Predictability as a Personality Trait: Consistent Differences in Intraindividual Behavioral Variation

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ABSTRACT: Although animal behavior is generally repeatable, most behavioral variation apparently occurs within rather than across individuals. With the exception of very recent interest in individual behavioral plasticity (consistent differences in responsiveness), this within-individual variation has been largely ignored despite its importance in the study of proximate and ultimate questions about behavior. Here, we repeatedly scored the undisturbed activity of 30 adult male mosquitofish across multiple observation bouts spanning 132 days ($n = 37$ observations per fish). We found that the behavior of some individuals was consistently more predictable in a given context than others. Repeatability for this "intraindividual variation" (IIV; $r = 0.29$) was evident after accounting for individual differences in activity trends across days, and activity responses due to fine-scale temperature variation (i.e., individual plasticity in response to both variables). To our knowledge, this is the first evidence that predictability of behavior is a repeatable characteristic of individual animals. We suggest that IIV represents an important axis of consistent behavioral variation that has previously not been formally considered. Finally, individual differences in predictability may similarly exist for labile morphological and physiological traits but have seemingly not been studied.

Keywords: intraindividual variation, within-individual, IIV, temperament, repeatability, behavioral consistency, plasticity, labile traits, metabolism, hormones.

Introduction

Researchers studying variation in animal behavior have traditionally focused on individual differences in behavior (Clark and Ehlinger 1987; Hayes and Jenkins 1997; Gosling 2001). More recently, there has been a surge of interest in the study of consistent individual differences in behavior (i.e., coping styles, temperament, personality, and behavioral syndromes), because it may hold important answers to proximate and ultimate questions about animal behavior (Réale et al. 2007; Sih and Bell 2008). When a group of animals is observed repeatedly within a given context, we can estimate the proportion of behavioral variation explained by individual differences in their mean values, termed repeatability (Lessells and Boag 1987). Significant repeatability provides evidence for consistent individual differences in behavior.

A recent meta-analysis revealed that behavior is generally repeatable and that roughly 37% of behavioral variation can be attributed to between-individual differences (Bell et al. 2009). These and similar studies of variation in repeatability across ecological contexts may prove important in our efforts to understand how and when individual differences in behavior arise (van Dongen et al. 2010; Jenkins 2011). However, since repeatability is a function of the relative contributions of between- and within-individual variation in behavior for a group of animals and because the majority of behavioral variation (on average) is within individuals (63%), it is crucial that we develop a biological understanding of sources of within-individual behavioral variation (Bell et al. 2009). The same might also be said for other labile traits with similar levels of repeatability as behavior, such as metabolic rate or circulating hormone levels (Nespolo and Franco 2007; Williams 2008).

Within-individual variation in behavior has quite recently attracted interest in the context of individual behavioral "plasticity," whereby individuals may differ in their responsiveness to some gradient or context (Dingemanse et al. 2010; Stamps and Groothuis 2010). For example, individuals may differ in their response to changes to the environment (e.g., temperature: Biro et al. 2009; or with experience: Adriaenssens and Johnsson 2011; see also review in Mathot et al. 2012). Although this form of behavioral variation (plasticity) is often referred to as within-

individual variation, strictly speaking it is not, because it represents across-individual differences in intercepts and slopes with respect to some gradient (Singer and Willett 2003; Littell et al. 2006).

However, even after experimentally and/or statistically controlling for factors that affect average behavior across individuals (e.g., size, gender) and statistically controlling for individual differences in responses to some gradient(s), substantial within-individual variation still remains (for graphical depictions of this variation, see Martin and Réale 2008; Eriksson et al. 2010; Biro 2012; Carter et al. 2012; Stamps et al. 2012). Studies almost invariably treat this remaining within-individual ("residual") variation as random variation around an individual's expected mean, and assume it is the same for all individuals (Singer and Willett 2003; Littell et al. 2006). While some of this variation could result from low precision of observational methods, a recent study revealed that this nonsystematic variation can differ across individuals (Stamps et al. 2012). In other words, some individuals can be much more predictable in a given context than others.

Whereas within-individual behavioral variation has been largely ignored in nonhuman animal research (Stamps et al. 2012), psychologists have studied it for some time now and refer to it as intraindividual variation (IIV; Nesselroade 1991; Siegler 1994; Salthouse 2007; Ram and Gerstorf 2009). In contrast to systematic behavioral variation as a function of time or variation in external stimuli, termed "contextual plasticity" (Dingemanse et al. 2010; Stamps and Groothuis 2010), IIV is the variation that remains after accounting for systematic changes over time or across a contextual gradient and any other factors that could affect behavioral variation within individuals such as hunger, temperature, light levels, or any other factor not controlled for experimentally. In other words, IIV is nonsystematic behavioral variation expressed over time. In order to quantify IIV, one should use individual-specific residuals obtained from a statistical model that accounts for (*a*) systematic changes over time that could differ among individuals, (*b*) the effects of covariates such as size/gender, and (*c*) any other confounding factors not controlled for experimentally (for a full explanation of these methods, see Stamps et al. 2012).

