Overwinter temperature has no effect on problem solving abilities or responses to novelty in Black-capped Chickadees (*Poecile atricapillus*)

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A B S T R A C T

Birds overwintering at northern latitudes face challenging environments in which refined cognitive and behavioural responses to environmental stimuli could be a benefit. Populations of the same species from different latitudes have been shown to differ in their cognitive and behavioural responses, and these differences have been attributed to local adaptation. However, individuals overwintering at intermediate latitudes experience great breadth and variation in environmental conditions, and thus it is reasonable that these individuals would alter their responses based on current conditions. To determine within-species responses to environmental conditions we sampled birds from a single population at an intermediate latitude and assessed their problem solving abilities and their responses to novelty. We held birds overwinter in one of three experimental temperature regimes and assessed problem solving abilities and responses to novel stimuli in the spring. We found that overwinter temperature had no effect on problem solving ability. We also show that overwinter temperature had no effect on an individual's response to novelty. These findings strengthen the argument that differences in these behaviours seen at the population level are in fact driven by local adaptation, and that current environmental condition may have limited effects on these behaviours.

1. Introduction

As the cost of living in an environment increases, animals might be expected to alter their cognitive and behavioural responses to better exploit the resources in that environment (Shettleworth, 1998; Pravosudov and Clayton, 2002). Current research has increasingly focussed on responses to changing environments in birds (Crick, 2004). It has been shown, for example, that House Sparrows (*Passer domesticus*) invading urban areas have less neophobic responses to novel food sources than established birds (Martin and Fitzgerald, 2005). Urbanized Common Mynas (*Acridotheres tristis*) inhabiting novel complex environments are more innovative when working for a food reward compared to rural conspecifics (Sol et al., 2011). In addition to these anthropogenic factors, climatic factors can influence cognitive and behavioural responses as well. Mountain Chickadees (*Poecile gambeli*) from high elevations solve problems faster than individuals from low elevations (Kozlovsky et al., 2015), and Black-capped Chickadees (*Poecile atricapillus*) from northern latitudes solve problems more efficiently, and are less neophobic, than more southern conspecifics (Roth et al., 2010). Differences between populations across climatic gradients

extend beyond problem solving ability and neophobic responses. Differences between populations of Black-capped Chickadees in food-caching ability and spatial memory have also been found, in which individuals from higher latitudes cache more and recover caches more accurately than individuals from lower latitude populations (Roth et al., 2011). These differences may occur because, in order to survive, individuals from harsh high elevation or high latitude environments must exploit novel or more difficult to obtain food sources.

These results suggest that natural selection has acted differently on high vs low elevation populations producing differences in cognition and behaviour. Some recent work, however, indicates that genetic differences may not always explain the observed differences between populations. In a comparison of high and low elevation populations of Mountain Chickadees, Branch et al. (2017) found no evidence of genetic differences in population structure. Differences between populations of animals can occur, however, as a result of individual responses to the different environments in which these animals live. We examined whether individual experience rather than the effects of natural selection, might explain observed differences in behaviour and cognition between populations of chickadees living in more and less harsh
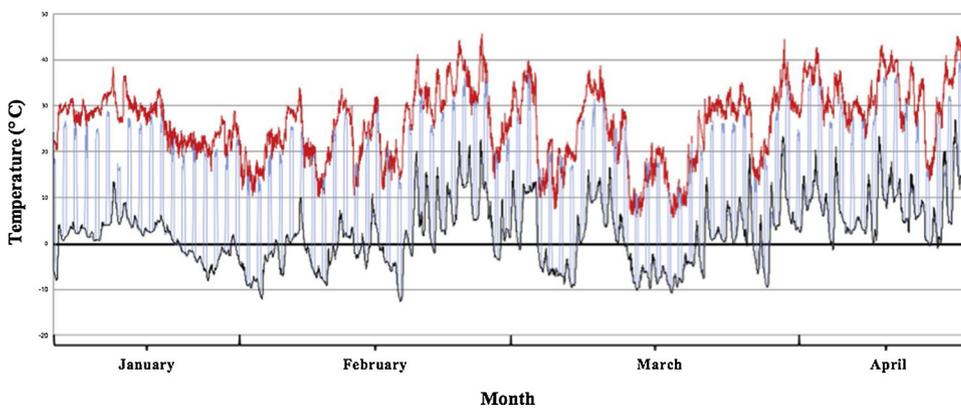
Fig. 1. Temperatures experienced by birds in each group. Mean temperatures recorded from outside roosting boxes for each treatment in 2016 shown as an example for clarity: Control in black, 24H in red, 6H in blue. The 24H condition was always warmer than Control, and the 6H group oscillated between Control (during non-heating hours) and 24H (during heating hours).

