Heat stress inhibits cognitive performance in wild Western Australian magpies, *Cracticus tibicen dorsalis*

Grace Blackburn [a, *, 1] , Ethan Broom [a, 1] , Benjamin J. Ashton [a, b] , Alex Thornton [c] , Amanda R. Ridley [a]

[a] School of Biological Sciences, University of Western Australia, Crawley, WA, Australia
[b] Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia
[c] Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Exeter, U.K.

Cognition enables animals to respond and adapt to environmental changes and has been linked to fitness in multiple species. Identifying the potential impact of a warming climate on cognition is therefore crucial. We quantified individual performance in an ecologically relevant cognitive trait, associative learning, to investigate the relationship between heat stress and cognition in wild Western Australian magpies over 2 consecutive years. We found that heat stress had a significant negative effect on performance in both years, with individual pass rates much lower under heat stress than under nonheat stress conditions. The long-term repeatability of cognitive performance within temperature conditions was high (i.e. consistent fails under heat stress and consistent passes under nonheat stress conditions between years), but repeatability between conditions was low. This suggests that the observed effect could not be attributed solely to natural fluctuation in cognitive performance. This study is one of the first to reveal the negative influence of heat stress on cognitive performance in a wild animal, drawing attention to the potential cognitive consequences of rising temperatures.
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Cognition, defined as the mechanisms through which animals acquire, process, store and act on information from the environment (Shettleworth, 2001), underpins a number of behaviours crucial to fitness (Sayol et al., 2016; Sol et al., 2005). Determining the factors that influence cognition is therefore essential. Anthropogenic climate change is forecast to increase global temperatures by 0.2 °C per decade (Intergovernmental Panel on Climate Change, 2018) and is predicted to become the single biggest threat to global biodiversity and wildlife (Foden et al., 2013; Urban, 2015). Until recently, the effect of rising temperatures on cognition in wild animals had not been explored, despite evidence that environmental conditions impact cognitive performance (Ashton et al., 2018a; Cauchoix et al., 2020) and that cognition is linked to survival and reproductive success in a variety of taxa (Ashton et al., 2018b; Cole et al., 2012; Keagy et al., 2009; Maille & Schradin, 2016; Shaw et al., 2019; Sonnenberg et al., 2019; Wetzel, 2017). There is therefore an urgent need for more research into the impact of environmental change on cognitive performance (Soravia et al., 2021).

Environmental conditions such as altitude, predation pressure and unpredictability of resources have been identified as determinants of intraspecific variation in cognitive performance (Brown & Braithwaite, 2005; Brydges et al., 2008; Freas et al., 2012; Pravosudov & Clayton, 2002; Tebbich & Teschke, 2014). For example, across a range of chickadee species, individuals living at higher altitudes exhibit elevated performance in spatial memory tasks (Freas et al., 2012). Environmental unpredictability has also been found to affect reversal learning in woodpecker finches, *Cactospiza pallida*, with individuals from habitats with variable food availability performing better than individuals from habitats with stable food abundance (Tebbich & Teschke, 2014).

While evidence for a relationship between environmental variation and cognitive performance is both compelling and important for our understanding of the potential impacts of anthropogenic change on animal cognition, research into how heat stress may impact animal cognition has been confined to captive studies (Dayananda & Webb, 2017; Triki et al., 2017; Coomes et al., 2019; Danner et al., 2021). In captive cleaner fish, *Labroides dimidiatus,* individuals were observed to be less adept at making

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strategic decisions to maximize their food intake following an environmental disturbance that increased water temperature (Triki et al., 2017). In captive zebra finches, *Taeniopygia guttata*, the ability of females to discriminate between intraspecific and heterospecific mating signals was impeded in hot conditions (Coomes et al., 2019). More recently, it was found that detour-reaching task performance (an assay of inhibitory control) in captive zebra finches was reduced when focal individuals were exposed to higher temperatures (Danner et al., 2021). In addition, this study found that performance on a colour association task was maintained at high temperatures, but birds were more likely to overlook located food rewards at these temperatures, suggesting a cognitive decline (Danner et al., 2021). Evidence for a temperature–cognition relationship has also been identified in humans, whereby heat stress negatively influences cognitive performance and increases the likelihood of lethal and sublethal workplace accidents (Hancock & Vasmatzidis, 2003; Ramsey et al., 1983). Combined, these findings support the hypothesis that wild animals may suffer cognitive decline while experiencing heat stress.

