**Simulated heat waves reduce cognitive and motor performance of an endotherm**

Running Head: Heat stress affects endotherm behavior

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**Abstract.** Recent heat waves have led to mortality of animals, including humans, across the globe. This is drawing new attention to how animals cope with thermal stress. Most research focuses on characterizing lethal limits of thermal stress to predict how changing climates will affect populations. Less well studied are the sublethal effects of thermal stress on behavior, which may influence both survival and reproductive success. Here we present the first experimental evidence in endotherms that birds exposed to simulated heat waves exhibit reduced performance of cognitive tasks. These results provide a potential mechanistic link between the effects of thermal stress on an individual’s physiology to recently observed phenomena at the population-level, including mortality, range shifts and breeding failure. Further, these results expand our understanding of animal cognitive conditions during thermal stress. Our findings will be of interest to those involved in modeling climate change impact on animal populations and in animal production and welfare.

**Keywords:** Climate change, heat stress, cognition, cognitive performance, behavior, zebra finch.

**Introduction**

Current global temperatures are higher than those during 90% of the entire Holocene [1], resulting in evolutionarily unprecedented temperatures for much of life on earth. In particular, January to June of 2016 marked the world’s warmest ever six month period [2]. Not only are average temperatures higher, but there is also an increase in the frequency of 'extreme events', including increases in extreme high temperatures [3]. For example, in both Australia and New Zealand the number of days exceeding 30°C has increased over time [4]. Whereas these hot extremes were limited to less than 1% of the Earth's surface in the past, extreme anomalies in high temperatures now cover more than 10% of land area [5]. Thus, terrestrial organisms are experiencing not only a long-term increase in temperature but also marked stretches of high heat, or 'heat waves', yet we know relatively little about the impact of heat waves on animal populations.

Changing temperatures impose selective pressures on animals. Predicting how animals will respond to increasing temperatures requires knowledge of the effects of thermal stress on animal behavior, such as cognition, and physiology, such as metabolism, as well as the genetic capacity of a species to adapt to changing temperatures [6]. Our knowledge of these effects is woefully limited for most species, inhibiting our ability to make specific predictions about the effects of climate change on populations. In particular, we know little about how high temperatures affect the behavior and physiology of endotherms, such as humans, mammals, birds and many fish, despite a literature on the effects of heat on performance in ectotherms, such as reptiles, amphibians and insects (see review in Angilletta *et al.* 2002). As such, these gaps in knowledge have spurred recent interest in measuring these effects in endotherms [8–13].

Thermoregulation in endotherms is achieved through several behaviors as ambient temperatures rise. Within the thermoneutral zone, animals expend a minimal amount of energy by moving to cooler locations and making minor postural changes that increase the body surface area in order to shed heat through convection. The upper critical temperature of the thermoneutral zone is defined by an increase in metabolic rate, which is caused in part by increased frequency and extent of thermoregulatory behaviors. As ambient temperatures approach and exceed body temperature, heat loss through convection from body surfaces becomes ineffective and animals must shift to sweating and panting to shed heat through evaporative water loss [14]. Hyperthermia ensues when behavioral and physiological mechanisms are insufficient to dissipate excess heat.

Time spent engaged in cooling behaviors may limit the time that endotherms spend on other fitness related behaviors, such as foraging, parental care and attracting potential mates. For example, recent field studies provide evidence that passerine birds forage less efficiently [10], spend less time incubating eggs [15], and sing less in hot weather [16]. In addition to time budget trade-offs, typical motor pattern performance (e.g., motor speed) may also be altered when individuals slow their movements to reduce heat generation or when muscle performance declines. However, it is not known whether or how reductions in motor speed would affect fitness-related behaviors.

High temperatures may also affect cognition. For example, environmental factors such as thermal stress can affect neural development and permeability of the blood brain barrier, thereby affecting cognitive function [17–19]. Periods of heat stress outside of the developmental period may also affect cognitive function by leading to activation of glial cells and induction of inflammatory molecules in the hippocampus, causing memory loss, neuronal death and impaired adult neurogenesis [19–21]. Studies on human workers observe lower performance on work tasks at higher temperatures [22]. Like humans, other endotherms likely experience reduced cognitive performance in response to heat stress, but this hypothesis has not been tested.

