

Small within-day increases in temperature affects boldness and alters personality in coral reef fish

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Consistent individual differences in behaviour, termed personality, are common in animal populations and can constrain their responses to ecological and environmental variation, such as temperature. Here, we show for the first time that normal within-daytime fluctuations in temperature of less than 3°C have large effects on personality for two species of juvenile coral reef fish in both observational and manipulative experiments. On average, individual scores on three personality traits (PTs), activity, boldness and aggressiveness, increased from 2.5- to sixfold as a function of temperature. However, whereas most individuals became more active, aggressive and bold across temperature contexts (were plastic), others did not; this changed the individual rank order across temperatures and thus altered personality. In addition, correlations between PTs were consistent across temperature contexts, e.g. fish that were active at a given temperature also tended to be both bold and aggressive. These results (i) highlight the importance of very carefully controlling for temperature when studying behavioural variation among and within individuals and (ii) suggest that individual differences in energy metabolism may contribute to animal personality, given that temperature has large direct effects on metabolic rates in ectotherms.

Keywords: plasticity; metabolism; behaviour; consistency; temperament; syndrome

1. INTRODUCTION

We now know that personality is common in animal populations, and that this phenomenon may have far-reaching implications for understanding how animals respond to ecological and environmental challenges (e.g. Sih *et al.* 2004; Reale *et al.* 2007). For instance, variation across individuals in personality traits (PTs), such as activity and boldness, can affect food acquisition and encounter rates with predators (Biro *et al.* 2006; Stamps 2007), and can even affect the likelihood of an individual being captured by sampling or harvesting gear (Biro & Dingemans 2009). PTs are assumed to result from underlying tendencies that affect behaviour in different contexts, that vary across individuals and that are reasonably stable across time (Reale *et al.* 2007).

Of the many contexts that might affect the expression of PTs, one of the most important is ambient temperature, given that the vast majority of animal species on Earth are ectotherms. It is well known that large differences in ambient temperature can affect the mean values (across individuals) of a variety of ecologically important behaviours (Brodie & Russell 1999; Angilletta *et al.* 2003). However, most researchers have ignored small temperature fluctuations of a few degrees or less, particularly when these fall within an organism's normal daily temperature range (e.g. Magellan & Magurran 2007), and even temperature-controlled regimes in the laboratory have operating variance that is typically disregarded. Ignoring the effects of minor variation in

temperature on personality may be risky because (i) metabolic rate increases exponentially with temperature in ectotherms, meaning that small increases in ambient temperature have large effects on energy metabolism (e.g. Schmidt-Nielsen 1991; Clarke & Johnston 1999) and (ii) individual differences in energy metabolism might be linked to PTs in animals (Biro & Stamps 2008; Careau *et al.* 2008). Given strong direct effects of temperature on mean metabolic rates in ectotherms, we might expect compensatory increases in PTs related to food intake rates when temperatures rise. For example, an increase in temperature of less than 3°C resulted in large increases in average fish activity rates across identical replicate fish populations; higher activity increased feeding rates, allowing individuals to maintain high growth rates despite higher metabolic costs, but at a cost of higher predation mortality (Biro *et al.* 2007).

To date, studies of the effects of temperature on consistent individual differences in behaviour are virtually absent. We found only one article on this topic, which focused on anti-predator behaviour (Brodie & Russell 1999). As a result, it is currently unknown whether individual differences in multiple PTs, or correlations between PTs, are maintained over the range of temperatures that an ectothermic individual would normally experience during its daily activities.

Here, we show not only that individual fish consistently differed with respect to three PTs (aggressiveness, boldness and activity rates) at a given temperature, but that small daily temperature increases of just a few degrees had

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dramatic effects on mean-level activity, boldness and aggressiveness. Even more important, individuals differed with respect to their responses to minor variations in temperature, whereby rank order of individual scores on each of these traits (personality) changed as a function of temperature. At the same time, correlations between different PTs were maintained at different temperatures. Our results suggest that strict experimental (or statistical) control of temperature is absolutely essential in studies of behaviour and personality in ectotherms, a point that has previously been overlooked.