environments.

One of the most important variable factors individuals are exposed to is environmental temperature. For small, non-migratory birds such as the Black-capped Chickadee, winter temperature in particular can be extremely important. The home range of the Black-capped Chickadee in winter was between 0.5 °C warmer and 6 °C colder in 2016 than in 2015 and between 0.5 °C colder and 5.8 °C warmer in 2017 than in 2016 (Hansen et al., 2010; GISTEMP Team, 2016). Annual variation in temperature is capable of modulating behavioural responses in birds. For example, temperature is known to affect foraging behaviour in birds. Chatelain et al. (Chatelain et al., 2013) demonstrated that a reduction in ambient temperature increases the predation of toxic prey by European Starlings (*Sturnus vulgaris*). Caraco et al. (Caraco et al., 1990) also demonstrated that temperature influences foraging choice. In a two-choice task, Yellow-eyed Juncos (*Junco phaeonotus*) in cold environments favoured a variable high-risk, high-reward option, while birds in warmer environments opted for the constant low-risk, low-reward option.

As environmental temperature can modulate behaviour in a foraging context, it is possible that the experience of seasonal temperature variation could produce differences in cognition and behaviour between populations previously attributed to adaptive differences between populations. In this study we examined the effects of winter temperature on problem solving ability and responses to novelty in Black-capped Chickadees. We hypothesized that seasonal winter temperature would have an effect on behaviour and predicted that birds experiencing a colder winter environment would solve problems faster and be less neophobic than conspecifics that experienced a warmer winter environment.

2. Methods

2.1. Subjects

We caught forty-nine Black-capped chickadees between October and December of 2015 (27 birds; 8F:19 M) and 2016 (22 birds; 10F:12 M), on the University of Western Ontario campus. Each bird was given a unique colour band combination for identification. We group housed all birds in large, outdoor, free-flight rooftop aviaries (from 2.5 × 3.0 m to 3.0 × 3.5 m, all were 2.5 m in height) at the Advanced Facility for Avian Research shortly after capture in groups of six to 12. On January 8 in both years, we moved individuals to individual outdoor cages (45.75 × 45.75 × 45.75 cm). Mazuri Small Bird Diet (PMI Nutrition International, Brentwood, MO, U.S.A.) and powdered sunflower seeds were provided *ad libitum*, and water was provided twice daily (approx. 9am and 2 pm) to avoid freezing in sub-zero temperatures. Mealworms and whole black oil sunflower seeds were given daily. Individuals were provided with a roosting box (7.6 × 7.6 × 7.6 cm) with straw, cotton and yarn for insulation. Birds remained in these home cages until the completion of the experiment.

2.2. Treatments and heating

Beginning January 15 in both years we assigned birds to one of three treatment groups: Control (n = 16), six hours of heat overnight (6H, n = 17), or twenty-four hours of heat (24H, n = 16). Birds in the Control group experienced natural temperatures in their outdoor cages. Individuals in the 6H treatment experienced natural temperatures, but received six hours of additional heat every twenty-four hours, between 10 pm and 4am. These birds thus avoided what is typically the coldest daily temperature. Individuals in 24H treatment experienced twenty-four hours of additional heat daily to simulate a warmer winter. Heat was provided by PrimeGLO Telescopic Electric Heaters (AZ Patio Heaters, Peoria, AZ), placed directly above each cage. The Control, 6H and 24H treatments all experienced variation in temperature as a result of outdoor housing and exposure to naturally changing weather. For the Control group this was normal daily variation in winter temperature, while for the 24H group it was natural variation with a warming effect superimposed. For the 6H group, temperature oscillated between the natural temperature experienced by the Control group during the day, and the warmer temperature experienced by the 24H group at night (Fig. 1). To quantify the effect of our temperature manipulations we recorded temperature on the exterior of a subset of the birds' roosting boxes (2 each for Control and 6H, 3 for 24 H) in all treatments using HOBO® Pendant® Data Loggers (Onset Computer Corporation, Bourne, MA). Birds were housed in heated treatments until the completion of cognitive testing.

