



Original Article

Between- and within-individual variation in activity increases with water temperature in wild perch

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In contrast to a growing interest in the ecological implications of consistent individual differences in behavior, it is still unclear how consistent those differences are across environmental gradients, especially under ecologically relevant contexts and timescales. We investigated how individual variation in swimming activity of Eurasian perch (*Perca fluviatilis*) changes in response to natural fluctuations of water temperature as a proxy for an ecological gradient for ectothermic animals. Using an automated acoustic telemetry system, we tracked individual positions of adult perch in a whole natural lake for about 1 year and compared several model frameworks for the individual responses to water temperature. The best-fit model revealed that rising water temperature led to an increase in both between- and within-individual variation in activity, thereby stabilizing behavioral repeatability across temperature. Further, including temporal autocorrelation significantly improved the model performance, suggesting that consistent individual differences in behavior could be partially explained by factors such as slowly changing states in the wild. By using ecologically relevant data, our results revealed complex patterns of behavioral variation in response to an environmental change represented by water temperature.

Key words: animal personality, behavioral plasticity, heteroscedasticity, reaction norm, variance partitioning.

INTRODUCTION

Animals of many taxa show behaviors that are consistently different from one another in a wide array of traits, such as activity, exploration, aggression, sociability, and boldness (Bell et al. 2009; Dingemanse et al. 2010). Recent applications of biotelemetry have further provided evidence for consistent individual differences in behavior under ecologically relevant conditions and timescales (Taylor and Cooke 2014; Harrison et al. 2015), opening the door to the ecological implications of animal personality (Grootuis and Trillmich 2011; Sih et al. 2012; Wolf and Weissing 2012). In the wild, however, many animals adjust their behavior in response to environmental changes (i.e., behavioral plasticity), and moreover, the extent of behavioral plasticity may differ between individuals (Nussey et al. 2007; Biro et al. 2010; Carter et al. 2012). If so, individual variation in behavioral plasticity could add complexity to understanding how individual differences in behavior

are expressed in response to environmental changes (Dingemanse et al. 2010).

Statistically, consistent individual differences in behavior are usually investigated with linear mixed-effects models fitted to repeated behavioral measures of individuals (Dingemanse and Dochtermann 2013). When behavior is measured repeatedly across environmental gradients, environmental variables can be included in the model to estimate between-individual variance (Nakagawa and Schielzeth 2010; Brommer 2013). However, within-individual variance may also change across environmental gradients (Brommer et al. 2008; Pruitt et al. 2011; Briffa 2013; Briffa et al. 2013; Highcock and Carter 2014), which violates the assumption of homoscedasticity in standard linear models. Another ecologically important, yet overlooked, complication is temporal autocorrelation. Due to the nature of repeated measures, behavioral measures are potentially nonindependent from one another, thereby violating the assumption of independence of errors in standard linear models (Biro and Stamps 2015). If behavioral measures are autocorrelated in time, the presence of consistent individual difference in behavior does not necessarily represent the underlying individual variation in life history (Wolf et al. 2007; Réale et al. 2010). Rather, the observed individual variation in behavior

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may be confounded by other factors such as slowly changing states (Sih et al. 2015). Although these potential complications need to be explored to understand consistent individual differences in behavior in the wild, thus far it has been difficult due to the need for large, robust, and yet ecologically relevant data sets.

Recent technological advances have enabled automated collection of long-term, high-resolution movement data on animals in the wild, which can be used for investigating individual variation in movement traits under ecologically relevant conditions and timescales (Krause et al. 2013; Hussey et al. 2015). Activity, often measured as distance travelled, is an ecologically relevant movement trait that governs growth (Martin-Smith and Armstrong 2002) and predation risk (Strobbe et al. 2011). Furthermore, activity is also important for population dynamics, as it could influence distribution, dispersal, and gene flow (Johnson et al. 1992). Activity is a personality trait in many animals (Réale et al. 2007; Bell et al. 2009), and recent telemetry studies show consistent individual differences in activity in the wild (Taylor and Cooke 2014; Harrison et al. 2015). When combined with environmental data, the large amount of movement data provides a unique opportunity to investigate how individual variation in activity responds to changes in natural environments. For example, Biro et al. (2010) reported that under laboratory conditions even small temperature fluctuations significantly altered the rank order of activity in damselfish, *Pomacentrus wardi*, which raises the question of whether this is also the case in the wild.