2. MATERIAL AND METHODS

Our study consisted of two laboratory experiments examining temperature effects on PTs of young damselfish. The first was an observational study using recently settled juvenile *Pomacentrus moluccensis* as subjects, where the daytime water temperature of aquaria fluctuated across the range of temperatures that would normally be experienced by these fish in the field. This first experiment was not designed to study the effects of temperature on personality, but rather to quantify aspects of personality in coral reef fish. The large effects of temperature on personality revealed in the first experiment led us to conduct a second experiment in order to establish a causal link between PTs and temperature. The second laboratory experiment used newly settled juvenile *Pomacentrus bankanensis*, and directly manipulated water temperatures across a similar range as in the first experiment.

(a) *Observational experiment*

The first experiment was conducted in the laboratory at One Tree Island Field Research Station (University of Sydney), located on the southern Great Barrier Reef (GBR), Australia (23°30' S, 152°5' E). We captured recently settled lemon damselfish (*P. moluccensis*) while snorkelling, using hand nets and 5 per cent clove oil solution, and immediately transferred them to a large holding aquaria with fresh flow-through sea water. This species is common and widespread on shallow reefs on the southern GBR. All fish were captured from a single area of a shallow patch reef, less than 2 m deep at low tide. From a much larger sample of fish, we selected 33 individuals with a relatively narrow range of body sizes (mean total length = 16 mm, s.e. = 0.1, range = 14–22 mm). Fish of this size had lived on the reef for about one week. We placed each individual into its own opaque plastic aquarium (30 × 13 × 16 cm, filled to depth of 8 cm), each of which contained a piece of coral rubble (ca 7 × 5 × 1.5 cm) under which fish could shelter. Light levels were maintained constant using artificial lights during daylight hours. We fed the fish newly hatched live *Artemia* nauplii several times a day to provide ad libitum food prior to and during the experiment. Excess live food was thus present in aquaria at all times. As fish were housed individually and fed to excess, any behavioural differences observed among individuals should not reflect differences in recent feeding opportunity. Water in the aquaria was changed at the end of every second day with fresh sea water (changing 90% of the water) after all observations were complete to allow fish to settle overnight before observations the next morning. Aquaria were immediately restocked with live food after changing the water. Fish were acclimated to their new surroundings for 1.5 days prior to the first behavioural observations.

We focused on three behavioural traits that have been considered to be PTs in previous studies: activity, boldness and aggressiveness (Reale *et al.* 2007). Direct behavioural observations were made while seated motionless on a tall chair with wheels from a short distance away; slow and careful movement between aquaria while seated did not appear to disturb fish. Activity was estimated by quantifying the cumulative distance moved during a 3 min observation period. To aid this estimation, we marked the rectangular aquarium into three 10 cm sections and noted the position occupied by the fish at the end of each 5 s interval. Boldness was estimated as the latency for the fish to emerge from its shelter following a simulated predation attempt. We simulated a predatory threat by rapidly dipping an aquarium dip net handle into the centre of the aquaria; all fish responded by taking refuge underneath the coral rubble. Aggression was measured as the response of the fish to the introduction of a live conspecific contained within a tiny glass jar (4.5 cm diameter, 6 cm tall). We selected a fish that was smaller than all the test fish to encourage aggressive behaviour, and used the same individual for successive tests. We chose this method because a pilot experiment indicated that using a mirror test for assessing aggressiveness elicited no responses from fish. We quantified the frequency of rapid swimming directly towards the intruder ending with either a sudden stationary posture immediately in front of the intruder or actually hitting the jar with its nose.