2.3. Body composition and sex

We measured body composition for each individual at three time points during the experiment using a quantitative magnetic resonance (QMR) scanner (Echo-MRI-B, Echo-Medical Systems, Houston, TX, USA). QMR scans provided measures of both fat and lean mass ± 0.01 g (Guglielmo et al., 2011). Pre-treatment measurements were taken at least one week after capture, but before birds were allocated to a treatment group. This waiting period between capture and measurement allowed birds to habituate to captivity and allowed food intake and energy expenditure to stabilize prior to taking body composition measures. During-treatment measurements were taken three days prior to the beginning of testing in order to get an accurate measure of body composition for the testing period without subjecting the birds to body composition scans on testing days. Post-testing measurements were taken within one week of the end of testing for the final bird. Due to extended testing in the first year, however, the post-testing dates differ between years. Year one birds' post-testing measurements were taken in May, while year two birds' post-testing measurements were taken in April. The sex of each individual was determined by gonadal inspection at the time of sacrifice. At the end of this study birds were sacrificed for neuroanatomical analyses reported elsewhere.

2.4. Behavioural testing

In both years, behavioural testing began on March 20 and all trials were conducted in the birds' home cages. All tasks were video recorded, and the tasks were completed in the order described below. Birds in year 1 only received *Problem Solving I* and birds in year 2 received *Problem Solving II*.

2.5. Problem solving I

We assessed problem solving using a modified version of the problem-solving task from Roth et al. (2010). The problem solving task assessed a bird's ability to obtain a partially obstructed food reward. The apparatus was a wooden board (40 cm x 18 cm) with 15 identical wells (1.5 cm diameter). In experimental trials, a stainless-steel washer (3.5 cm diameter, 1.5 cm center hole), with a clear plastic cover on the center hole (Con-Tact Brand®, Kittrich Corporation, La Mirada, CA) covered a single well. The covered washers allowed birds to see the food reward, but not access it without removing the washer. Mealworms were placed in the covered well as a food reward. Two days prior to testing, birds were exposed to both the board and the washer for at least 36 h for habituation. During habituation, the board contained mealworms in 8 of the 15 wells (at least one in each row, and column), and the covered washer was fastened adjacent to the central well such that the birds could interact with it, but not move it. Birds were allowed 24 h to interact with both the board and the washer, and habituation was considered successful if food was retrieved from all 8 baited wells. All birds successfully cleared all wells and moved on to experimental trials.

Before experimental trials we food deprived birds for one hour. Testing occurred in three phases: pre- motivation, experimental, and post- motivation. The three phases were performed in succession, with as little inter-phase time as possible. The pre- and post- motivation phases were used to ensure that motivation did not vary before and after the experimental phase. The 'first-touch' score (time to first contact the apparatus in the experimental phase) was used to control for potential neophobic responses. Each bird was assigned one rewarded well and that well remained the same for all three phases. In the pre- motivation phase, a mealworm was placed in the rewarded well, and the board was placed in the bird's home cage. After 5 min had elapsed, the board was removed. A new mealworm was placed in the rewarded well and a washer was placed over the well. The board was returned to the home cage, beginning the experimental phase. Birds were allowed 30 min to retrieve the meal worm. The post- motivation phase followed the same procedure as the pre- motivation phase and immediately followed the experimental.

