass (*Micropterus salmoides*) in Warner Lake, Ontario.

Seasonal comparison	N	Daily distance traveled		Mean daily swimming speed	
		Spearman's ρ	P	Spearman's ρ	P
Fall	20	0.17	0.48	0.23	0.32
Winter	20	0.49	0.03*	0.35	0.13
Spring	20	0.19	0.43	-0.35	0.27
Summer	19	-0.57	0.06	1.30	0.19

Note: *, $P < 0.05$.

Table 4. Between-season repeatability of largemouth bass (*Micropterus salmoides*) swimming performance hierarchies for daily distance traveled and mean daily swimming speed in Warner Lake, Ontario.

Seasonal comparison	N	Daily distance traveled		Mean daily swimming speed	
		Spearman's ρ	P	Spearman's ρ	P
Spring vs. fall	12	0.36	0.12	0.33	0.16
Winter vs. fall	12	-0.16	0.50	0.06	0.81
Winter vs. spring	12	-0.16	0.49	0.05	0.83
Summer vs. fall	12	0.03	0.93	0.36	0.26
Summer vs. spring	12	-0.24	0.46	-0.43	0.17
Summer vs. winter	12	-0.12	0.71	0.33	0.30

population of the lake that share common traits that made them vulnerable to angling at the time of capture. However, given that stable performance hierarchies have been noted in multiple fish species that were collected or reared through a variety of methods (Kolok 1992; Kolok and Farrell 1994; Martínez et al. 2002; Claireaux et al. 2007; Hanson et al. 2007b; Hanson et al. 2008; Nelson et al. 2008), we do not believe that the results of the current study are an artifact of sampling, and the observed context-dependant performance hierarchies are stable within the population as a whole. Unfortunately, we were not able to look at any other biotic or abiotic factors in this study. This question should be addressed in the future and will require greater sample sizes and more explicit contrasts of individuals in different groups.

Consistent with the idea that performance may be context sensitive, when the same set of individuals was sampled in 2 years with similar thermal regimes, these individuals did not assort into the same performance hierarchy as the previous year (Table 5). These data suggest that water temperature alone is not the only predictor of individual performance and that other environmental and intrinsic biological variables that were not measured in the current study could be sufficiently different between years to affect indi-

vidual swimming performance. For example, dissolved oxygen concentration, habitat differences, or prey distribution and abundance could fluctuate between years, thereby altering individual fish behaviour.

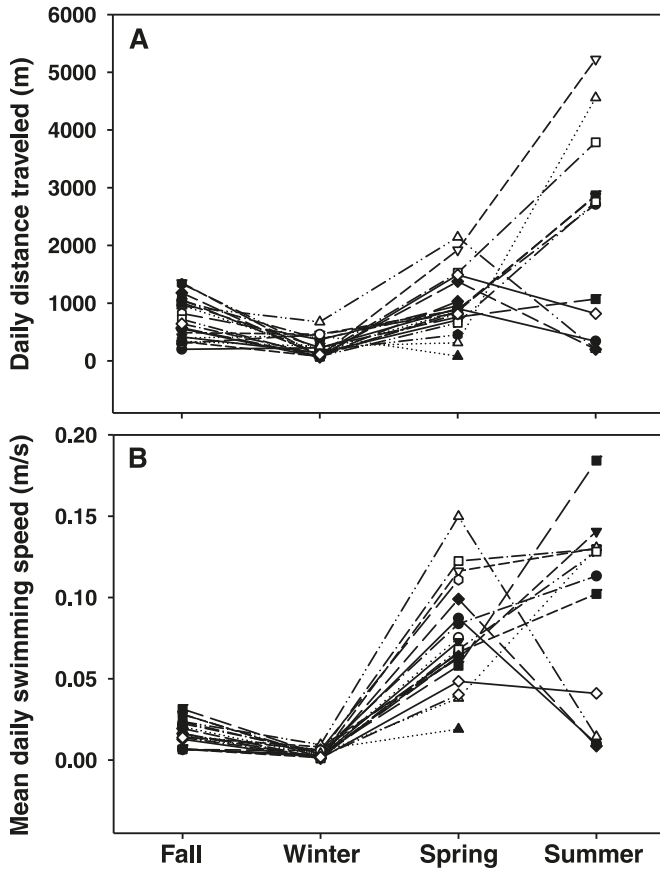
The results from the current study have grave implications for the interpretation of performance data in the context of individual fitness. Typically, studies relating individual locomotory performance to individual fitness rely on very few trials across a discrete temporal period with similar abiotic conditions (Adolph and Pickering 2008). These study designs rely on the underlying assumption that the differences measured among individuals are related solely to phenotypic variation and that individual animals will exhibit relatively stable levels of locomotory performance throughout their life (i.e., once a fast animal, always a fast animal; Adolph and Hardin 2007; Adolph and Pickering 2008). As such, any correlations made between locomotory performance and phenotypic traits (biochemical, physiological, morphological, evolutionary) employ the tacit assumption that the measured differences in locomotory performance will be stable in many, if not all, situations (e.g., predator-prey interactions, territory acquisition and defense, migratory movements) under a range of abiotic conditions (e.g., varying water temperatures associated with seasonality, habitat

Table 5. Within- and between-year repeatability of largemouth bass (*Micropterus salmoides*) swimming performance hierarchies for daily distance traveled and mean daily swimming speed in Warner Lake, Ontario.