We observed fish over an 11-day period (1–11 February), from 10.00 to 12.00 and from 14.00 to 17.00 each day. These sampling hours were well outside the dawn and dusk periods (sunrise: 05.33, sunset: 18.38), when greater levels of activity, aggression and foraging effort are typically observed for fish in general, and coral reef fish in particular (Boujard & Leatherland 1992; Kadri *et al.* 1997a,b; Jennings *et al.* 1998; Blyth *et al.* 1999). We collected data on each PT in a manner to ensure a relatively even distribution of data on each individual from morning and afternoon sampling periods and across days. Only one PT per time period was measured (e.g. activity in the morning, boldness in the afternoon); the order of PTs that were quantified was randomly chosen. We always observed fish in the same order when quantifying a particular PT in order to minimize potential disturbance, and if present, to keep any order-related disturbance effects consistent across trials. Water temperatures fluctuated naturally according to ambient air temperatures inside the open-air but shaded laboratory, and ranged from a minimum of 24°C to a maximum of 28°C. Most observations of behaviour were obtained at late morning temperatures of 25°C (range 24–25.5°C) and afternoon temperatures of 27°C (range 26–28°C). Daily temperature fluctuations of this range are common at this time of year at One Tree Island lagoon (P. A. Biro 2007, unpublished data). A study at Heron Island lagoon, 2 km away, indicated that daytime fluctuations in water temperature ranged from 26 to 33°C at low tide and from 25 to 29°C at high tide within ponded lagoon sites like that at One Tree Island at this time of year (Jimenez *et al.* 2008). Our sampling regime provided data for each fish for all three PTs across an approximately three-degree range of temperatures, with similar numbers of data points per individual at low and high ends of the temperature range. For analyses, we had approximately 15, nine and six observations per individual for activity, aggression and boldness, respectively, spread out across the 11-day experiment.

(b) Manipulative experiment

The second experiment was conducted in a temperature-controlled laboratory at Lizard Island Research Station (Australian Museum), located on the northern GBR, Australia (14°41' S, 145°27' E). Using light traps anchored just outside the reef crest (Meekan *et al.* 2001), we captured large numbers of a different species of damselfish (*P. bankanensis*) that were settling on the reef at the end of their planktonic larval stage. These fish were naive to life on the reef, in contrast to the fish in the first experiment. Fish were transferred to a large holding aquarium with fresh flow-through sea water at ambient (ca 28°C) temperature. We selected 30 individuals with a near-equal body size (mean standard length = 12.9 mm, range = 12.7–13.5) and placed each individual into its own plastic aquarium (25 × 16 × 17 cm, filled to a depth of 10 cm) containing a layer of sand on the bottom and a short section of a plastic pipe at one end for shelter. The aquaria were visually isolated from one another and from the observer using plastic sheeting. Fish were acclimated, fed ad libitum and their water changed, as in the previous experiment. Water temperature was maintained at an average of 29.0°C (range 28.4–29.5°C) for the first half of the experiment, and an average of 26.2°C (range 25.0–27.2°C) for the second half. We measured temperatures in each aquarium at the end of observations and used tank-specific values in analyses as before.

Based on the results from the first experiment, we decided to gather more data on fewer PTs (activity and boldness), in order to increase our power to detect individual differences in response to temperature (§2c). Activity was estimated by quantifying the number of times the fish crossed over the midpoint of the aquarium during a 2 min observation period. To aid estimation, we marked the rectangular aquarium into two equal sections. We chose to alter the methods for this particular PT as we were working with a new species and felt this method better captured the movements of the fish owing to many rapid movements over short time intervals that the previous method would not capture as well. Boldness was measured as in the previous experiment. We quantified both PTs twice each day, once in the morning (9.00–11.30) and once in the afternoon (14.00–16.30). Within each observation period, we allowed approximately an hour to elapse between scoring a PT (e.g. activity) for an individual and scoring another PT (e.g. boldness) for that same individual; the fish were always observed in the same order for reasons as outlined above. We observed fish over a 13-day period (26 November–8 December), yielding a total of approximately 24 observations per individual per PT, evenly distributed across morning and afternoon sampling.