In ectothermic animals, temperature is one of the most critical environmental factors that influence activity. In fish in particular, water temperature tightly regulates metabolism and, consequently, influences energetic demands (Clarke and Johnston 1999; Cossins and Bowler 1987). Water temperature can also act as a controlling factor of primary productivity (Keller 1989; Regaudie-de-Gioux and Duarte 2012), which influences the abundance of prey fish (Downing et al. 1990) and, consequently, the activity of predator fish (Jacobsen et al. 2014). Although activity of fish is influenced by many other environmental factors such as light (Cerri 1983; Diehl 1988) and seasonality (Jacobsen et al. 2002; Hanson et al. 2007), water temperature is thus a useful proxy for a broader ecological gradient, considering that many environmental factors are cross-correlated in the wild. Consequently, many fishes show elevated activity as water temperature increases (Neuman et al. 1996; Hanson et al. 2007). However, we do not know whether individuals respond differently from one another to changes in water temperature in the wild, which can only be understood by measuring activity of wild fish experiencing natural fluctuations of water temperature.

We used wild adult Eurasian perch, *Perca fluviatilis*, as a model species to investigate how between- and within-individual variation in activity responds to natural changes in water temperature. Perch are a common predatory fish in many temperate freshwater systems (Persson et al. 2003), and adults actively hunt benthic prey and small pelagic fish during the daytime (Allen 1935; Eklöv 1992). Perch would experience stronger intraspecific competition as water temperature increases because of the increase in food demand and escape ability of fish prey (Abrahams et al. 2007). Considering that animal personality emerges from a trade-off between intraspecific competition for food and risk-taking behavior (Wolf et al. 2007; Edenbrow and Croft 2013), we hypothesized that perch would increase between-individual variation in swimming activity as water temperature increases. To test our hypothesis, we estimated the daily swimming activity of each individual using acoustic telemetry

and investigated how individual activity responded to changes in water temperature by comparing several ecologically plausible models. Further, as a possible mechanism of individual differences in activity, we explored a correlation between activity and location such as depth use and distance from shore. We did this because individuals could experience different habitats regarding ambient temperature, light, prey availability, and predation risk, which could lead to individual differences in activity.

MATERIALS AND METHODS

Study site and telemetry system

We set up 20 wireless hydrophones (WHS 3050; Lotek Wireless Inc., Newmarket, ON, Canada) fully covering a temperate natural lake (Kleiner Döllnsee, 25 ha, 52°59'40"N, 13°34'53"E) located about 80 km northeast of Berlin, Germany. This slightly eutrophic shallow lake (average depth about 4 m, maximum depth about 8 m) was characterized by dense submerged macrophytes and a surrounding reed belt in the littoral zone (Zajicek 2012). The water temperature is nearly constant at 2 m depth across the lake (Pagel et al. 2015). The perch population was natural and self-reproducing, and no commercial and recreational fishing took place before and during the study period. Other relevant top predators in the study lake were northern pike, *Esox Lucius*, and European catfish, *Silurus glanis* (Kobler et al. 2009). The average data yield (i.e., the percentage of transmissions yielding a valid position) of the whole-lake telemetry system was 40%, and the accuracy was 3.1 m for horizontal position and 0.3 m for vertical position. Further details of the system can be found in Baktoft et al. (2015).

Capture and tagging

In autumn 2010, we caught 20 adult piscivorous perch using gill nets ($n = 10$) and angling ($n = 10$) throughout the entire lake. After capture, all fish were anesthetized in a 50 mg/L solution of clove oil (9:1, clove oil:ethanol), and we implanted ultrasonic transmitters with pressure and temperature sensors (CH-TP-11-25; 11 × 65 mm, 12 g; Lotek Wireless Inc.) into the body cavity following the protocol described by Hühn et al. (2014). Fish fully recovered after 15–30 min and were then released back into the lake near the capture point. Each transmitter was set to emit a uniquely encoded ultrasound at 9-s intervals, which was recorded by the hydrophones in the lake. In addition, each transmitter sent pressure and temperature information at 27-s intervals, which was later used to estimate fish depth. The experiment was conducted under the approval by State Office of Environment, Health and Consumer Protection in Brandenburg, Germany (protocol number 23-2347-15-2010).