Four latency scores were obtained for each individual. The pre- motivation phase score was the latency to remove a mealworm from the baited board. Two latency scores were obtained from the experimental phase: 1) the latency to first contact the apparatus, the 'first-touch' score and 2) the latency to move the washer and retrieve the worm, the 'problem solving' score. The post- motivation phase score was the latency remove a mealworm from the baited board.

2.6. Problem solving II

Problem Solving II followed the same procedure as Problem Solving I, with the experimental phase extended to 1 h. This manipulation was done in response to the low completion rate of birds in Problem Solving I and was designed to increase the number of birds that were able to solve the task without receiving a maximum time score. Birds 28–49 were allowed this 1-hour retrieval period.

2.7. Response to novelty

We assessed responses to novel stimuli in a modified version of the task described in Roth et al. (2010). Silver coloured food cups were used as the standard food dish. Novel food cups were created by altering the birds' standard food dish with blue and yellow paint, and metal nuts and bolts. Food dishes and rewards were presented by sliding a bottom tray out of the home cage, placing the dish on the tray, and sliding the tray back into the home cage. Individuals were presented with a single mealworm in the standard food dish each day for four days in order to allow the birds to habituate to the dish. Birds were food deprived for one hour prior to testing. Testing occurred in three phases; pre- motivation, experimental, and post- motivation. The three phases were performed in succession, as quickly as possible. In the pre-motivation phase, birds were presented with a single mealworm in a standard food dish and allowed 5 min to retrieve it. After 5 min had elapsed, the dish was removed and replaced with a novel food dish containing a single mealworm to initiate the experimental phase. Individuals were allowed 15 min to complete this trial. The post-trial motivation phase was performed in the same manner as the pre- motivation phase and immediately followed the experimental phase.

Three scores were obtained on each trial: 1) The pre- motivation phase score was the latency of a bird to remove a worm from a standard food dish; 2) The experimental phase score was the latency of a bird to remove a worm from a modified food dish; 3) The post- motivation phase score was the latency of a bird to remove a worm from a standard food dish

2.8. Video recording and analysis

All trials for Problem Solving I, Problem Solving II, and Response to Novelty were recorded remotely to minimize effects of direct visual observation. Videos were recorded using one of four different cameras (GoPro® HERO4 Silver camera, GoPro Incorporated, San Mateo, CA, USA; Canon VIXIA HF R40, Canon Canada Incorporated, Mississauga, ON, Canada; Activeon CX Action Camera, Activeon Incorporated, San Diego, CA, USA; CX Gold Action Camera, Activeon Incorporated, San Diego, CA, USA). Videos were uploaded to a computer and analysed upon the completion of all trials. Videos were analysed by observers blind to temperature treatment. Each video was scored twice, and the mean latency for each phase (see task specific sections) score was used for analysis. The onset of a trial was marked by the testing apparatus being stationary in the cage, with the experimenter out of the frame. In the case that the latency scores differed by more than 5 s, a third score was obtained from the video record and mean of the two most similar scores was used for analysis.

2.9. Statistical analysis

All statistical analyses were done using SPSS (version 24, IBM Corporation) unless otherwise noted. All significant interactions and main effects are reported; interactions not reported were non-significant. For all behavioural measures, untransformed data are presented visually for clarity. All statistical analyses were done on log transformed values.

3. Results

3.1. Temperature treatments

Temperature between years and among temperature treatments was compared by two-way ANOVA and Tukey's post hoc tests using R (R Core Team, 2017). There was a significant difference between years in mean temperature (the first year was colder by a mean of 2 °C, $F_{1,96} = 8.60$, $p = 0.004$, $\eta_p^2 = 0.03$) and between temperature treatments ($F_{2,96} = 120.2$, $p < 0.0005$, $\eta_p^2 = 0.69$). Tukey's multiple comparisons, however, showed no differences between years for the same temperature treatment (Tukey's adjusted p: Control: p = 0.95; 6H: p = 0.53; 24H: p = 0.14).