(c) Statistical analyses

In order to assess the consistency of behaviour across different temperatures, we used a general linear model with mixed effects (fixed and random) using Proc Mixed (SAS Institute). We specified water temperature as our main fixed effect of interest, and the intercept and slope of the PT with temperature as random effects (covariance structure type = 'unstructured'). In this type of model, the random intercept effect describes the extent to which individual differences in behaviour are consistent across contexts (i.e. contextual generality), e.g. whether individuals who had higher behavioural scores than others at one temperature also tended to have relatively higher scores at other temperatures. Thus, the

random intercept effect describes the extent to which the rank order of individual scores is maintained across contexts, which is one of the key criteria for PTs. In statistical terms, this approach fits a separate 'regression' line for individuals that all possess the same slope with temperature, but differ in their intercept. In contrast, the random slope effect describes the extent to which different individuals within the group differ in response to changes in temperature context (i.e. contextual plasticity; *sensu* Stamps & Groothuis in press), e.g. whether some individuals in the sample have much stronger behavioural responses to differences in temperature than others. This approach to determining levels of context generality in behaviour has also been referred to as quantifying 'behavioural reaction norms' (reviewed in Dingemans *et al.* in press).

We tested whether the variance components associated with random intercepts and random slopes were statistically significant using the 'covtest' option. In addition to temperature, we also added the body size of fish and the observation number as covariates to statistically control for any body size effects or potential habituation to experimental protocols, respectively. In the second experiment, we conducted the same analysis, and in addition to temperature also tested for observation number, time of day and body size.

We began model-fitting with a saturated model that included the random effects of intercept and slope and all fixed effects, then removing non-significant ($p > 0.1$) fixed effects and refitting the model. If the variance estimate for the random slope effect was not significant, we omitted it from the model and refit with only the random intercept effect; the random intercept effect was significant in all cases, indicating consistent differences in behaviour across contexts (i.e. evidence for PTs). We used the Kenward–Roger method to calculate degrees of freedom for the fixed effects, and tested the significance of each using a type III approach. Activity and aggression data were $\log_e(x + 1)$ and square root $(x + 1)$ transformed prior to analyses to normalize the data.

In order to test for correlations among the PTs, we first calculated model-predicted values for each individual at 25 and 27°C (for experiment 1) and 26 and 29°C (for experiment 2) by using the best linear unbiased predictors and holding significant fixed effects constant. We then used these predicted values to examine the Spearman correlations among PTs at each of the two temperatures (e.g. we computed the correlation between activity and aggressiveness across individuals at 25°C, and again for the same two PTs at 27°C).

3. RESULTS**(a) Observational study of temperature effects**

On average, individual activity rates increased fivefold with only a small increase in temperature ($F_{1,33} = 19.9$, $p < 0.0001$; figure 1a). However, individuals consistently and substantially differed in their activity levels at lower temperatures (random intercept effect: $p < 0.001$), and the extent to which activity increased with temperature also differed among individuals (random slope effect: $p < 0.02$; figure 1a). As a result, the rank order of scores for the individuals in the group changed with temperature context, altering personality. Some individuals had virtually the same levels of activity at all temperatures (low contextual plasticity), but most