Here, we test the effect of simulated heat waves on cognitive and motor performance of cognitive tasks, using zebra finches (*Taeniopygia guttata*), an emerging model system for studies on cognition (reviewed in Healy *et al.* 2010). Cognitive tasks measure how animals collect, retain and use information from the environment, which is essential in fitness related behaviors, including foraging, predator avoidance and mating (Morand-Ferron *et al.* 2016). We tested zebra finches using two different established assays of cognitive performance: a color association task and a detour-reaching task. Color association tasks measure associative learning, which has been linked to foraging success in free-living animals [25,26]. Detour-reaching tasks measure self-control, also referred to as inhibitory control, which is important for making decisions related to foraging [27]. For both tasks, we tested performance at typical housing temperatures and at temperatures above the published thermoneutral zone for zebra finches. Their thermoneutral zone is approximately 36 to 42°C, with an upper critical temperature of 40–42°C and mortality above 45°C [28–31]. There is no apparent difference between domesticated and feral zebra finches in their physiological response to heat stress [29]. We predicted that heat stressed birds would show reduced cognitive and motor performance on both tasks. Consistent with our predictions, heat stressed birds made cognitive errors, moved more slowly, and spent time on thermoregulatory behaviors, all of which reduced foraging efficiency. To place these results in a relevant ecological context, we built maps from climate data to determine whether free-living zebra finches in their native range in Australia would experience temperatures at which captive birds exhibited reduced behavioral performance. During the past year, ambient temperatures experienced by free-living zebra finches in their native range exceeded temperatures causing cognitive decline during 28% of days during the austral summer and exceeded temperatures causing motor decline during 70% of days during the austral summer. This work represents the first experimental test of the sublethal effects of heat stress on behavioral performance in endotherms and further places those results in the context of the organism's environment. We anticipate that these findings will stimulate new research and planning objectives for climate change.

**Materials and Methods**

**Subjects.** We obtained two groups of adult male zebra finches from an avian breeder (Magnolia Farms); one group was housed at Tulane University for the color-association task, and one group was housed at the University of North Carolina Wilmington (UNCW) for the detour-reaching task. Birds were housed individually for trials in wire cages with perches and cuttlebone. Food and water were provided ad libitum. Birds were kept on a 12:12 light-dark cycle at ambient temperature of 22°C and relative humidity of 50–75%.

**Heat stress.** We assessed whether birds showed behavioral indicators of heat stress, including panting, wing spreading, and taller posture, at the four ambient temperatures used in this study (22°C, 40°C, 43°C and 44°C). Assessing these behaviors allowed us to determine whether and at what temperature individuals experienced thermal stress.

**Color-association task.** We taught birds to remove lids fitted snuggly into six wells drilled in a grey composite plastic block (10cm x 14cm) in order to reach millet seed following Boogert *et al.* (2011). This task had three phases: habitation, training and testing. Habitation and training included five stages of trials: (i) no lids, (ii) lids next to wells, (iii) lids tipped into wells, and (iv) lids covering wells. Birds had to eat from at least two of four baited wells within two minutes to pass a trial, and had to pass three out of four consecutive trials to move to the next stage. The pattern of baited wells was random and changed every trial. For the last stage, (v) birds were taught to associate seed with only one color of lid (yellow or blue), which was assigned randomly. For this stage, two blocks were used and eight of the 12 wells baited (four yellow and four blue). To pass a trial, birds had to flip the four lids of the reward color before trying lids of the other color. To pass the stage, birds had to pass six out of seven consecutive trials. Birds stuck on a stage were moved back a stage. Birds that did not complete a stage in two weeks (60 trials) were removed. To ensure motivation, food was removed from cages five hours before trials began and after trial completion a motivation test was done in which food dishes were placed in the cages and the time it took birds to approach was recorded. All birds approached food dishes in less than one minute, which is considered sufficiently motivated [32].