Year	Day comparison	N	Daily distance traveled		Mean daily swimming speed	
			Spearman's ρ	P	Spearman's ρ	P
2005	16 vs. 17 December	9	0.68	0.042*	0.79	0.01*
	17 vs. 18 December	9	0.38	0.31	0.38	0.32
	18 vs. 19 December	9	0.72	0.03*	0.83	0.006*
	19 vs. 20 December	9	0.72	0.03*	0.71	0.031*
2006	16 vs. 17 December	6	0.94	0.005*	0.94	0.005*
	17 vs. 18 December	6	0.49	0.33	0.24	0.65
	18 vs. 19 December	6	0.50	0.25	0.43	0.34
	19 vs. 20 December	6	0.94	0.005*	0.87	0.025*
Yearly	2005 vs. 2006	6	-0.43	0.39	-0.41	0.43

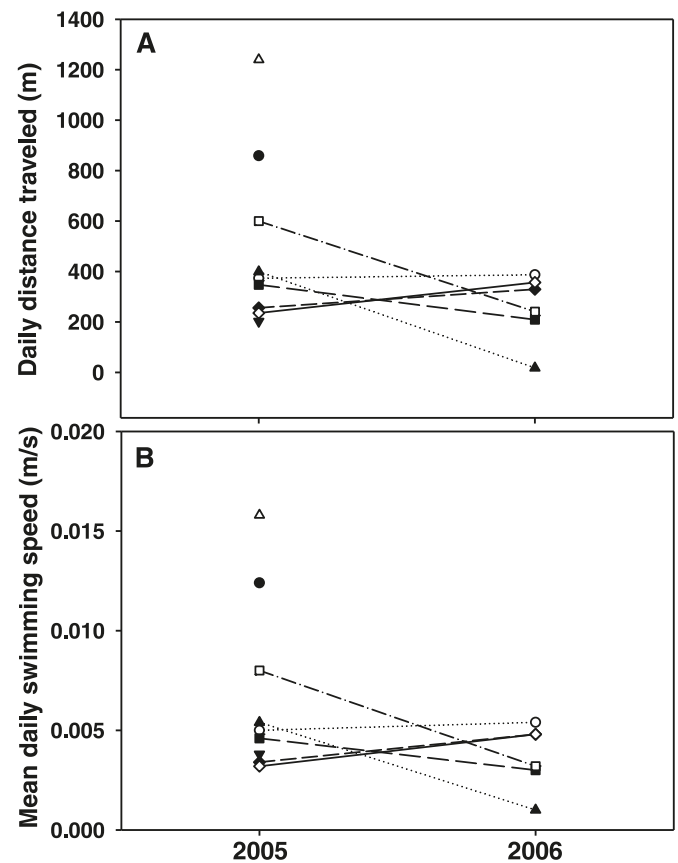
Note: *, $P < 0.05$.

Fig. 5. Repeatability of mean individual largemouth bass (*Micropterus salmoides*): (A) daily distance traveled (m) and (B) mean daily swimming speed (m/s) between successive 5-day sampling periods during each season in 2004–2005.



utilization; Adolph and Hardin 2007). Given the results of this study, where swimming performance hierarchies were not stable across seasons and water temperatures, inferences of organismal performance and fitness based upon a data set generated during a single season would generate an inaccurate representation of organismal performance in other seasons. Researchers should be cognizant of this situation and should design studies to evaluate intraindividual variation in measurements so that a correction factor can be applied dur-

Fig. 6. Repeatability of mean individual largemouth bass (*Micropterus salmoides*): (A) daily distance traveled (m) and (B) mean daily swimming speed (m/s) between 5-day sampling periods in winter 2005 (December 2005) and winter 2006 (December 2006) in Warner Lake, Ontario.



ing analyses (Adolph and Hardin 2007). If this is not taken into account, extrapolations from a single set of performance estimates determined within one discrete set of environmental conditions to a different set of environmental conditions, let alone an estimation of individual fitness, are highly suspect. Knowing the precise factors that influence changes in the shuffling of organismal performance hierarchies would be useful for understanding variability in individual fitness and population demographics (Ricklefs and Wikelski 2002).

The present study provides evidence that swimming performance and daily activity hierarchies remain stable within seasons during an annual cycle for a wild population of largemouth bass. However, seasonal changes in environmental conditions appear to result in a reshuffling of performance hierarchies. Future research should examine the stability of swimming performance hierarchies in relation to seasonally variable abiotic factors, including dissolved oxygen concentrations, prey distribution and abundance, and habitat configuration, as well as water temperature. It may also be possible that shuffling is related to organismal condition or other intrinsic biotic factors. Once the biotic and abiotic factors that may contribute to the stability of performance hierarchies are characterized, an improved understanding of potential fitness consequences can be gained. Further examinations of whole organism performance will aid in characterizing the mechanistic connections between phenotypic traits and adaptive evolution.

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