Elevated temperatures can have both lethal (McKechnie et al., 2012) and sublethal impacts on wild animals (Andreasson et al., 2020; Conradie et al., 2019; Stillman, 2019; Urban, 2015). The small body size and diurnal activity of many bird species leave them particularly vulnerable to high temperatures (McKechnie & Wolf, 2009; du Plessis et al. 2012; Gardner et al., 2016), leading to changes in behaviour, gut microbiome, thermoregulation, evaporative water loss and survival (Conradie et al., 2019; Davidson et al., 2020; Nilsson et al., 2016; Smit et al., 2013). These sublethal costs of heat exposure are likely to lead to rapid population declines, particularly in arid regions (Conradie et al., 2019; Ridley et al., 2021). There is also evidence for behaviour–thermoregulatory trade-offs in birds under hot conditions, whereby vital foraging or reproductive behaviours are traded off against the increasing need to dissipate heat through behaviours such as panting and wing splaying (Cunningham et al., 2013, 2021; Edwards et al., 2015; Funghi et al., 2019; Wiley & Ridley, 2016). If cognitive processing experiences a similar trade-off with thermoregulation, cognitive performance may decline as temperatures increase. Such trade-offs could compound the physiological effects of heat stress on the brain, such as heat-induced neuroinflammation (Lee et al., 2015). Given the growing amount of evidence linking cognitive traits to foraging behaviours (Morand-Ferron, 2017; Rosati, 2017; Shaw et al., 2015), impairment of foraging behaviours as temperatures increase may be partially induced by declines in cognitive performance.

Several studies have identified that there is likely to be a critical temperature point at which behavioural–thermoregulatory trade-offs occur (Bourne et al., 2020; Cunningham et al., 2013, 2021; Edwards et al., 2015; Wiley & Ridley, 2016). In Western Australian magpies, for example, time spent foraging rapidly decreases above 32 °C, concomitant with an increase in heat dissipation behaviours (Edwards, 2014). The fitness implications of this are potentially severe; for instance, research on pied babblers, *Turdoides bicolor*, in the Kalahari Desert shows that a reduction in foraging efficiency during elevated temperatures is associated with body mass decline (du Plessis et al., 2012) and lower provisioning rates to young (Wiley & Ridley, 2016). These sublethal effects are expected to increase dramatically in the coming decades as temperatures increase (Conradie et al., 2019). If critical temperatures are present for cognitive processing, as they are foraging (Edwards et al., 2015), rapid heat-induced declines in cognitive performance may also occur.

A range of studies revealing a direct link between cognition and fitness have further highlighted the importance of identifying factors that may adversely affect cognitive performance. For instance,

variation in tendencies to solve novel problems has been positively correlated with reproductive measures such as clutch size (Cole et al., 2012), mating success (Keagy et al., 2009) and survival of offspring to fledging (Wetzel, 2017) across various species. Another important cognitive skill, spatial memory, has been positively correlated with reproductive success in male New Zealand robins, *Petroica australis* (Shaw et al., 2019), and survival in male African striped mice, *Rhabdomys pumilio* (Maille & Schradin, 2016). Associative learning has been identified in numerous studies as a key cognitive trait underpinning foraging, intraspecific competition and predator avoidance behaviours (Morand-Ferron, 2017; Shaw et al., 2015). In Western Australian magpies, females with higher cognitive performance across multiple cognitive tasks (including associative learning) raised more fledglings that survived to independence per year (Ashton et al., 2018b). This cognition–fitness relationship suggests that heat-induced declines in cognitive performance may have longer-term implications for the ability of individuals to survive and reproduce.

In this study, we compared the intraindividual performance of wild Western Australian magpies in an associative learning task when they were displaying heat stress behaviours (panting and/or wing splaying) versus normal (no heat stress) behaviours in a paired design and we identified a critical temperature point for rapid decline in cognitive performance. We then compared repeatability of cognitive performance within and between heat stress and nonheat stress conditions to determine the robustness of observed patterns in cognitive performance.

METHODS

Study Animals and Site

The Western Australian magpie is a sexually dichromatic medium-sized bird (250–370 g) that lives in cooperatively breeding groups of 3–16 individuals, with a life span of up to 25 years in the wild (Ashton et al., 2018b; Edwards et al., 2015). These birds are found throughout the southern half of Western Australia and are common throughout the southwest of the state (Johnstone & Storr, 1998). Summer temperatures in this region are predicted to increase by 0.5–1.2 °C by 2030 and up to 1.1–4.2 °C by 2090 (Department of Primary Industries and Regional Development, 2020).

Nine habituated magpie groups (group size 4–16) located in Guildford (31°89'S, 115°96'E) and Crawley (31°98'S, 115°81'E), Perth, Western Australia were observed for this study. Each group was habituated to the presence of humans (Pike et al., 2019), thus allowing for close observation and individual presentation of cognitive tasks, and has been monitored since 2013 (Ashton, 2017; Ashton et al., 2018b). The majority of individuals were ringed to allow for individual identification and collection of life history information (Ashton et al., 2018b; Pike et al., 2019).

Experimental Design

Cognitive performance was quantified using an associative learning task. This domain-general cognitive trait was chosen due to its ecological relevance; it is likely that associative learning underlies a number of behaviours related to foraging, intraspecific competition and predator avoidance (Ashton et al., 2018b; Morand-Ferron, 2017; Shaw et al., 2015). Two rounds of testing were carried out on the study population over two consecutive summer periods (February – April 2018 and 2019) to determine robustness and repeatability of results.