Only birds that learned the color association task were used for test trials (n = 6). These birds were tested with two blocks with their reward color baited. We repeated the color association task for each bird at three ambient temperatures with treatment order randomized within temperature pairs: 22°C and 40°C, and then 22°C and 43°C. Experiments were conducted in home cages placed in an environmental chamber (Conviron A1000, Winnipeg, Canada). We recorded all test trials using webcams as described above. We took five behavioral measures from these trials. We measured the lengths of time taken to begin the task (time from trays were added to the first lid flipped), complete the task (from first to last lids flipped), and eat individual seeds (from picking up a seed to finishing chewing the seed; for similar methods see 36), the number of seeds eaten per well, and the error ratio of lid flips (the number of incorrectly-colored lids flipped divided by the number of correctly-colored lids flipped within 5 minutes of beginning the task). We tested for differences in performance among temperatures by fitting linear models with R [34]. Models included a factor variable for either signs of thermoregulatory stress (i.e. whether or not the bird panted during the exam) or exam temperature. All models included bird identification as a fixed effect in order to account for repeated measures within individuals. We present effect sizes (B) ± standard errors estimated from the linear models and measures of support for models, including test statistics (t or F) and p-values for specific terms and the full models, and r2adjusted for the full models.

**Detour-reaching task.** Birds were taught to reach into a tube to retrieve a food reward following [32]. This task had three phases: habituation, training and testing. For all phases, a trial consisted of placing a tube (5cm length, 4cm diameter) mounted on a thin piece of wood in a bird's home cage for 10 minutes with a food reward (freshly killed mini-mealworm) at the center of the tube. Trials were repeated sequentially until the bird passed each phase, with no more than 20 trials per day. During the habituation phase, birds were taught to associate an opaque tube with food and passed habituation by taking food in three consecutive trials. Birds were in the main housing room during habituation but visually isolated from other birds with opaque black plastic partitions. For training and testing, birds were moved in their home cage to an environmental chamber (Caron 7000-10, Winnipeg, Canada). During the training phase, birds were exposed to the same temperature and relative humidity as in the main housing room (22°C, 55–65% rH), and were taught to reach around the opaque tube to remove food instead of pecking on the surface. They passed training when they no longer pecked on the side of the tube before removing the food in four out of five consecutive trials.

Only birds that passed the training phase were used in the testing phase (n=9). In the testing phase, birds were presented with baited clear tubes, and passed when they no longer pecked on the side of the tube before removing the food in four out of five consecutive trials. The testing phase was repeated at two ambient temperatures: 22°C and 44°C in a repeated measures design with treatment order randomized across birds. We recorded all test trials to a computer using webcams mounted inside the environmental chamber. We tested for differences in the number of trials to pass the task among temperature treatments by fitting linear models using package nlme [35] that included trial temperature as a fixed effect and bird identification as a random effect. We also tested if trial number influenced performance. We calculated r2 using package r2glmm [36].

**Ethical treatment.** We habituated birds to thermal chambers immediately prior to the test trials and on days preceding test trials. Habituation immediately before the trial was for 30 minutes at trial temperature. For the color-association task, we also habituated birds to the environmental chamber on separate days at 22°C for 2 hours and at an elevated temperature (36°C) for 1.5 hours. For the detour-reaching task, we also habituated the birds to the chamber on a separate day at 22°C for 1 hour. We monitored birds continuously during trials via webcams and removed one bird from a test trial because it exhibited signs of prolonged stress. Following each trial, we supplied fresh food and water to the birds’ cages.

**Ambient temperature in native range.** We mapped ambient temperature in the native range of the zebra finch subspecies (*T. g. castanotis*) used in our captive studies. We downloaded daily maximum temperature maps from the Australian Bureau of Meteorology (http://www.bom.gov.au/jsp/awap/temp/archive.jsp). These maps are interpolated based on data from several hundred weather stations around Australia. We used the bindings for the Geospatial Data Abstraction Library [37] as well as the raster package [38] in the R project [34] to read these maps and to calculate the number of days that reached threshold temperatures (40°C and then 44°C) for each geographical coordinate. We then overlayed the outline of Australia using the maps package [39]. Finally, we clipped the temperature data to the zebra finch range. We obtained this range from BirdLife International [40] and 'ground-truthed' the range using sightings from eBird [41] and museum collection sites from VertNet (vertnet.org).