It is not clear what the biological importance of IIV might be, yet there are several studies providing clues (reviewed by Stamps et al. 2012). Research of human learning and cognition suggests that IIV can change over time and with experience (MacDonald et al. 2009; Bielak et al. 2010). Studies such as these and others (reviewed by Sliwinski et al. 2006; Stamps et al. 2012) indicate that IIV is not just random noise about an expected mean value but could reveal biologically important information about behavior and individual differences in behavior not just in humans but in any animal. Indeed, IIV may represent a form of behavioral flexibility that is generated by the brain in order to increase unpredictability of behavior or to facilitate learning (Maye et al. 2007; Brembs 2011; see also "Discussion"). Clearly, our understanding of IIV for nonhuman animals is in its very beginning stages, and we therefore need studies to quantify and describe it before we can efficiently design studies aimed at unraveling its proximate underpinnings and/or ultimate function (Stamps et al. 2012).

One critically important and outstanding question is whether IIV is repeatable. In other words, does predictability consistently differ across individuals in a population? Human studies suggest that individual predictability might well be repeatable (Allaire and Marsiske 2005; Detto et al. 2008). If so, IIV might need to be viewed as another aspect of consistent individual behavioral differences, along with animal personality (consistent differences in mean levels of behavior over time or across contexts), and individual behavioral plasticity (individual differences in responsiveness; Dingemanse et al. 2010; Stamps and Groothuis 2010). And if predictability is repeatable, this also has implications for our statistical models that almost invariably assume each individual has the same residual variance (see "Discussion").

Here, we repeatedly measured the activity rates of individually housed mature male mosquitofish (*Gambusia holbrooki*) over a 4-month interval, using a "multiple burst" sampling design suggested for human studies of IIV (Nesselroade 1991; Salthouse and Nesselroade 2010). For each individual, we estimated IIV using data from each of several bursts and used these estimates of IIV over time to test for repeatability, and we show for the first time that animals do indeed consistently differ in IIV over extended periods of time.

Methods

Sampling Fish from the Wild

Adult mosquitofish were collected February 16, 2011, from the littoral zone of a pond on Centennial Parklands in Sydney, Australia (33°53′ 55″S, 151°14′29″E, surface area ~8,000 m^2). Following recent suggestions (Biro and Dingemanse 2009), we used two different types of sampling gear to minimize behavioral sampling bias; we used large dip nets (50-cm diameter) and also a 12 × 1.5-m beach seine to encircle fish from distance. After transport in a large aerated and insulated box, fish were transferred to one of two 150-L mixed-sex stock tanks. One-half of the surface area of each stock tank was covered from incoming light and filled with dense artificial vegetation. Water was aerated and filtered using two large canister filters (J and T

Industry, JHW-303A, flow ~10 L/min) and one-third of the water was changed each week. During acclimation in stock tanks, photoperiod followed the natural day/night cycles and temperature varied with ambient temperatures in the room (20°–25°C). Fish were fed approximately 0.5-g pellets (500–800 μm, NRD5/8, INVE Aquaculture) four times daily through automated feeders, and an air stone ensured the food was spread out across the surface.

Sampling of Focal Individuals

After more than 2 months, we sampled 30 individuals from one of these laboratory stocks with a dip net (30 × 23-cm net area). In order to minimize the potential for behavioral sampling bias, we dragged the dip net across the open area of the stock tank and separated individuals in order of their vulnerability to capture. This procedure was preceded with five initial hauls from which individuals were returned to the stock tank to avoid the risk of surprise effects on catching. Individuals caught during the first 30 catches ($N = 122$) and those remaining after 50 catches ($N = 117$) represented two groups with different catching vulnerability from which we then selected our fish. Fifteen size-matched males were selected from each group of fish for our experiment (total $N = 30$; difference in mass: $t = 0.889$, $P = .382$, mean ± SE = 0.225 ± 0.004 g; difference in length: $t = 0.251$, $P = .804$, mean ± SE = 28.66 ± 0.21 mm).

Each individual was randomly allocated to its own home tank on April 26, which was placed within a temperature-controlled room with a 12L : 12D photoperiod (fluorescent tubes), where they resided until September 10 (20 cm × 13 cm × 13 cm, 2.8 L water volume). The bottom of each tank was covered with 2 cm of sand, and we used transparent mosquito mesh above the tanks to prevent fish from jumping out. Each tank was subdivided to produce a sheltered area and an open area. All lateral sides of the tank were covered with dark (shelter area) or white (open area) plastic except for the short side of the open area through which observations occurred. All experimental tanks were continuously supplied with clean water from the same flow-through filtration system (ca. 1.8 L/h). Approximately every 14 days, the windows of each tank were cleaned with cotton wool before replacing one-third of the water with fresh water to avoid excessive buildup of nitrates and algae. No observations took place during the 24 h after a cleaning event. Dissolved oxygen in the water remained above 8 mg/L, and levels of ammonia did not exceed 0.1 ppm. Temperature of the room was set to 25°C, and fluctuations from this set temperature were monitored with a data logger (accuracy ± 0.2°C) inside the filter. Water temperature ranged from 24.4° to 26.3°C over the 135-day experiment. On three occasions, tanks were randomly swapped position within the room to avoid any systematic position effects on behavior.