Data processing

We recorded the positions of fish for about 1 year (from 23 September 2010 to 13 September 2011). We downloaded the data every 4–6 weeks from the data loggers (hydrophones) and calculated the positions of individual fish using a proprietary postprocessing software (ALPS v.2.22; Lotek Wireless Inc.) as described in Baktoft et al. (2015). Fish were assumed to be dead when they stopped moving within 15 m until they eventually disappeared (most likely due to sedimentation blocking signals). We discarded 2 individuals from the analysis due to the malfunction of the transmitter (abnormally sporadic signal transmission after release) and 2 individuals due to death immediately after the release. All remaining fish ($n = 16$) were adult females of similar sizes (35.8 ± 2.5 cm, mean \pm standard deviation [SD]).

Assessment of swimming activity, location, and water temperature

We obtained over 12 million effective positions of 16 individuals (about 0.8 million positions per individual on average) over a period of about 1 year. From these positions, we estimated the daily swimming distance (km) of each individual as a measure of activity by summing the linear distances between consecutive positions within each day (24 h). When fish do not move, it may overestimate swimming distance by accumulating the positioning errors over time. To avoid this problem, we performed spatial discretization by filtering out the positions when a fish did not move more than the 95% confidence interval of the system's positioning errors. This procedure reduced the daily swimming distance by 23.6% on average per individual. In addition to swimming distance, we estimated for each individual the mean daily distance from shore (m) and the mean daily depth from water surface (m) from all data collected within a given day, which were used to test for a correlation with swimming distance.

Daily mean water temperature (°C) was obtained from an in-lake sensor installed at 2 m water depth. In this lake, water temperature was virtually constant (± 0.25 °C) at 2 m depth (Pagel et al. 2015). Missing data due to late installation of the sensor by December 2010 (23 September–16 December 2010) and due to malfunction of the sensors (i.e., no data record, 5 April–8 October 2011) were predicted from a local weather station near the study site (20 km south of the lake, Deutscher Wetterdienst, Angermünde) using a generalized additive model. This model explained 94.1% of deviance in water temperature data and was thus well suited to predict daily variation in water temperature (see Supplement 1 for details). Water temperature during the observation period showed the profile of a typical temperate lake, with an average of 11.3 ± 6.9 °C, ranging from 1.8 to 23.0 °C (Supplement 2).

Data analysis

We investigated how between- and within-individual variance of swimming distance responded to changes in water temperature using linear models with different specifications following Dingemanse and Dochtermann (2013). To that end, we explored 5 ecologically plausible models (Table 1). Model 1 is a null model, in which the swimming distance is drawn from the same normal distribution for all individuals. Model 2 specifies the individual as a random effect, assuming that mean swimming distance was consistently different between individuals (individual-only model, I).

Model 3 included water temperature as a fixed effect, without taking into account individual differences (environment-only model, E). Model 4 included water temperature as a fixed effect and individual as a random effect (I, E). This model assumed that individuals have different intercepts of their behavioral reaction norms but share the same slope, resulting in constant between-individual variance in swimming distance across the temperature gradient. Finally, model 5 was a random regression model, in which individuals could exhibit varying plasticity in their swimming distance in response to changes in temperature, in addition to varying intercepts between individuals ($I \times E$ interaction). In this model, between-individual variance was estimated as a function of temperature, between-individual variance of slope and intercept, and covariance between slope and intercept (Brommer 2013).

To test for the temporal autocorrelation of activity and nonconstant within-individual variance across the temperature gradient, we included an autoregressive term and a heteroscedastic error structure in each model. An autoregressive term was added in each model as $\sum_{k=1}^k \varphi_k (y_{i-k,j} - \mu_{i-k,j})$, where φ_k is an autoregressive coefficient of k th autoregressive term, and y_{ij} and μ_{ij} are the observed and predicted activity of individual j on day i , respectively. In each model, a higher order was sequentially added until the model did not improve further based on the deviance information criterion (DIC). Heteroscedastic errors were specified such that swimming distance was drawn from a normal distribution with mean zero and temperature-dependent within-individual variance ae^{bx} , where parameters a (>0) and b are constants, and x_i is water temperature on day i . In this way, within-individual variance was allowed to change across the temperature gradient. For example, model 5 ($I \times E$) with a k th autoregressive term and heteroscedastic errors was specified as