**Results**

**Heat stress.** When exposed to higher temperatures, birds showed behavioral indicators of heat stress, including panting, wing spreading, and taller posture. At low temperatures (22°C), birds never showed these behaviors (n=9 in detour reaching study, n=6 in color association study). At 40°C, 4 of 6 birds showed all three behaviors during color association trials. At 43°C and 44°C, all birds (n=15) showed all three thermoregulatory behaviors during trials for both tasks. These data indicate that zebra finches experience thermal stress starting at approximately 40°C under these experimental conditions, and that there is inter-individual variation in the threshold of thermal stress.

**Color association task.** Heat reduced motor performance of the color association task. Birds completed the task more slowly when showing signs of thermal stress (Fig. 1A, t13=3.6, p=0.003, full model: F6,13=5.4, p=0.005, r2adjusted=0.58). Compared to the ambient low temperature (22°C), the time to finish the task was slightly longer per individual at 40°C, though not significant (B = 33 seconds ± 45 s.e., t12=0.737, p=0.47), and was significantly longer at 43°C (B = 139 seconds ± 47 s.e., t12=3.0, p=0.011, full model: F7,12=3.5, p=0.03, r2adjusted=0.48). One individual took four times longer to complete the trial at 43°C than at 22°C. The slower completion times at higher temperatures were attributed to two factors. First, birds paused to perform thermoregulatory behaviors, which caused them to take longer between flipping lids of the correct color (Fig. 1B, t12=3.8, p=0.003, full model: F6,12=5.2, p=0.007, r2adjusted=0.59). Similar to results from completion time, the time between correct flips was slightly longer per individual at 40°C, though not significant (B = 4 seconds ± 5 s.e., t11=0.76, p=0.46), and was significantly longer at 43°C (B = 22 seconds ± 6 s.e., t11=3.7, p=0.004, full model: F7,11=4.2, p=0.02, r2adjusted=0.55). Second, birds chewed the food rewards more slowly when showing signs of thermal stress (Fig. 1C, B = 0.7 seconds ± 0.07 s.e., t152=9.5, p<0.0001, full model: F6,152=20.2, p<0.0001, r2adjusted=0.42). Compared to 22°C, the time to eat a seed was significantly longer at both 40°C (B = 0.49 seconds ± 0.07 s.e., t151=6.2, p<0.0001) and 43°C (B = 0.72 seconds ± 0.09 s.e., t151=8.2, p<0.0001, full model: F7,151=16.1, p<0.0001, r2adjusted=0.40).

Heat did not have as strong of an effect on cognitive performance of the color association task. Accuracy of the color association task was not related to high temperatures or signs of thermal stress (Fig. 2A, both t < |1.4| and p > 0.2). Birds missed significantly more food rewards when showing signs of thermal stress (Fig. 2B, t178=-2.65, p=0.0088), suggesting that thermal stress caused cognitive errors, but the full model explained a small amount of variation in the data (F6,178=3.2, p=0.005, r2adjusted=0.07). Further, birds missed more rewards at 40°C (t177=-2.0, p=0.049) and tended to miss more rewards at 43°C (t177=-2.0, p=0.056), although the full model explained little variation in the data (F7,177=2.5, p=0.017, r2adjusted=0.05). Latency to begin the exam was generally short ( = 9 seconds ± 12 s.d. for completed trials) and did not differ significantly based on signs of thermal stress or temperature (both t < |0.3| and p > 0.5), although during one incomplete exam at 40°C, the bird performed thermoregulatory behaviors for over four minutes before beginning the exam. Trial number did not influence performance in any of the above measurements (all t < 1, p > 0.3), indicating that birds did not improve or decline in performance in successive trials.

**Detour reaching task.** Heat limited cognitive performance of the detour-reaching task. Birds required more trials to complete the task at the higher temperature (Fig. 3; B = 3 trials ± 1.0 s.e. t8=3.1, p=0.01, r2=0.25), indicating lower cognitive performance at the higher temperature. Trial number did not influence performance (t8=-0.23, p=0.82), indicating that birds did not perform higher in later trials as a result of learning in previous trials.

**Heat stress in the wild.** Free-living zebra finches in Australia experienced ambient temperatures that caused cognitive and motor declines in our captive birds. During the austral summer months of December 2016­–February 2017, ambient temperatures exceeded temperatures causing motor decline (40°C) on up to 63 days (70% of the austral summer days) and exceeded temperatures causing cognitive decline (44°C) on up to 25 days (28% of the austral summer days) (Fig 4). During this time period, zebra finches experienced at least one day at or above 40°C in 42% of their range and 44°C in 18% of their range.