3.2. Body composition

A general linear model (GLM) was used to analyze body composition data, and Tukey's multiple comparisons were used to compare each phases of the experiment. Phase of the experiment (Pre-Treatment, During-Treatment, Post-Treatment) was included as a within-subjects variable, and temperature treatment (Control, 6H, 24 H), sex, and year were included as between-subject variables. There were no significant differences in fat mass between temperature treatments ($F_{2,46} = 2.250$, $p = 0.12$), sex ($F_{1,47} = 3.491$, $p = 0.07$) or year ($F_{1,47} = 0.315$, $p = 0.57$). The During-Treatment fat mass however, was significantly higher ($F_{2,76} = 15.58$, $p = 0.000003$, $\eta_p^2 = 0.31$) than the Pre-Treatment ($p = 0.01$) and Post-Testing ($p < 0.001$) fat mass which did not differ from each other ($p = 0.50$).

Temperature treatment had no effect on the lean mass ($F_{2,46} = 1.627$, $p = 0.21$). Males consistently had greater lean mass than females ($F_{1,47} = 11.388$, $p = 0.002$, $\eta_p^2 = 0.0245$). Birds from year one also had greater lean mass than birds from year two ($F_{1,47} = 9.151$, $p = 0.005$, $\eta_p^2 = 0.207$), however, these differences are due to the sex ratio of males to females in each year (Year 1 = 8F:19 M, Year 2 = 10F:12 M).

3.3. Problem solving I

A GLM was used and included phase (Pre-Trial Motivation, Experimental Trial, Post-Trial Motivation) as a within-subject variable, and temperature treatment (Control, 6H, 24 H), sex and year as between-subject variables. There was no significant effect of temperature treatment ($F_{2,46} = 1.667$, $p = 0.20$, $\eta_p^2 = 0.09$), sex ($F_{1,47} = 1.010$, $p = 0.32$, $\eta_p^2 = 0.028$), or year ($F_{1,47} = 1.633$, $p = 0.21$, $\eta_p^2 = 0.05$) on problem solving latency (Fig. 2). There was, however, a significant interaction between temperature treatment and year ($F_{2,43} = 5.723$, $p = 0.001$, $\eta_p^2 = 0.25$). This interaction appears to be due to the failure of some birds to retrieve the worm before the maximum allowed time (Fig. 3). In year one, significantly fewer individuals in the Control group

completed the task compared to individuals in the 6H and 24H groups (chi-square test: $\chi^2 = 7.67$, $p = 0.022$). In year two however, all Control birds competed the task, while some individuals from the 6H and 24H groups failed to do so. In year one the rank order of mean latencies from fastest to slowest was: 6H (790.6 s; 78% completion), 24H (823.5 s; 78%), Control (1446.6 s; 22%). In year two the rank order was; Control (255.1 s; 100%), 24H (885.1 s; 57%), 6H (1166.2 s; 63%).

3.4. Problem solving II

Problem Solving II was the same task as Problem Solving I above, but with the maximum trial time extended to 60 min. Temperature treatment had no effect on problem solving ability ($F_{2,19} = 2.202$, $p = 0.15$, $\eta_p^2 = 0.28$) and there was no difference between males and females ($F_{1,20} = 0.460$, $p = 0.51$, $\eta_p^2 = 0.03$).

3.5. Response to novelty

Neither temperature treatment ($F_{2,36} = 1.258$, $p = 0.30$, $\eta_p^2 = 0.07$; Fig. 4), nor year ($F_{1,36} = 0.262$, $p = 0.61$, $\eta_p^2 = 0.01$) had an effect on birds' response to novelty. Males had significantly shorter latencies on this task than females ($F_{1,36} = 5.938$, $p = 0.02$, $\eta_p^2 = 0.14$).

4. Discussion

This paper reports a variety of null results, and as a result seems to provide evidence that temperature is not, in any part, responsible for behavioural changes seen in previous studies. We want to acknowledge that our results do not exclude the possibility that there was an effect, and we simply did not have the power to detect it, however we suggest that this does provide evidence that any effect of temperature is slight and thus is probably not capable of behavioural modulations similar to those seen in previous work.