$$\mu_{ij} = (\beta_0 + \text{ind}_{0j}) + (\beta_1 + \text{ind}_{1j})x_i$$

$$y_{ij} = \mu_{ij} + \sum_{k=1}^k \varphi_k (y_{i-k,j} - \mu_{i-k,j}) + \varepsilon_i$$

$$\begin{bmatrix} \text{ind}_0 \\ \text{ind}_1 \end{bmatrix} \sim \mathcal{N} \left(0, \begin{bmatrix} \sigma_{\text{ind}_0}^2 & \text{cov}(\text{ind}_0, \text{ind}_1) \\ \text{cov}(\text{ind}_1, \text{ind}_0) & \sigma_{\text{ind}_1}^2 \end{bmatrix} \right)$$

$$\varepsilon_i \sim \mathcal{N}(0, ae^{bx_i})$$

where β_0 and β_1 are group-mean intercept and slope, ind_{0j} and ind_{1j} are random intercept and slope for individual j . Random intercept and slope are drawn from a bivariate normal distribution, and

Table 1
Model specifications for observed swimming activity (y_{ij}) of individual j on day i

Model	Specification	Error distribution	Random effect(s)
1. null	$y_{ij} = \beta_0 + \varepsilon_i$	$\varepsilon_i \sim \mathcal{N}(0, \sigma^2)$	—
2. I	$y_{ij} = \beta_0 + \varepsilon_i$	$\varepsilon_i \sim \mathcal{N}(0, \sigma^2)$	ind_{0j} (intercept)
3. E	$y_{ij} = \beta_0 + \beta_1 x_i + \varepsilon_i$	$\varepsilon_i \sim \mathcal{N}(0, \sigma^2)$ or $\mathcal{N}(0, ae^{bx_i})$	—
4. I, E	$y_{ij} = \beta_0 + \beta_1 x_i + \varepsilon_i$	$\varepsilon_i \sim \mathcal{N}(0, \sigma^2)$ or $\mathcal{N}(0, ae^{bx_i})$	ind_{0j} (intercept)
5. $I \times E$	$y_{ij} = \beta_0 + \beta_1 x_i + \varepsilon_i$	$\varepsilon_i \sim \mathcal{N}(0, \sigma^2)$ or $\mathcal{N}(0, ae^{bx_i})$	ind_{0j} (intercept), ind_{1j} (slope)

Daily swimming activity of adult perch was modeled as a function of water temperature (x_i) and normally distributed errors (ε_i), with either constant or temperature-dependent variance (see Materials and methods). In some models, individual differences were included as random effects (ind_{0j} for random intercept, ind_{1j} for random slope of individual j) when estimating group-mean intercepts (β_0) and slopes (β_1).

errors (ϵ_i) are drawn from a normal distribution with temperature-dependent variance.

In this way, each of the 5 models was further investigated with an autoregressive term (models 1–5), with a heteroscedastic error structure (models 3–5), and with both an autoregressive term and a heteroscedastic error structure (models 3–5), resulting in a total of 16 competing models. We compared the DIC between these models to investigate the most plausible framework within which between- and within-individual variance responded to changes in water temperature. The model performance was considered poorer when $\Delta\text{DIC} > 5$ compared to the best-fit model (Spiegelhalter et al. 2002). In the best-fit model, we estimated repeatability as the proportion of between-individual variance over the sum of between- and within-individual variance (Nakagawa and Schielzeth 2010).

Model parameters were estimated using a Bayesian Markov Chain Monte Carlo (MCMC) sampling method with noninformative priors. All data were analyzed on the original scales. For each model, we ran 3 chains of 600 000 resamples, each with 100 000 burn-in and 100 thinning in JAGS v3.4.0 (Plummer 2003) under R package “R2jags” ver. 0.5-7 (Su and Yajima 2015). The parameter estimates, diagnostic plots, and the model script for the best-fit model are found in Supplement 3.

Lastly, we tested whether individual swimming distance covaries with location. To that end, we fitted a bivariate linear mixed-effects model to swimming distance and fish depth as dependent variables and individual as a random effect and estimated between- and within-individual correlation coefficients from the variance-covariance matrices. Between-individual correlation explains how much individual differences in swimming distance correspond to individual differences in depth, whereas within-individual correlation explains how much individual changes in swimming distance correspond to individual changes in depth. Thus, the strong between-individual correlation would indicate that individual differences in swimming distance are linked to individual differences in depth use. In the same way, we investigated correlations between swimming distance and distance from shore. Parameters were estimated using a Bayesian MCMC sampling method in R package “MCMCglmm” ver. 2.21 (Hadfield and Kruuk 2010). All data were analyzed on the original scales. We ran 1 500 000 resampling with 500 000 burn-in and 100 thinning using noninformative priors.