**Discussion**

Our findings support the hypothesis that heat stress limits behavioral performance in an endotherm. The behavioral output of animals is composed of motor patterns (e.g. food manipulation) and cognitive processing (e.g. recall of foraging sites), and our findings suggest that both are affected by thermal stress. When heat stressed, birds took longer to complete the color association task, demonstrating reduced motor performance. Heat stressed individuals also required more trials to retrieve the food reward in the detour-reaching task and also missed food rewards during the color association task, indicating lower cognitive performance on these tasks. Taken together, our findings indicate that heat stress reduces motor and cognitive performance in zebra finches.

There are multiple avenues by which thermal stress could have reduced motor performance. First, birds under thermal stress stopped performing the color association task in order to perform thermoregulatory behaviors. This time budget trade-off between behaviors led to slower completion of the color association trials. Second, we found heat stress reduced performance of chewing behaviors. Individuals could be slowing movement to reduce heat generation or as a result of muscle function decline. Indeed, sublethal heat stress has been shown to alter muscle physiology in birds [11], which could reduce muscle performance, though this relationship has not been established. Together, the time budget trade-off and slowed muscle performance contributed to a slowdown in completing the color association task at higher temperatures.

Heat stress also reduced cognitive performance, but not for all cognitive abilities. We found strong effects of heat stress on inhibitory behavior. Birds had to inhibit the unproductive behavior of pecking on a clear barrier between themselves and the food reward in order to reach around the tube to acquire the food. The same individuals that could solve this task quickly at temperatures within their thermoneutral zone were significantly slower to do so at temperatures above their upper critical limit. In contrast, heat did not have as strong of an effect on discrimination behaviors, as assayed in the color association task. Birds missed food rewards but did not make more mistakes in selecting the correct lid color during color association. Therefore, heat stress may have different effects on different cognitive processes. This could be because thermal stress has differential effects on different regions of the brain [19], warranting further investigation. Further work is also needed to assay additional cognitive processes important to endotherms, such as spatial memory.

The cognitive assays used in our experiments should map onto functional behaviors in the wild. Although there are few studies of the evolutionary ecology of cognitive behaviors [24], there is increasing evidence that these types of cognitive processes explain variation in fitness. Our color association task measured associative learning. In bumblebees (*Bombus terrestris dalmatians*), associative learning speed is correlated with foraging rate [26]. Our detour-reaching task measured inhibitory behaviors, which are predictive of problem-solving skills (reviewed in Hauser 1999) and have been correlated with offspring fledged and mating success in wild birds [24,43,44]. Both of our tasks also measure aspects of flexible behavior that allow animals to respond to environmental variation, including novel environmental challenges or rapidly changing environmental conditions [45,46]. In mammals and birds (both endotherms), flexible behaviors are thought to be favored in species that use diverse food resources [47], inhabit environments with unpredictable resources [48] and have complex social systems [49]. Thus, there is evidence that variation in cognitive ability is linked to a number of different measures of fitness at the individual level and life-history traits at the species level.

We argue that a reduction in performance of cognitive tasks is due to a change in the thermal environment. Alternate explanations for variation in cognitive ability among individuals include variation in personality (e.g. risk taking), motor ability (e.g. dexterity), motivation (e.g. hunger) and perceptual ability (e.g. visual acuity) [24]. By comparing an individual's performance against themselves using a repeated measures design, we limit the potential confounds of variation in personality, motor ability and perceptual ability among individuals. Of course, variation in motor ability and even perceptual ability within an individual at different temperatures is likely part of the explanation for reduced performance. The remaining variable that could explain variation in performance among individuals is motivation. However, we assessed motivation to feed immediately after each assay, and all individuals showed motivation. Therefore, we suggest that our findings provide strong experimental evidence that heat stress affects behavioral performance in zebra finches.