Assays of Individual Activity

The activity level of each individual was scored 37 times between May 4 and September 9, a total duration of 128 days. Each trial lasted 1 h, during which a single observer (B. Adriaenssens) repeatedly scanned each tank every 2 min and noted whether the fish was active or inactive (motionless), for a total of 30 scan samples each. Fish were scored inactive if they did not change position during the first 3 s after being spotted. We expressed activity as the proportion of scans in which the fish was moving, and therefore, this measure of activity approximates the proportion of time spent moving over 1 h. Fish were viewed while the observer sat motionless in the room, and the bright lights over the tanks (no other lighting) helped conceal the observer's presence.

Observations were made twice per day (except May 18 when only one observation was made), once in the morning and once in the afternoon between 1030 and 1700 hours, clustered over three consecutive days (or bursts) of sampling. In order to increase sample size and gain better estimates of IIV, we pooled these short 3-day bursts to create four larger ones as follows: burst 1 (May 4–12, 10 observations per fish), burst 2 (May 13–27, 9 observations per fish), burst 3 (July 20–29, 12 observations per fish), burst 4 (September 7–9, 6 observations per fish). Fish mass was measured at the outset of the experiment and again at the end of June, August, and September, and these data were later included in our statistical models. Our data are available from the Dryad Digital Repository, http://dx.doi.org /10.5061/dryad.h8c10 (Biro and Adriaenssens 2013).

Feeding Protocol

The frequency of feeding varied throughout the experiment as part of a concurrent experiment studying effects of fine-scale food restriction on mosquitofish. The number of feeding occasions was varied across days but was identical for all individuals, whereby each fish received approximately 0.05-g pellets between zero and three times a day, representing >10% of fish body wet weight and well above the amount of food required to feed to satiation; as a result, the time since last feeding varied from 14 to 500 min (mean = 219) and was accounted for in our statistical models (see below).

Statistical Analyses

Repeated observations over time were analyzed using general linear mixed effects models (see Singer and Willett

2003; West et al. 2010). We used the days since the first observation as our principal variable of interest to quantify any systematic changes in activity over time (e.g., acclimation to individual housing) while also controlling for the effects of any potentially confounding variables (i.e., "covariates"; these included water temperature, time of day, time since last feeding, and fish mass).

We began model fitting with a saturated model containing all predictors (intercept, observation day, and the covariates) across the entire observation period. In order to test for individual differences in average initial activity, in activity change across days, in activity patterns with time of day, in response to temperature variation (Biro et al. 2010), and in responses to time since last feeding, we specified the intercept, observation day, water temperature, time of day, and time since last feeding as random effects, respectively. Specifying these effects as random fits a parameter describing the population mean and an associated variance parameter describing variation across individuals for that effect (see Singer and Willett 2003; West et al. 2010). These models are often referred to as random regression. This method generates predictions for individual-specific intercepts and slopes (BLUPs; best linear unbiased predictors). Note that this method generates individual-specific predictions but does not fit individual-specific parameters.

We arrived at the final best model by sequentially culling factors one at a time that were not significant ($P > .1$), starting with those fixed (mean-level) factors with the largest P value (Crawley 2005). Mean-level parameters were not culled if the corresponding random effect (variance parameter) was significant. All analyses were implemented using SAS Proc Mixed, where mean-level effects are evaluated using F-tests, and random effects were tested using z-tests (which are conservative relative to likelihood-based assessment). The Kenward-Roger method was used to estimate degrees of freedom for fixed effects, and we used a Type III sums of squares approach (SAS Institute, Cary, NC). In order to normalize the data, activity was logit transformed as a better alternative to the more traditionally used arcsine–square root transformation for proportion data (Warton and Hui 2010).

After arriving at the final model using the entire data set, and therefore accounting for any systematic changes in behavior across days and/or with respect to variation in the covariates (including time of day), we then used the model predicted values generated by Proc Mixed to compare to the observed values and calculated the residual individual standard deviation (RISD) for each individual within each burst of data, following the suggestions of Stamps et al. (2012). We then used the four estimates of RISD for each fish in a second mixed model analysis where we estimated repeatability of IIV over time by specifying

the intercept and the midpoint observation day within each burst as random intercept and random slope effects. We also tested for simple correlations between IIV and mean levels of behavior across individuals within each burst of samples.

Results

Overall, we observed that individuals differed in initial activity at the outset of the experiment, differed in the rates at which activity changed across days, and differed in their responsiveness to temperature. As a result, plastic responses of individuals to experience and temperature differed between individuals. After accounting for these systematic differences in behavior across individuals using random regression, we found that IIV was repeatable. Some individuals were therefore consistently more predictable in a given context than others.

Model Fitting to Obtain Residuals for IIV Calculation

Mean-Level Effects. Across all of the subjects, activity did not vary systematically as a function of time across the 132 days of observations ($F_{1,27.4} = 0.39$, $P = .54$; $b_{day} = 0.002$, $b_0 = 17.6$), but activity was greater in late afternoon than in the morning ($F_{1,945} = 104.3$, $P < .0001$; $b = 6.4$). On average, activity decreased slightly with temperature ($F_{1,27.5} = 9.2$, $P < .006$; $b_{temp} = -0.87$), but activity did not vary with time since last feeding ($F_{1,39.2} = 0.46$, $P = .50$) or with body mass ($F_{1,27.6} = 0.46$, $P = .50$).