RESULTS

Daily swimming distance was on average 3.8 ± 1.6 km (mean \pm SD) for all individuals, whereas it varied between individuals from 1.2 ± 1.7 km to 5.9 ± 4.5 km. Daily distance from shore was on average 94.0 ± 14.7 m, and daily mean depth was 4.5 ± 0.1 m for all individuals (Supplement 2).

When daily swimming distance was investigated with different model specifications, including an autoregressive term and a heteroscedastic error structure improved model performance in all cases (Table 2). The best-fit model (i.e., the model with the lowest DIC) was the one with random intercept and slope ($I \times E$) with an autoregressive term AR(7) and a heteroscedastic error structure. The slope of the behavioral reaction norm was estimated as 0.24 ± 0.09 (mean \pm SD), with individual's slopes ranging from 0.00 [95% credible intervals: $-0.27, 0.25$] to 0.34 [0.11, 0.64] among individuals (Figure 1a). There was no correlation between the slope and body size ($t_{14} = 1.77, P = 0.099$), or swimming distance and body size ($t_{14} = 1.69, P = 0.113$ at mean temperature).

Table 2
Rank of the models when allowing heteroscedastic within-individual variance and including autoregressive terms

Model	AR(k)	Within-individual variance	ΔDIC
$I \times E$	7	Heteroscedastic	—
I, E	6	Heteroscedastic	6.4
E	7	Heteroscedastic	42.0
I, E	5	Constant	969.3
$I \times E$	5	Constant	969.5
Null	6	—	973.5
I	6	—	977.8
E	6	Constant	1002.2
$I \times E$	—	Heteroscedastic	1813.4
I, E	—	Heteroscedastic	1980.9
E	—	Heteroscedastic	2802.0
$I \times E$	—	Constant	2980.3
I, E	—	Constant	3104.8
I	—	—	3659.7
E	—	Constant	3718.9
Null	—	—	4204.0

Individual variation in behavioral plasticity led to greater between-individual variance as water temperature increased, from 0.51 km^2 [0.09, 2.26] at $1.8 \text{ }^\circ\text{C}$ to 12.48 km^2 [1.88, 50.51] at $23.0 \text{ }^\circ\text{C}$ (Figure 1b). By contrast, between-individual variance was 2.42 km^2 in model 2 (i.e., random intercept only) with no autocorrelation, and 0.07 km^2 in model 2 with AR(6). Within-individual variance also increased with rising water temperature ($a = 1.49$ [1.36, 1.63], $b = 0.14$ [0.13, 0.15]), ranging from 1.9 km^2 [1.8, 2.1] at $1.8 \text{ }^\circ\text{C}$ to 33.9 km^2 [29.7, 39.0] at $23.0 \text{ }^\circ\text{C}$ (Figure 1c). As a consequence of concurrent changes of between- and within-individual variance, repeatability did not change much across the temperature gradient (Figure 1d), ranging from 0.21 [0.04, 0.54] at $1.8 \text{ }^\circ\text{C}$ to 0.33 [0.10, 0.65] at $12.7 \text{ }^\circ\text{C}$. All coefficients of the autoregressive term were positive except the highest order ($\varphi_1 = 0.48$ [0.44, 0.51], $\varphi_2 = 0.06$ [0.02, 0.10], $\varphi_3 = 0.08$ [0.04, 0.11], $\varphi_4 = 0.14$ [0.10, 0.17], $\varphi_5 = 0.04$ [0.002, 0.08], $\varphi_6 = 0.05$ [0.01, 0.09], $\varphi_7 = -0.03$ [−0.07, 0.001]), indicating that swimming distance up to 6 days before a given measurement day positively influenced the current swimming distance (Figure 2).

We did not find a strong correlation between swimming distance and fish depth between individuals ($r = -0.367$ [−0.765, 0.110]), but they were negatively correlated within individuals ($r = -0.361$ [−0.388, −0.332]). Similarly, we did not find a strong correlation between swimming distance and distance from shore between individuals ($r = -0.205$ [−0.650, 0.298]), but they were negatively correlated within individuals ($r = -0.032$ [−0.066, −0.001]).