Motor and cognitive performance changed at different physiological transitions during thermoregulation. We found that zebra finches consistently exhibited behavioral indicators of heat stress, including panting, wing spreading, and taller posture, at 40°C. This observation is consistent with previous physiology studies that demonstrated 40°C as the upper critical temperature for zebra finches [29–31], though Cade *et al.* (1965) found it to be 42°C. At the upper critical temperature, we found reduced motor performance. Once above the upper critical temperature, this effect on motor performance was four times higher with an increase in 3°C, and we began to find reduced cognitive performance. This result suggests an increasing effect of heat stress on behavior with each degree outside the thermal neutral zone for endotherms. Such temperature response curves are known for some physiological processes [8,9,50] but have not been described for behavioral processes in endotherms. Because the progression of thermoregulation is conserved across endotherms, we can predict that other endotherms should show similar reductions in motor and cognitive performance above their upper critical temperature. For example, another well-studied passerine, the white-crowned sparrow (*Zonotrichia leucophrys*) has an upper critical temperature of 37°C [51]. We therefore predict a reduction in motor performance of cognitive tasks starting around 37°C, with a reduction in cognitive performance following at higher temperatures. Our findings of temperature dependent effects on behavioral performance suggest important avenues of future work at the interface of thermal and behavioral biology.

Our findings highlight the need for modeling approaches to predict the likelihood of sublethal effects of climate change. Existing models predict lethal effects, but not sublethal effects, of changing temperatures on endotherms. For example, temperature increases of 3.5–5.5°C by 2080 are expected to increase mortality from dehydration for several bird species in the US southwest [52,53]. However, our data indicate that sublethal heat stress leads to less efficient foraging, which could result in heat-induced mortality sooner and for longer stretches of time, suggesting that our current predictions of future mortality resulting from heat waves are conservative.

**Ethics**

Tulane IACUC 0427R and UNCW IACUC A1516-018 approved housing and experimental conditions.

**Data Accessibility**

We uploaded datasets of behavioral performance to Dryad. Climate and zebra finch range data are available online and from Birdlife International as described in the Methods section. We uploaded all R scripts for data analyses as supplementary materials.

**Authors’ contributions**

RMD conducted behavioral trials, carried out statistical analyses and computer modeling, participated in design of the study and helped draft the manuscript; CMC conducted behavioral trials, participated in design of the study and helped draft the manuscript; EPD participated in design of the study, contributed to computer modeling, and helped draft the manuscript. All authors gave final approval for publication.

**Competing interests**

We have no competing interests.

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**Figures**

Macintosh HD:Users:dannerr:Dropbox:Thermal cognition:ThermCog association and detour ms:Figures:Fig 1 Color association speed.pdf

**Figure 1.** Zebra finches required longer to complete a color-association task when showing signs of thermal stress (i.e. panting) at higher temperatures. This was reflected in total time to finish the trial (A), and resulted from longer times between flipping correct lids (B) and slower chewing speeds (C) when exhibiting signs of thermal stress (all p < 0.005 for 6 birds at three temperatures). Birds showed signs of thermal stress during all trials at 44°C and some trials at 40°C.

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**Figure 2.** Zebra finches showed evidence of cognitive declines at high temperatures. Finches maintained high accuracy in a color association task, despite signs of thermal stress (p > 0.2 for 6 birds at three temperatures) (A), though they skipped more food rewards (p = 0.0088 for 6 birds at three temperatures) (B), suggesting that thermal stress reduced cognitive performance. Birds showed signs of thermal stress during all trials at 44°C and some trials at 40°C.

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**Figure 3.** Zebra finches required more trials to complete a detour-reaching task at a higher temperature. Lines connect paired measurements of performance of individual birds at two temperatures (p=0.01 for 9 birds at two temperatures); dots and error bars represent model-based averages and standard errors.

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Macintosh HD:Users:dannerr:Dropbox:Thermal cognition:ThermCog association and detour ms:Figures:Fig 4B Temp maps with letter.pdf

**Figure 4.** Geographical areas within the zebra finch range during austral summer 2016–2017 in which ambient temperatures caused (A) motor decline (40°C) and (B) cognitive decline (44°C) in our captive studies. Data taken from the austral summer months of December 2016 to February 2017. Presented as a heat map with the maximum number of days that reached or exceeded that temperature in red and zero days in white. Zebra finch range is outlined in gray.