Individual-Level Effects. After accounting for the significant time of day effect, it was evident that individuals consistently differed in activity levels at the start of the experiment (random intercept effect, $P < .004$; variance = 1,073.8), consistently differed in the rates of change in activity across days (random slope effect, $P < .002$; variance = 0.00023), and consistently differed in their responses to temperature variation (random slope effect, $P < .004$; variance = 1.70). All these effects were therefore accounted for in the model when estimating the RISD as our measure of IIV (see fig. 1 for four example individuals and their activity patterns over time). Individuals did not differ in their responses to the time since last feeding (random slope effect, $P = .47$) or in activity patterns within a day (random slope effect, $P = .13$). There was no significant relationship between initial activity and rates of change in activity over time ($P = .12$, covariance = 0.21). Individuals with high initial activity had lower predicted slopes with respect to temperature ($P < .007$, covariance = -42.7), whereby some individuals increased activity with temperature (those with lower initial activity on average) and some decreased with tem-
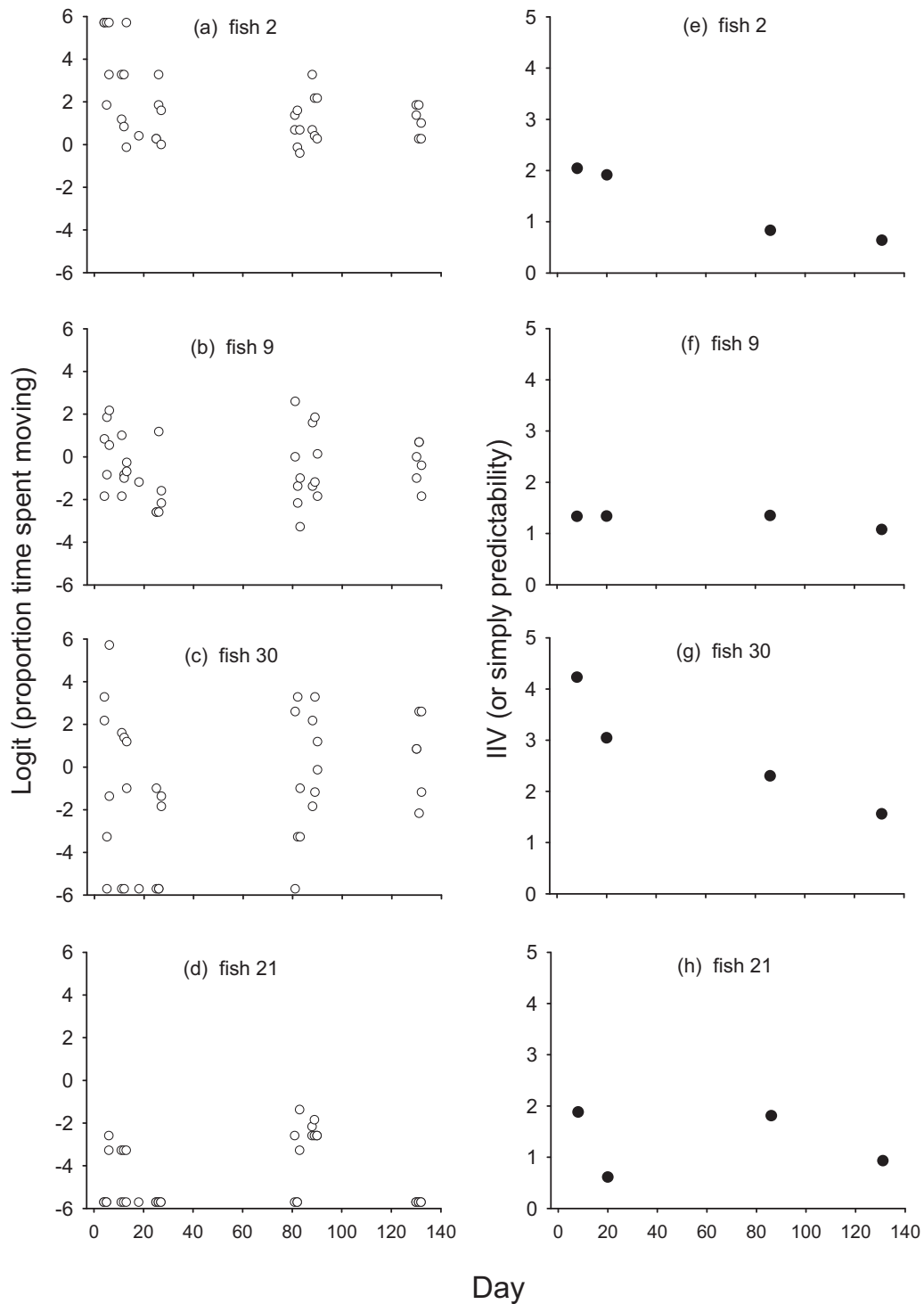
Figure 1: Spontaneous activity of adult male mosquitofish over the 132 days following transfer to individual home tanks experiment (*a–d*) and the corresponding estimates of intraindividual variability (IIV; or simply predictability) of those same three individuals (*e–h*). Shown are four individuals that help to illustrate the range of average activity levels and IIV observed among the fish in the sample. Fish 2 displays generally high levels of activity on average (*a*) and low IIV (*e*). Fish 9 (*b*) and 30 (*c*) display intermediate levels of average activity but very different levels of IIV (*f*, *g*). Fish 21 is rather sedentary (*d*) and with relatively low IIV (*h*). IIV is expressed as the residual individual SD (see "Methods"). Note that IIV values appear a little higher than one would expect for fish 21 given the patterns in the activity data; this is due to some bias inherent in these models, termed "regression to the mean," in instances where there are frequent floor or ceiling values present in an individual sample.