DISCUSSION

Our results revealed complex patterns of behavioral variation in response to natural fluctuations of water temperature. Specifically, individual perch differed from one another in how they altered their mean swimming activity in response to changes in water temperature. Subsequently, between-individual variation became more pronounced as water temperature increased. On the other hand, within-individual variation in activity also changed across the temperature gradient, in such a way that individual activity became less predictable with increasing temperature. As a consequence, the concurrent changes in between- and within-individual variation in activity stabilized behavioral repeatability across the temperature gradient by counterbalancing each other. Therefore, our

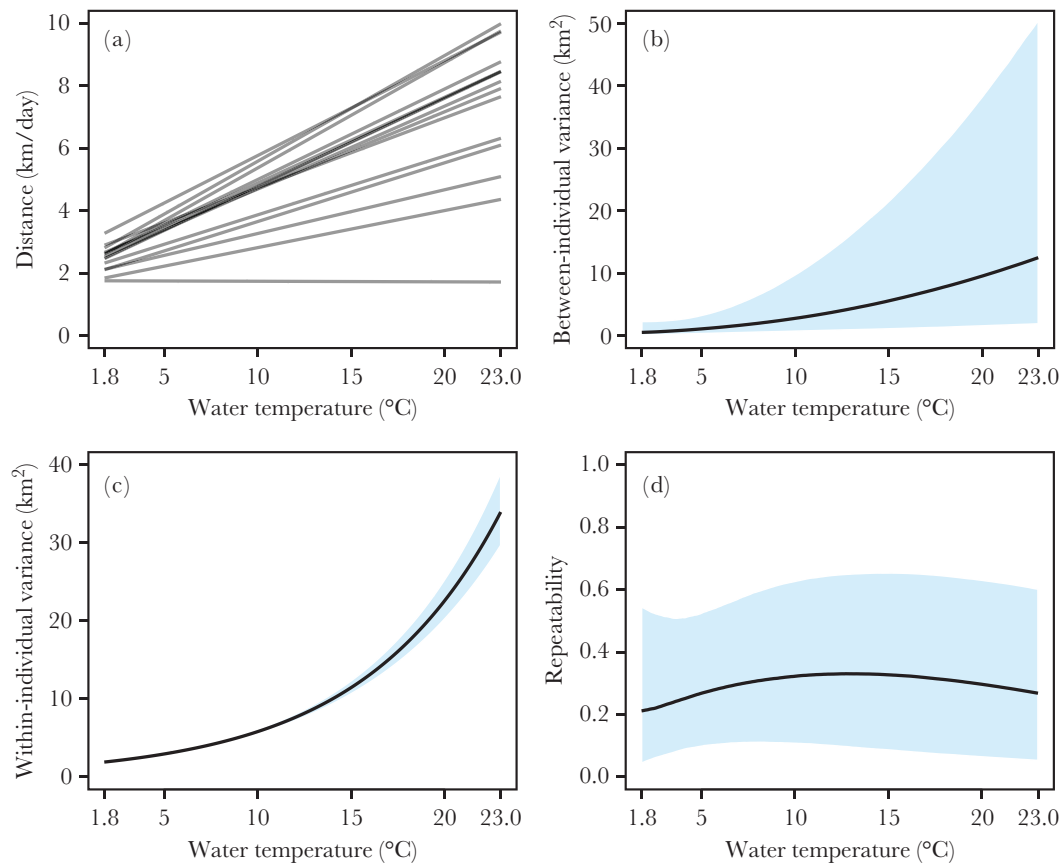


Figure 1

Estimations from the best-fit model ($I \times E$ model with heteroscedastic error and the seventh-order autoregressive term). (a) Estimated individual reaction norms of daily swimming distance (km), (b) between-individual variance, (c) within-individual variance, and (d) repeatability over observed water temperature.

results indicate that a group of perch can simultaneously manage dynamically changing between-individual variation and relatively stable behavioral repeatability across water temperature by adjusting within-individual variation.