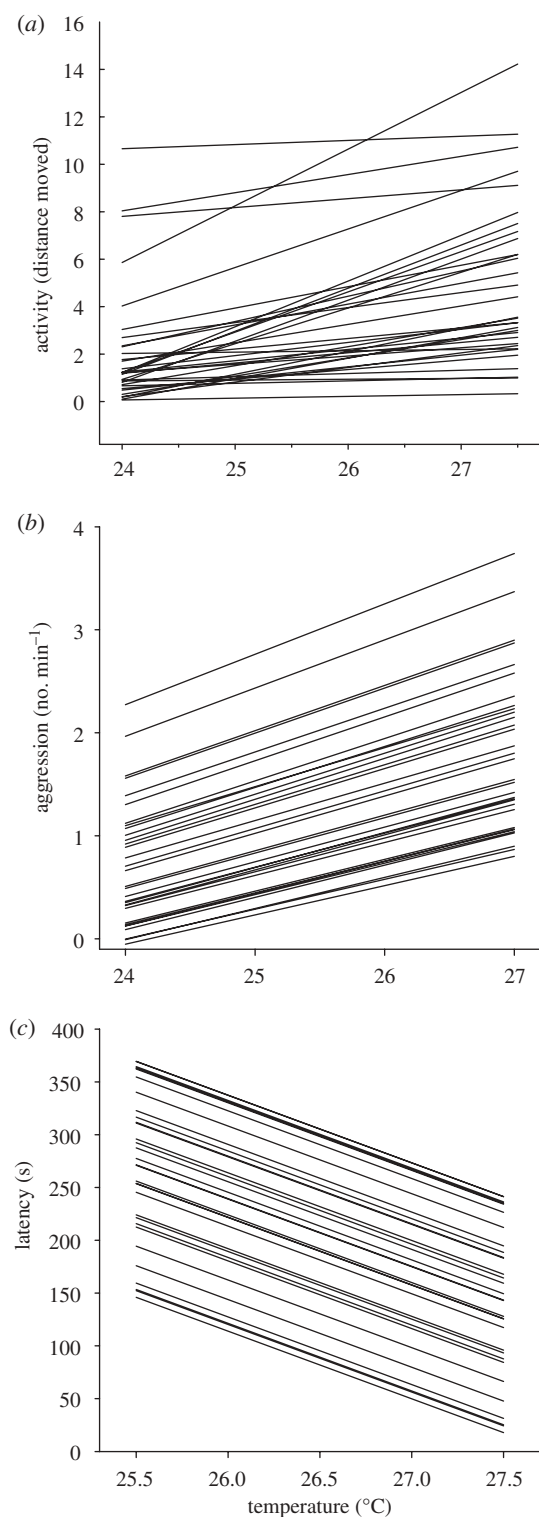


Figure 1. (a) Predicted activity, (b) aggressiveness and (c) boldness (latency to emerge from shelter after threat) trajectories for individual yellow damselfish across temperature contexts obtained from an experiment where within-day temperature varied. Shown are the back-transformed response functions for all 32 individuals from a mixed-model analyses of behavioural consistency, reflecting the temperature range across which data were collected for each PT. Note that shorter latencies to emerge following predatory threat indicate greater boldness, and that this PT was not transformed for analysis. Interindividual differences in the slopes for aggressiveness and latency as a function of temperature were not statistically significant, so estimates of individual slopes for these behaviours are not included in this figure.

increased activity substantially (high contextual plasticity, figure 1a). Individuals with low plasticity tended to be sedentary or highly active across the range of temperatures. Based on predicted values that were back-transformed to their original units, activity increased with temperature from as little as 1.06 to as much as 30-fold among individuals, with the average being fivefold (figure 1). There was no indication that activity changed as a function of time (observation number: $F_{1,144} = 1.8$, $p > 0.15$), but larger individuals were slightly less active than smaller ones (size: $F_{1,30} = 5.7$, $p < 0.05$).

On average, individual aggressiveness increased fourfold as a function of temperature ($F_{1,198} = 56.7$, $p < 0.0001$; figure 1b). In addition, we detected consistent and substantial individual differences in damselfish aggression (random intercept effect: $p < 0.001$). In this case, we did not detect significant differences among the fish in the slope of their regression lines (random slope effect: $p > 0.25$), so the results in figure 1b illustrate individual differences in intercept. Based on predicted values that were back-transformed to their original units, aggressiveness increased from 1.6 to 11-fold, with the average being fourfold (figure 1b). Aggressiveness did not significantly change as a function of observation number ($F_{1,114} = 0.9$, $p > 0.3$) nor did it vary with fish body size ($F_{1,30} = 0.02$, $p > 0.9$).