Temperature treatment did not have a significant effect on either
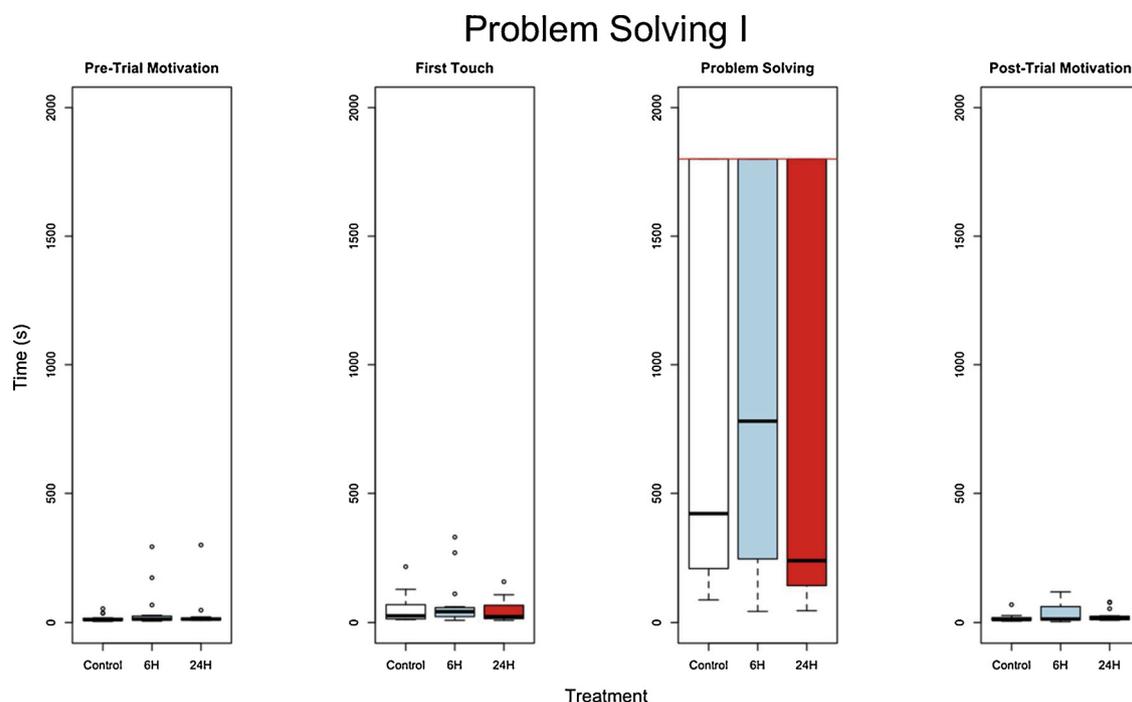
Problem Solving I