In many aquatic ecosystems, water temperature acts as a major ecological gradient (Magnuson et al. 1979), leading to elevated activity with increasing water temperature in wild perch (Neuman et al. 1996). While we found that perch generally increased their activity with temperature, individuals also responded differently from one another to changes in water temperature, in such a way that individual differences in activity were more pronounced as water temperature increased. One possible explanation is the multiplicative effects of temperature on metabolism. Considering that metabolism increases exponentially with temperature (Clarke and Johnston 1999; Cossins and Bowler 1987), rising temperature should increase individual differences in metabolism, which could be translated into pronounced individual differences in activity. In addition, given that environmental stressors modify the link between metabolism and behavior (Killen et al. 2013), higher water temperature could strengthen the link between activity and metabolism and, consequently, increases individual differences in behavior. Thus, it is possible that water temperature reinforced individual differences in activity by controlling metabolism, in a similar way that water temperature diversifies behavioral traits among species (Ohlberger et al. 2013).

Alternatively, water temperature might have influenced individual differences in activity through altering the fitness landscape. Water temperature could influence the strength of intraspecific

competition by regulating basal metabolism (Brown et al. 2004; Abrahams et al. 2007; Ohlberger et al. 2012) and the escape ability of prey (Jacobsen et al. 2004). Considering that consistent individual differences in behavior can arise from a trade-off between feeding and risk-avoidance behavior (Wolf et al. 2007), individual variation in behavior could vary across the environmental gradient when the environment mediates the trade-off between growth and mortality. In this species, the trade-off between growth and mortality can be solved by engaging either in a risky, active strategy, or in a less active strategy to save energy, thus generating individual differences in behavior seen here. Considering the ecological importance of activity on distribution, dispersal, and population dynamics (Johnson et al. 1992), our findings support recent calls for the integration of individual variation in behavior within an ecological framework (Groothuis and Trillmich 2011; Sih et al. 2012; Wolf and Weissing 2012).

In the wild, individual differences in activity could simply arise from individual differences in location. Especially, considering the importance of temperature on activity in ectothermic animals, activity can strongly be influenced by depth, as deeper water is generally colder. This is supported by a negative within-individual correlation between activity and depth, which indicates that individuals were less active when they stayed deeper. However, although a similar trend was observed at a between-individual level, we could not find a strong between-individual correlation, indicating that between-individual variation in activity may not be tightly linked to between-individual variation in depth use. By contrast, we found that activity was negatively correlated with distance from shore

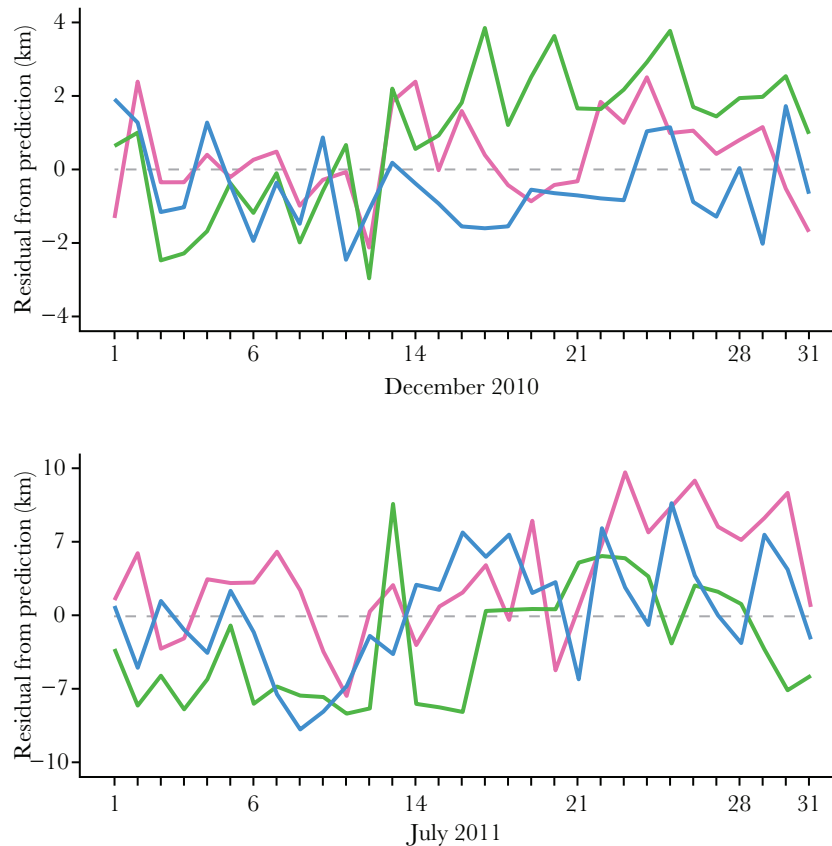


Figure 2

Temporal autocorrelation in activity in 3 example individuals. Residuals from individual reaction norms (the point estimates using posterior medians of the best-fit model) show that individual activity on a given day is strongly correlated with that on the previous days. Top: December 2010, bottom: July 2011.