perature (those with higher initial activity on average). There was no significant correlation between individual-level changes in activity over time and changes in activity with temperature (covariance between slopes = -0.0089, $P = .10$; residual variance = 3.55).

Due to the presence of random slope effects, we could not calculate repeatability using standard approaches that only consider a random intercept variance as the sole contributor to between-individual variation. Thus, we followed the general approach to decompose variance as presented by Singer and Willett (2003) in order to calculate day- and temperature-specific repeatability values. In our case, with two random slope effects and covariances, the variance across individuals is composed of a random intercept variance (Var_{int}), two random slope variances (Var_s), covariance between intercepts and slopes (Cov_{is}) and between slopes (Cov_{ss}) and residual variance ($Var_{residual}$). Thus, context-specific repeatability was calculated as repeatability = variance across individuals/total variance = ($Var_{int} + 2^* Cov_{is}^* X_1 + Var_s^* X_1^2 + 2^* Cov_{is}^* X_2 + 2^* Cov_{ss}^* X_1^* X_2 + Var_s^* X_2^2$)/numerator + $Var_{residual}$), where X_1 and X_2 represent day of experiment and temperature.

Using this formula we evaluated repeatability with respect to day by first setting temperature to 24.4°C (lowest value encountered) and found that $r = 0.37$, 0.38, and 0.55 at days 4, 65, and 132 respectively; when we evaluated at 26.3°C (highest value encountered), $r = 0.49$, 0.30, and 0.27.

Is IIV Related to Average Activity Levels?

There was no indication that individual IIV was related to the average predicted activity levels within burst 1 ($F_{1,24} = 0.98$, $P = .33$), burst 2 ($F_{1,24} = 0.3$, $P = .58$), burst 3 ($F_{1,24} = 0.20$, $P = 0.66$), or burst 4 ($F_{1,24} = 0.48$, $P = .49$). Inspections of data plots provided no indication of a quadratic relationship within any of the bursts.

Do Fish Consistently Differ in Levels of IIV over Time?

Individuals consistently differed in the levels of IIV over 128 days (repeatability = 0.29, random intercept $P < .02$, variance = 0.119, SE = 0.056; residual variance = 0.292). There was a trend of declining IIV over time ($F_{1,77} = 54.2$, $P < .0001$), whereby all individuals followed a similar rate of decline, because there was no evidence that individuals significantly varied in the rate of decline (random slope effect, $P = .23$; fig. 1).

To ensure that these results were not simply due to variation in sample size across the bursts (i.e., IIV was lowest in burst 4, which had fewer observations), we also calculated repeatability of IIV when assessed from the short 3-day bursts of data (see "Methods"). Assessment of IIV within these much smaller bursts of data also revealed consistent individual differences in the levels of IIV (repeatability = 0.20, random intercept $P < .02$, variance = 0.125, SE = 0.059; residual variance = 0.486) and declining IIV over time ($F_{1,129} = 45.7$, $P < .0001$). Again, there was no evidence that individuals varied in the rate of decline of IIV over time (random slope effect, $P = .31$) and again there were no correlations between IIV and mean levels of activity within any of the six (3-day) bursts (all $P > .28$).

Discussion

Overall, we observed that individuals consistently differed in activity rates, in their patterns of activity across days (some increased over time; others decreased), and in their activity responses to fine-scale temperature variation (again, some increased with temperature, others decreased). After accounting for these systematic, predictable differences in behavior across individuals, and a tendency for fish to be more active late in the day on average, we observed that (*a*) substantial intraindividual variation remained, (*b*) this intraindividual variability (IIV) differed across individuals, and (*c*) IIV was consistent within individuals over an extended period of time. Here, for the first time to our knowledge, we have demonstrated that IIV is repeatable in animals and might therefore be considered as another axis of animal behavioral variation in addition to personality (consistent individual differences across time or contexts) and plasticity (consistent individual differences in response to some contextual gradient). Therefore, consideration of IIV is likely to provide us with a richer understanding of behavioral variation, not just within but also across individuals.

Realization that predictability (IIV) may be a consistent attribute of animals will add substantially to the way we view and study animal personality, and particularly, behavioral plasticity. Indeed, this study found that individuals differed in thermal responsiveness, in patterns of behavior over time (two forms of plasticity), and in IIV, suggesting complex patterns of behavioral variation that need to be considered when studying animal behavioral variation in future studies. A relevant next step is to attempt to explain the biological significance of this variation. As in studies of animal personality (Sih et al. 2004), explanations for individual differences in predictability can be broadly subdivided in two categories: nonfunctional or functional explanations. Nonfunctional differences in IIV could arise if behavioral predictability is a by-product of constraints inherent to the proximate architecture of behavior. Alternatively, individual differences in predictability themselves may be the result of adaptive processes fa-

voring variation within populations. Below we discuss these explanations in more detail.