Fig. 2. Latencies in the Problem Solving I task. Groups shown: Control in white, 6H in blue, 24H in red. Each pane shows the variation in response times in one of the 4 trial phases. The red horizontal line in the Problem Solving phase indicates the maximum trial time. Motivation was high both pre- and post-trial (panes 1 & 4), and the birds did not exhibit a neophobic response to the apparatus (pane 2). Birds took significantly longer to complete the task (pane 3), but there was no effect of temperature on completion time.
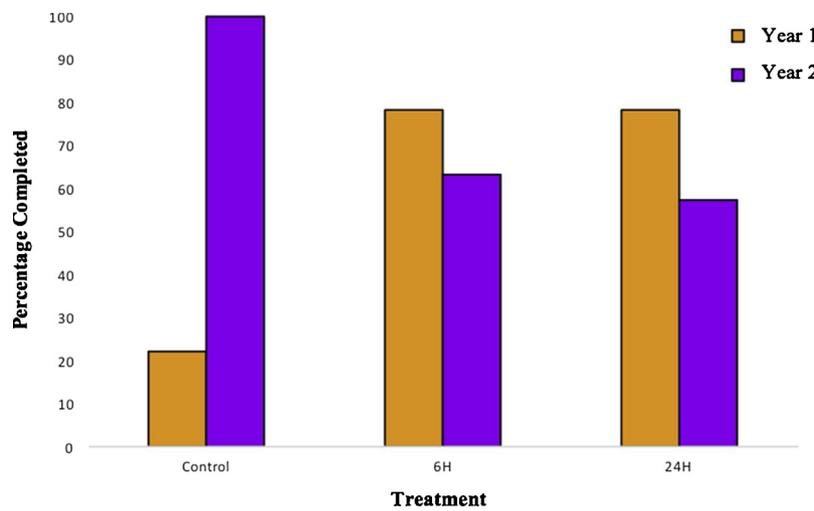
Fig. 3. Completion rates for problem Solving. Percentage of birds in each temperature treatment group that completed Problem Solving I up in each year. The greatest difference between years occurred in the Control treatment.
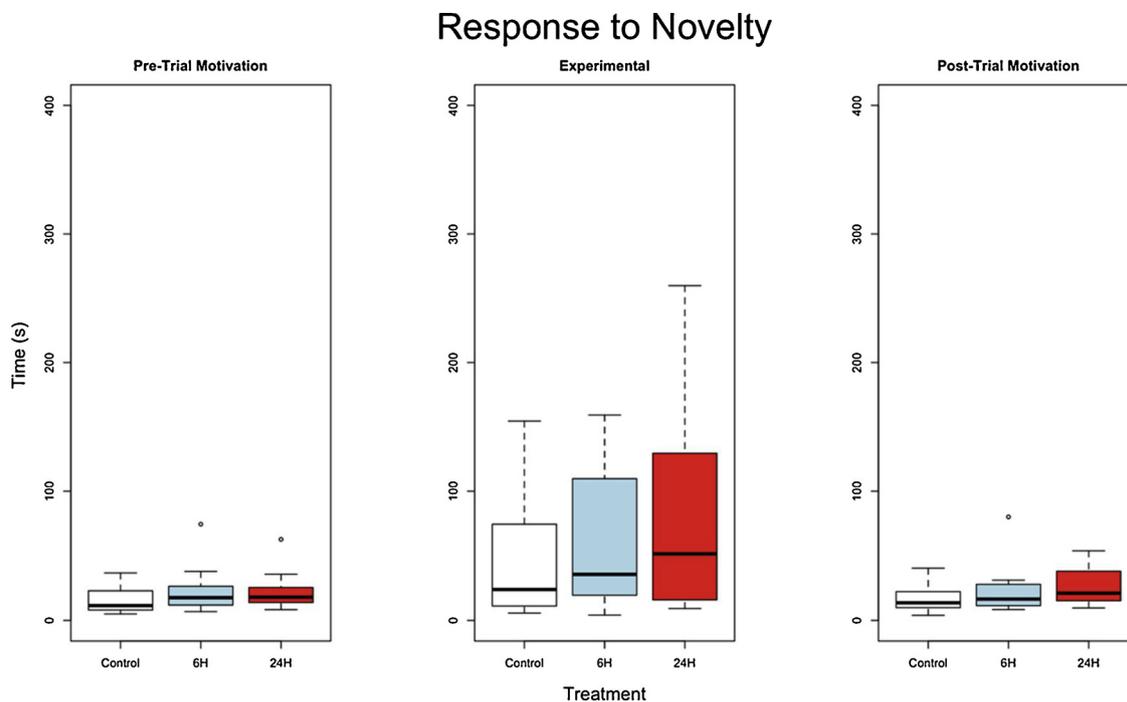

Fig. 4. Responses to novelty. Groups shown: Control in white, 6H in blue, 24H in red. Though motivation was high throughout the trial (panes 1 & 3), temperature treatment had no significant effect on response to novelty (pane 2).

problem solving or responses to novel stimuli and thus provide no evidence that individual experience with winter temperature causes changes in these behaviours in Black-capped Chickadees. These findings do, however, show there can be considerable variation among individuals within a population and that behavioural responses can change from year to year. The interaction in Problem Solving I, where the rank order of the problem solving latency among treatment means was reversed from year one to year two suggests that there may be other factors not controlled for in this study that modulate behavioural responses. There are many environmental and social factors that can affect birds' behaviour (Gosler, 1996; Grubb, 1975; Gerson and Guglielmo, 2011; Smith, 1991; Freeberg, 2006) and our birds' individual or social experience prior to capture may have differed between years.