within individuals, but the correlation was very weak ($r = -0.032$). Further, we could not detect a strong between-individual correlation, indicating that distance from shore may not be linked to activity, regardless of more structures along the shore that could lower predation risk. Further study is needed to understand how individual differences in location influence individual differences in behavior in the wild.

We found that swimming activity was better explained by the model that allows for individual variation in plasticity and a temperature-dependent within-individual variance, compared to the model in which both between- and within-individual variance is fixed across the temperature gradient. In addition, individual variation in behavioral plasticity led to dynamic between-individual variation in activity across water temperature. In line with our results, Fisher et al. (2015) reported that between-individual variation in behavior systematically changes over ontogeny in field crickets, *Gryllus campestris*. Further, within-individual variation in behavior could also change across ecological gradients (Brommer et al. 2008; Pruitt et al. 2011; Briffa 2013; Briffa et al. 2013; Highcock and Carter 2014), and accordingly, behavioral repeatability could also change dynamically across the gradient. Because failure to test these possibilities could potentially inflate the discovery of consistent individual differences in behavior, it is more informative to explore various model frameworks in studying animal personality (Nussey et al. 2007; Dingemanse et al. 2010; Brommer 2013).

We acknowledge that water temperature is without a doubt just one of the many environmental factors that influence activity of fish. For example, water temperature across a year should be highly

correlated with photoperiod, which influences daily activity of visual predators such as perch (Jacobsen et al. 2002). Also, activity of perch we measured not only represents foraging but also be confounded by other activities such as spawning in spring (Craig 1977; Neuman et al. 1996), which is difficult to disentangle in telemetry data. Therefore, our results show how between- and within-individual variation in activity responds to changes in water temperature of the epilimnion as a proxy for an ecological gradient, but it does not necessarily indicate the direct effects of water temperature on activity.

Temporal autocorrelation is often ignored when analyzing repeated measures of behavior, despite the fact that the nonindependence of the behavior violates the model assumption. Our results demonstrate that taking into account the temporal autocorrelation of behavior significantly improved the model performance. Specifically, the best-fit model took the seventh-order autoregressive term, with the correlation coefficients being positive up to the sixth autoregressive term. Thus, swimming activity up to 6 days before a given measurement still influenced the current swimming activity. Temporal autocorrelation in behavior could arise from autocorrelated environmental factors, such as turbidity and prey density. Also, it could arise from labile states that cannot change on very fast timescales, such as short-term memory about good food patches or predators, hormone levels, hunger, parasite, and injuries. These labile states can mask the “true” behavioral variation that may have arisen from life-history trade-offs (Wolf et al. 2007). Consequently, the repeatability estimated from autocorrelated behavioral measures does not necessarily represent the underlying

personality, and thus, the interpretation requires caution. Research on why and when behavior is autocorrelated will be the next step to understand the ecological impacts of consistent individual differences in behavior.

Animal telemetry is a promising tool to understand animal behavior under ecologically relevant contexts and timescales, and the rich data allow us to explore behavioral variation under natural environment. Meanwhile, rapidly developing statistical methods are opening new doors to investigating the complexity of individual variation in behavior. For example, when the interest lies in individual variation in behavioral predictability (i.e., intraindividual variability), one can specify within-individual variance to vary between individuals and quantify between-individual variation in within-individual variation (Bridger et al. 2015; Cleasby et al. 2015; Westneat et al. 2015). Here, by comparing various frameworks within which individual behavior is expressed in response to changes in water temperature, our results highlight the potential importance of the natural abiotic environment on consistent individual differences in behavior under ecologically relevant contexts and timescales. Studying consistent individual differences in behavior in the wild will contribute to understand the potential impacts they could have on the ecological processes and consequences (Groothuis and Trillmich 2011; Sih et al. 2012; Wolf and Weissing 2012).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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