Proximate constraints could give rise to nonfunctional variation in predictability across individuals. A common genetic or hormonal mechanism could, for example, cause IIV to be linked with other traits that have more direct fitness consequences (McGlothlin and Ketterson 2008). Genetic correlations could then constrain the evolution of IIV as an independent trait. Whereas some of the resulting links may at first hand appear nonintuitive (e.g., aggressive individuals tend to form routines; Benus et al. 1990), others may follow more logically from the proximate architecture of behavior. Fluctuating hormone levels triggered by the hunger status of the animal can, for example, lead to cycles in feeding related activity patterns throughout the day (Tolkamp et al. 1998). Individual differences in predictability may then reflect individual variation in digestive function or metabolism. Satiation is, however, unlikely to have affected differences in IIV across individuals in our study because time since last feeding did not affect behavior, and individuals were treated identically with respect to feeding. We also accounted for time of day effects on activity; activity levels tended to increase in late afternoon similarly for all individuals since time of day affected behavior only as a main fixed effect but not as a random slope effect.

Alternatively, nonfunctional differences in behavioral predictability could result as a side effect of individual variation in cognitive processes. Hermit crabs (*Pagurus bernhardus*), for instance, that took longer to emerge from their shell following disturbance also had a higher IIV within a single burst of sampling. It was suggested that this link reflects a cognitive constraint to the ability of hermit crabs to estimate time intervals when latencies were high (and presumably risk was perceived to be considerable; Stamps et al. 2012). In this study we observed no correlation between predictability and mean levels of activity, which could indicate a lesser role of this cognitive constraint.

Evolutionary theory for why individuals may differ in predictability has not been developed. However, two functional explanations for IIV were recently proposed by Brembs (2011), who suggested that IIV could be a form of adaptive stochastic variation in behavior facilitating trial and error learning or to reduce vulnerability to predators or competitors. Both explanations are consistent with our data showing declines in IIV over time. Coral reef fish also become more predictable in their activity rate over time as they apparently acclimate and settle down into relatively stable and repeatable patterns of behavior when given time to habituate to the risks and benefits of their new environment (Biro 2012).

Especially during the first days of isolation, variable behavior could be a result of habituation to a context where public information on optimal behavior is absent. Mosquitofish, in particular, are known to differ in social phenotypes (Burns et al. 2012) and make more accurate risk-taking decisions when in a group (Ward et al. 2011). The shift in use of public to private information may therefore initially force individuals into a strategy of trial and error (causing high IIV), before behavioral routines are developed (Danchin et al. 2004). Since the value of private versus social learning strategies depends on the frequency of social learners in the group, we would also expect individuals in a group to differ in their reliance on public information (Barnard and Sibly 1981). It seems thus that cognitive processes may play an important role in generating individual differences in predictability in our model species. Links between predictability and individual learning are further supported by human studies, where greater IIV was associated with rapid gains in cognitive task performance (Allaire and Marsiske 2005). Other studies reveal that human IIV can change over time and with experience (MacDonald et al. 2009; Bielak et al. 2010).

Alternatively, individuals may differ in predictability in response to varying perceived predation risks. The benefit of randomness in vigilance behavior has mostly been studied in the context of predator scanning in foraging groups. Theoretical studies in this field predict that unpredictable behavior is most efficient in reducing vulnerability to "stalking" predators that might key in on predictable patterns of prey movement (Bednekoff and Lima 1998, 2002). The observation of consistent individual differences in predictability now provides a starting point to study differential vulnerability of predictable and unpredictable individuals to predation.

Another way to discriminate between nonfunctional and functional explanations is to study whether patterns of IIV across populations correspond with some local gradient of selection (e.g., Dingemanse et al. 2007). Given the scarcity of studies in the field and unavoidable differences in power across studies, it is too early to discern specific patterns about the biological significance of IIV across studies. In practice, IIV could also result from individual differences in sensory sensitivity to some unaccounted external factor (e.g., individuals with a highly sensitive sensory system have greater IIV). Future studies should therefore carefully control, measure, and account for variation in environmental factors such as those demonstrated to be of importance in this study. Only this will allow certainty in discriminating between nonsystematic (IIV) and systematic (plasticity) behavioral variation. The difficulty of doing this in the field may obstruct our ability to understand how common IIV really is in natural populations. Yet, recent studies on migrating roach (*Rutilus rutilus*; Brodersen et al. 2012) showed that individual roaches tend

to differ in the variability of timing and destination of yearly migration movements, suggesting IIV in migration decisions in a wild population. Another difficulty with the study of IIV can follow from the requirement to collect a large number of repeated observations on the same animals, which increases the risk of observers getting to know individuals and introducing observer bias. In this study this effect was bypassed by the use of strict scoring categories and regular swapping the position of tanks throughout the experiment. Alternatively, future studies could use software to automatically score behavior from video recordings (e.g., Adriaenssens and Johnsson 2013).