In addition, we manipulated only a relatively short period of time in the life of a Black-capped Chickadee and did not include early

development. A longer period of exposure to different over winter temperatures or exposure at an important time during development may have produced different results. Birds were also only food restricted prior to testing. It is possible that this restriction was not long enough to trigger sufficient cognitive differences. Longer restrictions may have increased individual stress, thereby maximizing the value of the reward.

The temperature a bird experienced did not influence its fat mass or the amount of lean mass that an individual had. No difference in fat mass is particularly interesting because it has been proposed from theoretical considerations that temperature should be an accurate predictor of fat (Houston and McNamara, 1993), and observed empirically that the lower the temperature, the more fat an individual has (Gosler, 1996). It is worth noting that in all three temperature treatments, fat mass increased from Pre-Treatment to During-Treatment. This is consistent with many observations from the field (*e.g.* (Petit and

Vézina, 2014; Petit et al., 2014)) and in the wild is likely due to the unpredictability of food, along with energetically taxing cold nights. There are several possible reasons that the control, 6H and 24H birds did not differ in fat mass. First, it is possible that the time of day the measurements were taken affected fat mass. Many small birds, due to their a high metabolic rate, cannot carry more fat than will sustain them for about 1–2 days (King, 1972). As a result, many of these species, including the Black-capped Chickadee, undergo a significant daily variation in fat mass, with stores being depleted overnight and replenished during the day (Baldwin and Kendeigh, 1938; Chaplin, 1974). Because all body composition measurements were taken in the morning, it is possible that differences between treatments that emerge over the course of the day were not yet apparent. If the birds had been measured later in the day, the fat score might have been more indicative of the maximum fat mass of each individual. If this idea is correct, then it is possible that the data collected better represent the rate of fat replenishment in each treatment. As all individuals would have just used their fat stores through the night, the fat they had when measured would just be the fat they had replenished in the time before measurements were taken. Birds in all treatments were allowed between 1–2 hours of food access before being measured, and individuals were sampled in a pattern such that the mean access to food should be roughly equal among groups (Control, 6H, 24H, 24H…). It is possible then, that there are no differences in the replenishing rate of fat stores but the maximum value of the fat stores, immediately before nightfall, would be different between groups.

In general, the findings of this study suggest that behavioural and cognitive differences previously observed between populations of chickadees exposed to different degrees of environmental harshness at different altitudes or different latitudes are not due to plastic responses to winter temperature. If differences between populations in cognition and behaviour are the outcome of natural selection and not individual flexibility, this may indicate that responses to rapidly changing climate conditions are unlikely to occur quickly (Gaston et al., 2003). Populations of chickadees living under different environmental conditions differ in cognition and behaviour, presumable to better survive in these different environments (Kozlovsky et al., 2015; Roth et al., 2010, 2011). As the global climate changes and the ability to exploit changing resources becomes increasingly important, the absence of a rapid behavioural response to overwinter temperature that we observed suggests that population responses may not be rapid.

5. Conclusions

Behavioural differences have been described between populations of chickadees from different environments. These differences have been attributed to genetic differences resulting from long term selection on these populations. New evidence suggests that these genetic differences may not be present in every case (Branch et al., 2017). In this study, we tested experiential effects on the cognitive and behavioural traits examined in previous studies. The results show that short term experience of over winter temperature does not affect problem solving abilities responses to novel stimuli. These results lend indirect support to the genetic hypothesis for observed population differences in cognition and behaviour. Understanding the possible range of behavioural responses to changing environmental conditions can help inform conservation and policy decisions regarding the impact of climate change on natural populations.

Ethics

Birds were collected under a Canadian Wildlife Service Permit (CA 0236). This research was conducted in accordance with all local and federal regulations and was supervised by the University of Western Ontario (AUP 2015-019).

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