On average, individual boldness increased 2.5-fold as a function of temperature ($F_{1,122} = 16.9$, $p < 0.0001$). In addition, we detected consistent individual differences in boldness (random intercept effect: $p < 0.006$), but did not detect significant individual differences in contextual plasticity with respect to boldness (random slope effect: $p > 0.2$; figure 1c). Based on predicted values on the raw data, boldness increased from 1.5- to 8-fold, with the average being 2.5-fold (figure 1c). Boldness did not change over time ($F_{1,101} = 3.5$, $p > 0.06$) nor with fish body size ($F_{1,30} = 0.03$, $p > 0.8$).

Across individuals, we observed correlations between activity and aggressiveness and between activity and boldness. The correlation between activity and aggressiveness was similar at 25°C and at 27°C, and was significant at the higher temperature (25°C: $r_s = 0.33$, $p > 0.08$; 27°C: $r_s = 0.38$, $p < 0.03$, $n = 32$). Activity was positively correlated with boldness across individuals at both temperatures, and the strength of those correlations was similar at the two temperatures (i.e. activity was negatively correlated with latency to emerge; 25°C: $r_s = -0.45$, $p < 0.01$; 27°C: $r_s = -0.56$, $p < 0.0009$, $n = 32$). In contrast, there was no indication of a relationship between boldness and aggressiveness at either temperature (25°C: $r_s = -0.09$; 27°C: $r_s = -0.18$, both $p > 0.2$, $n = 32$). Adjustment of critical p -values for these six results by minimizing the false discovery rate (Verhoeven *et al.* 2005) indicated that correlations that were previously significant remained so. These results indicate not only that different PTs were correlated in juveniles in this species, but that these correlations did not change as a function of the minor changes in temperature.

(b) Manipulative study of temperature effects

On average, individual activity rates increased sixfold with a small increase in temperature ($F_{1,127} = 13$, $p < 0.001$; figure 2a). In addition, individuals differed consistently

and substantially in their activity levels at lower temperatures (random intercept effect: $p < 0.0001$), and the extent to which activity increased with temperature also differed among individuals (random slope effect: $p < 0.005$; figure 2a). Some individuals had similar activity levels across temperature contexts (low plasticity), but most dramatically increased activity with minor increases in temperature (high plasticity), thus changing the individual rank order and altering personality (figure 2a). Based on back-transformed predicted values, activity decreased for one individual (a 0.5-fold change), but increased for the remaining 28 individuals from onefold to as much as 23-fold, with the average being sixfold (figure 2a). On average, activity increased as a function of observation number over the course of the experiment ($F_{1,533} = 36$, $p < 0.0001$), but neither time of day nor body size had any effect (both $p > 0.2$).

On average, individual boldness increased fourfold with temperature ($F_{1,83} = 16$, $p < 0.0005$; figure 2b). Individuals consistently and substantially differed in boldness at lower temperatures (random intercept effect: $p < 0.0001$), and also differed in the extent to which their boldness changed as a function of temperature (random slope effect: $p < 0.005$), thus changing the individual rank order and therefore personality across temperature contexts (figure 2b). Across the individuals in the sample, boldness increased (i.e. latency decreased) from 1.5- to 15-fold as a function of temperature, with the average being fourfold (figure 2b). Again, individuals that were either consistently bold or shy at low temperatures also tended to maintain their relative level of boldness at higher temperatures (i.e. low plasticity across temperatures). Boldness increased as a function of observation number over the course of the experiment ($F_{1,486} = 14$, $p < 0.0005$), but neither time of day nor body size had any effect (both $p > 0.3$).