Whereas this study focused on individual differences in the predictability of behavioral traits, similar differences in predictability could exist in other labile traits. Average levels of metabolic rate or circulating hormone levels show comparable patterns of individual variation as behavioral traits (Nespolo and Franco 2007; Williams 2008). Closer scrutiny of the predictability of such traits could not only be helpful for our understanding of behavioral predictability, they could also increase our mechanistic understanding of physiological traits themselves (Romero 2004). Another area of research where the study of predictability could prove fruitful is the study of animal signaling, where individuals could differ in the temporal variability of acoustic or variable morphological traits (Riebel and Slater 2003; Delhey and Kempenaers 2006).

Finally, our results indicate that we should exercise caution when interpreting statistical analyses of behavioral data because nearly all parametric linear models assume that each individual has equal residual variance (but see Briffa et al. 2013, where a unique residual variance is fitted to each individual and shown to provide a near-identical result to the simpler approach employed here). Individual differences in IIV may therefore be important when we quantify repeatability, which is assessed across a group of individuals, and assess whether it is significantly different from zero. The statistical implications of IIV for hypothesis testing is beyond the scope of this article, but it has been shown that parameters derived from mixed models and individual-specific predictions derived from BLUPs appear robust and do not vary substantially from individual-specific models that (of course) do not assume constant variance across individuals (Stamps et al. 2012).

Acknowledgments

Literature Cited

Adriaenssens, B., and J. I. Johnsson. 2011. Shy trout grow faster: exploring links between personality and fitness-related traits in the wild. Behavioral Ecology 22:135–143.

———. 2013. Natural selection, plasticity and the emergence of a behavioural syndrome in the wild. Ecology Letters 16:47–55.

Allaire, J. C., and M. Marsiske. 2005. Intraindividual variability may not always indicate vulnerability in elders' cognitive performance. Psychology and Aging 20:390–401.

Barnard, C. J., and R. M. Sibly. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour 29:543–550.

Bednekoff, P. A., and S. L. Lima. 1998. Randomness, chaos and confusion in the study of antipredator vigilance. Trends in Ecology and Evolution 13:284–287.

———. 2002. Why are scanning patterns so variable? an overlooked question in the study of anti-predator vigilance. Journal of Avian Biology 33:143–149.

Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. Animal Behaviour 77:771–783.

Benus, R. F., S. Dendaas, J. M. Koolhaas, and G. A. Vanoortmerssen. 1990. Routine formation and flexibility in social and nonsocial behavior of aggressive and nonaggressive male mice. Behaviour 112:176–193.

Bielak, A. A. M., D. F. Hultsch, E. Strauss, S. W. S. MacDonald, and M. A. Hunter. 2010. Intraindividual variability is related to cognitive change in older adults: evidence for within-person coupling. Psychology and Aging 25:575–586.

Biro, P. A. 2012. Do rapid assays predict repeatability in labile (behavioural) traits? Animal Behaviour 83:1295–1300.

Biro, P. A., and B. Adriaenssens. 2013. Data from: Predictability as a personality trait: consistent differences in intraindividual behavioral variation. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.h8c10.

Biro, P. A., C. Beckmann, and J. A. Stamps. 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. Proceedings of the Royal Society B: Biological Sciences 277:71–77.

Biro, P. A., and N. J. Dingemanse. 2009. Sampling bias resulting from animal personality. Trends in Ecology and Evolution 24:66–68.

Brembs, B. 2011. Towards a scientific concept of free will as a biological trait: spontaneous actions and decision-making in invertebrates. Proceedings of the Royal Society B: Biological Sciences 278:930–939.

Briffa, M., D. Bridges, and P. A. Biro. 2013. How does temperature affect behavior? multilevel analysis of plasticity, personality and predictability in hermit crabs. Animal Behaviour 86:47–54.

Brodersen, J., P. A. Nilsson, B. B. Chapman, C. Skov, L.-A. Hansson, and C. Brönmark. 2012. Variable individual consistency in timing and destination of winter migrating fish. Biology Letters 8:21–23.

Burns, A. L. J., J. E. Herbert-Read, L. J. Morrell, and A. J. W. Ward. 2012. Consistency of leadership in shoals of mosquitofish (*Gambusia holbrooki*) in novel and in familiar environments. PLoS ONE 7:e36567.

Carter, A. J., R. Heinsohn, A. W. Goldizen, and P. A. Biro. 2012.

Boldness, trappability and sampling bias in wild lizards. Animal Behaviour 83:1051–1058.

Clark, A. B., and T. J. Ehlinger. 1987. Patterns and adaptation in individual behavioural differences. Pages 1–47 *in* P. P. G. Bateson and P. H. Klopfer, eds. Perspectives in ethology. Plenum, New York.

Crawley, M. J. 2005. Statistics: an introduction using R. Wiley, New York.

Danchin, E., L.-A. Giraldeau, T. J. Valone, and R. H. Wagner. 2004. Public information: from nosy neighbors to cultural evolution. Science 305:487–491.

Delhey, K., and B. Kempenaers. 2006. Age differences in blue tit *Parus caeruleus* plumage colour: within-individual changes or colour-biased survival? Journal of Avian Biology 37:339–348.

Detto, T., J. M. Hemmi, and P. R. Y. Backwell. 2008. Colouration and colour changes of the fiddler crab, *Uca capricornis*: a descriptive study. PLoS ONE 3:e1629.

Dingemanse, N. J., A. J. N. Kazem, D. Réale, and J. Wright. 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology and Evolution 25:81–89.

Dingemanse, N. J., J. Wright, A. J. N. Kazem, D. K. Thomas, R. Hickling, and N. Dawnay. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. Journal of Animal Ecology 76:1–11.

Eriksson, C. A., D. J. Booth, and P. A. Biro. 2010. "Personality" in two species of temperate damselfish. Marine Ecology Progress Series 420:273–276.

Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? Psychological Bulletin 127:45–86.

Hayes, J. P., and S. H. Jenkins. 1997. Individual variation in mammals. Journal of Mammalogy 78:274–293.

Jenkins, S. H. 2011. Sex differences in repeatability of food-hoarding behaviour of kangaroo rats. Animal Behaviour 81:1155–1162.

Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Littell, R. C., G. Milliken, W. Stroup, R. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. 2nd ed. SAS Institute, Cary, NC.

MacDonald, S. W. S., S.-C. Li, and L. Bäckman. 2009. Neural underpinnings of within-person variability in cognitive functioning. Psychology and Aging 24:792–808.

Martin, J. G. A., and D. Réale. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. Animal Behaviour 75:309–318.

Mathot, K. J., J. Wright, B. Kempenaers, and N. J. Dingemanse. 2012. Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. Oikos 121:1009–1020.

Maye, A., C.-H. Hsieh, G. Sugihara, and B. Brembs. 2007. Order in spontaneous behavior. PLoS ONE 2:e443.

McGlothlin, J. W., and E. D. Ketterson. 2008. Hormone-mediated suites as adaptations and evolutionary constraints. Philosophical Transactions of the Royal Society B: Biological Sciences 363:1611–1620.

Nespolo, R. F., and M. Franco. 2007. Whole-animal metabolic rate is a repeatable trait: a meta-analysis. Journal of Experimental Biology 210:2000–2005.

Nesselroade, J. R. 1991. The warp and woof of the developmental fabric. Pages 213–240 *in* R. Downs, L. Liben, and D. Palermo, eds. Visions of development, the environment, and aesthetics: the legacy of Joachim F. Wohlwill. Erlbaum, Hillsdale, NJ.

Ram, N., and D. Gerstorf. 2009. Time-structured and net intraindividual variability: tools for examining the development of dynamic characteristics and processes. Psychology and Aging 24:778–791.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews 82:291–318.

Riebel, K., and P. J. B. Slater. 2003. Temporal variation in male chaffinch song depends on the singer and the song type. Behaviour 140:269–288.

Romero, L. M. 2004. Physiological stress in ecology: lessons from biomedical research. Trends in Ecology and Evolution 19:249–255.

Salthouse, T. A. 2007. Implications of within-person variability in cognitive and neuropsychological functioning for the interpretation of change. Neuropsychology 21:401–411.

Salthouse, T. A., and J. R. Nesselroade. 2010. Dealing with short-term fluctuation in longitudinal research. Journals of Gerontology B 65:698–705.

Siegler, R. S. 1994. Cognitive variability: a key to understanding cognitive development. Current Directions in Psychological Science 3:1–5.

Sih, A., and A. Bell. 2008. Insights from behavioral syndromes for behavioral ecology. Advances in the Study of Behavior 38:277–281.

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology and Evolution 19:372–378.

Singer, J. D., and J. B. Willett. 2003. Applied longitudinal data analysis: modeling change and event occurrence. Oxford University Press, New York.

Sliwinski, M. J., J. M. Smyth, S. M. Hofer, and R. S. Stawski. 2006. Intraindividual coupling of daily stress and cognition. Psychology and Aging 21:545–557.

Stamps, J. A., M. Briffa, and P. A. Biro. 2012. Unpredictable animals: individual differences in intraindividual variability (IIV). Animal Behaviour 83:1325–1334.

Stamps, J. A., and T. G. G. Groothuis. 2010. The development of animal personality: relevance, concepts and perspectives. Biological Reviews 85:301–325.

Tolkamp, B. J., D. J. Allcroft, E. J. Austin, B. L. Nielsen, and I. Kyriazakis. 1998. Satiety splits feeding behaviour into bouts. Journal of Theoretical Biology 194:235–250.

van Dongen, W. F. D., K. Maldonado, P. Sabat, and R. A. Vasquez. 2010. Geographic variation in the repeatability of a personality trait. Behavioral Ecology 21:1243–1250.

Ward, A. J. W., J. E. Herbert-Read, D. J. T. Sumpter, and J. Krause. 2011. Fast and accurate decisions through collective vigilance in fish shoals. Proceedings of the National Academy of Sciences of the USA 108:2312–2315.

Warton, D. I., and F. K. C. Hui. 2010. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10.

West, S. G., E. Ryu, O. M. Kwok, and H. Cham. 2010. Multilevel modeling: current and future applications in personality research. Journal of Personality 79:2–50.

Williams, T. D. 2008. Individual variation in endocrine systems: moving beyond the "tyranny of the golden mean." Philosophical Transactions of the Royal Society B: Biological Sciences 363:1687–1698.