Similar to the observational experiment with a congener, activity and boldness were again correlated with each other, and these correlations were maintained across different temperatures. Activity was positively correlated with boldness across individuals at both temperatures, and the strength of those correlations was similar at the two temperatures (i.e. activity was negatively correlated with latency to emerge; 26°C: $r_s = -0.84$, $p < 0.0001$; 29°C: $r_s = -0.71$, $p < 0.0001$, $n = 29$). Interestingly, however, although we detected significant random slope effects (plasticity) for both activity and boldness (see above), these two slopes were not significantly correlated with one another across individuals ($r_s = -0.17$, $p > 0.3$, $n = 29$). In other words, the degree of plasticity in the activity of a given individual was unrelated to its boldness plasticity across temperature contexts.

4. DISCUSSION

Because most animals are ectotherms, it is critical to determine whether individual differences in PTs, and correlations among PTs, are maintained over the range of temperatures that ectothermic individuals normally experience during a typical day. We observed that most of the individuals in our experiments were very responsive to changes in temperature, dramatically increasing their levels of activity, boldness and aggressiveness as a function of increases of only a few degrees of temperature.

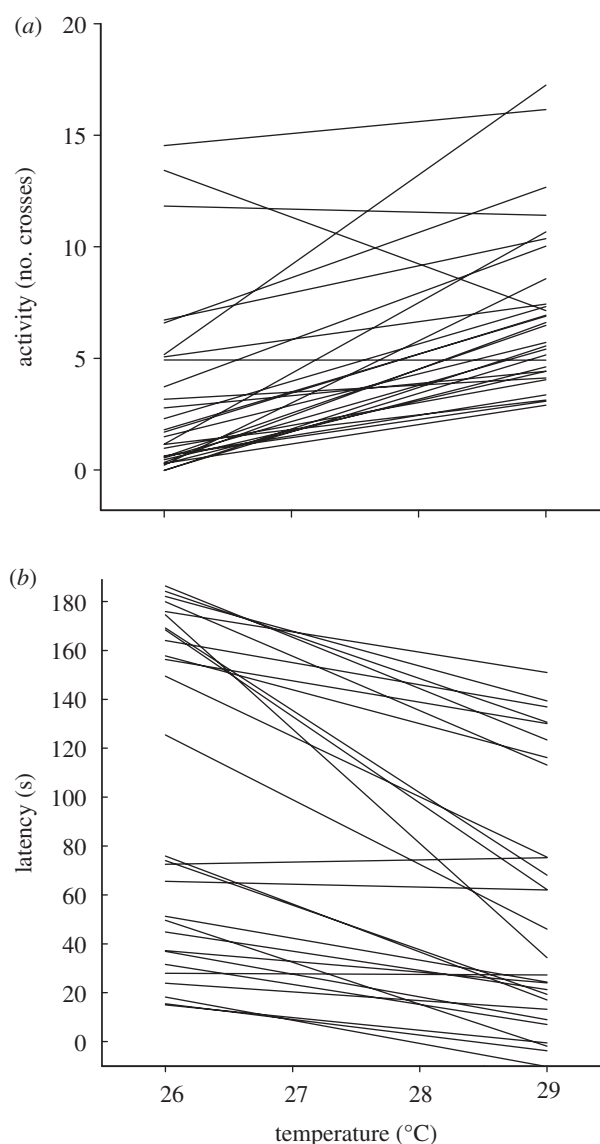


Figure 2. Predicted activity and boldness (latency to emerge from shelter after threat) trajectories for 29 individual *P. bankanensis* damselfish across temperature contexts, obtained from an experiment where temperature was directly manipulated. Shown are the (a) back-transformed and (b) raw data response functions for all 29 individuals, reflecting the temperature range across which data were collected for each PT. Note that shorter latencies to emerge following predatory threat indicate greater boldness.

In observational and manipulation studies involving two different species of damselfish, average scores for activity, boldness and aggressiveness increased 2.5- to 6-fold as a function of relatively minor (3°C or less) differences in temperature. If we had ignored temperature in these studies, and had measured different individuals at slightly different temperatures, our estimates of the 'personality' of any given individual would have been strongly affected by the temperature at which we measured its behaviour. For example, a generally shy individual who was observed under slightly warmer conditions could have appeared to be as bold as, or even bolder than, a generally bold individual who was observed under slightly cooler conditions.

In addition to the large mean-level effects of small temperature increases, we also observed that individuals

differed in their response to temperature. For example, some individuals had very similar activity rates when tested at different temperatures (low contextual plasticity), whereas others had dramatically higher activity rates when tested at higher temperatures (high contextual plasticity). Thus, even if we had measured all of the animals at exactly the same temperature, their behaviour, relative to the other individuals in the same sample, would depend upon the particular temperature at which we had measured them. In this situation, a less-plastic individual at a cooler temperature might appear to be relatively active and bold. That same individual, tested at a slightly warmer temperature would now appear to be relatively shy, in comparison to more-plastic individuals that respond more strongly to temperature.

Indeed, the only aspect of personality that did not change as a function of temperature were correlations between different PTs. For instance, the correlation between activity and boldness at a lower temperature was similar to the correlation between those same two PTs at a higher temperature. These results raise the question of why this should be the case, when other attributes of personality changed as a function of temperature? One possibility is that activity, boldness and aggressiveness work together to increase an individual's food intake rates under natural conditions. If so, consistent individual differences in productivity (growth in our case here for juveniles) might encourage consistent individual differences in behaviours that increase intake rates of the nutrients and energy that are required for growth (Stamps 2007; Biro & Stamps 2008). Increases in the overall levels of all three PTs as a function of temperature are consistent with individual fish compensating for the increased metabolic costs associated with increases in temperature (Schmidt-Nielsen 1991; Clarke & Johnston 1999; Holker 2006). That is, in order to maintain a preferred (intrinsic) growth rate across a range of temperatures, individual fish might need to increase their rates of food intake at higher temperatures to offset their higher metabolic costs (Biro *et al.* 2007; Biro & Stamps 2008). These results are also consistent with previous studies showing that individual differences in metabolic rates are consistent over time in a variety of animals (Nespolo & Franco 2007).

However, even though individuals may differ with respect to their metabolic responses to temperature (Lighton *et al.* 2001; Nespolo *et al.* 2003; Lardies *et al.* 2008), individual metabolic responsiveness cannot readily explain the individual differences in behavioural plasticity observed here. If individual differences in the effects of temperature on metabolic rates were directly responsible for behavioural plasticity, we should have observed a positive correlation between slopes for activity and boldness in experiment 2, but we did not. As we did not measure metabolic rates in these fish, further speculation about these results seems premature. Nonetheless, this topic is worth pursuing in future studies given the interesting suggestions that metabolism and personality might be linked in various ways (Biro & Stamps 2008; Careau *et al.* 2008).

The large increases in average levels of PTs across such a small range of temperatures (less than 3°C) underscore the importance of temperature in studies of personality and other behaviour patterns in ectotherms. What is novel here is not the fact that temperature affects scores

on behavioural traits, but rather that very modest changes in temperature changes can lead not only to dramatic changes in mean-level scores in behaviour, but also change the scores of individuals relative to others in the same sample. Further, these large behavioural effects can result from small temperature changes that are well within normal temperatures experienced by animals within a given day, or from one day to the next. Small variations in temperature of the magnitude that would confound results are probably commonplace, not only in nature, but also in the laboratory. For example, even in a temperature-controlled laboratory, we observed minor spatial and temporal differences in water temperature among aquaria (§2). Had we not carefully measured and statistically accounted for this 'minor' variation, we would have introduced variance into the data that would have distorted the 'true' personality differences among individuals. Clearly, it seems that future studies of ectotherm personality, or indeed behaviour generally, must either very carefully control temperature and/or measure and control for its effects statistically. Finally, from an applied perspective, our results suggest the possibility for increasingly disrupted patterns of behaviour in fishes and other ectotherms under a scenario of climate warming, with increases in mean-level activity, boldness and aggressiveness of a magnitude that has been shown to result in greater vulnerability to predation, and decreased survival in other fish populations (Biro *et al.* 2007).

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