Causally identical but visually distinct versions of the associative learning task have been presented to the study population

previously (Ashton et al., 2018b). To avoid previous experience confounding performance, visually distinct shapes were used as discrimination stimuli rather than colours, as used by Ashton et al. (2018b) in previous associative learning tasks. The shapes used in the two testing periods and in each treatment condition of this study were visually distinct to prevent any confounding effect of memory on performance (Ashton et al., 2018b). The associative learning task required individuals to learn an association between a particular shape on the lid of the task and a food reward (small piece of mozzarella cheese). The task consisted of a wooden foraging grid with two identical wells, each covered by black wooden lids with distinct white shapes painted on them (Appendix 1, Fig. A1). The food reward could be accessed by pecking one of two lids (the rewarded shape) on the task. Test subjects did not need training due to previous experience with similar cognitive tasks (Ashton et al., 2018b). Twelve shapes were used in the associative learning task, arranged into sets of two that were always on the array together. Different shapes were used in each of the two testing periods, as well as in each of the two treatment conditions for each bird (resulting in a maximum of four tests per bird), so that no individual was ever presented with the same shapes for multiple tests. Each cognitive test included a maximum of 30 trials, each trial spaced 1 min apart. The same shape was rewarded throughout the test (set of a maximum 30 trials). Lids were swapped randomly between trials so that the rewarded shape was not always on the same side of the array, ensuring the bird associated the shape with the food reward and not the spatial location of the well. To control for olfactory cues, cheese was rubbed around the inside of both wells prior to testing (see Ashton et al., 2018b). Following the protocol of Shaw et al. (2015), the first trial of each test allowed the bird to peck at both lids and explore both wells, to demonstrate that only one well contained a food reward. Testing did not progress past this first trial until the focal bird explored both wells. In all subsequent trials, the bird was only allowed to peck one of the lids before the array was removed by the experimenter. During trials, the array was placed approximately 3 m from the focal individual, with the experimenter standing approximately 5 m on the other side of the array in line with the middle of the task to avoid any possible cueing to either of the two wells. The individual then approached the task and pecked at one of the two wells. If the correct shape was pecked first, the trial was passed, and the individual could obtain and consume the food reward. If the incorrect shape was pecked first, the task was removed, and the individual did not obtain the food reward. Testing was completed in relative isolation, with group members other than the focal individual approximately 5 m from the task. This was achieved by placing the array behind an object (such as a tree or other plants) that would effectively separate the focal individual from the rest of the group or simply waiting until the focal bird moved sufficiently far from the rest of the group. This was easily achievable as magpies often forage over 10 m from each other (Ashton et al., 2018b). If another bird did approach the task of the individual being tested, the test was paused until the individual being tested was once again isolated. During each trial, air temperature was measured using an RS Pro RS42 digital thermometer (in the shade, where testing occurred) and time of day was recorded. For trials in 2019, we also recorded the ground temperature, each individual's body mass and neophobia (the time it took for the individual to interact with the task, which was used as a metric of motivation). Body mass, a measure of body condition, was measured within 30 min of testing using a top-pan scale which the magpies had been habituated to hop onto (Pike et al., 2019). In addition, during the 2019 testing season, a FLIR T530 thermal imaging camera (Teledyne FLIR, Wilsonville, OR, U.S.A.) was used to capture images of individuals within 30 min of completing testing. The FLIR ResearchIR software

package (FLIR Systems, Inc., 2015) was then used to determine minimum eye region surface temperature readings and the number of pixels that made up the eye in each image. Model selection revealed that eye temperature was not a better measure for predicting heat-induced cognitive decline than treatment condition and air and ground temperatures. We therefore do not include eye temperature as a variable in the analyses presented (for more in-depth discussion of the thermal imaging set-up and analysis used in this study, see Appendix 2). If an individual successfully pecked the rewarded shape in 10 of 12 consecutive trials, they passed the test, as this represented a significant departure from binomial probability (see Ashton et al., 2018b). If this was not achieved within 30 trials, the test was considered a fail. It was necessary to use binary (pass/fail) measures with an upper limit of 30 trials, rather than continuous measures of cognitive performance (as in previous studies where all individuals were tested until they passed; Ashton et al. 2018b) due to the time constraints of testing under heat stress versus nonheat stress conditions.

Testing was completed using a paired design whereby the same individuals were tested in both heat stress and nonheat stress conditions. An individual was considered heat stressed if it displayed observable markers of heat dissipation (panting and/or wing splaying) for at least 25% of the testing time (see du Plessis et al., 2012; Edwards et al., 2015). Heat stress behaviours were almost always exhibited at temperatures over 32 °C, a temperature determined to be a critical threshold for this species (Edwards, 2014). During both test years, for the first test of each individual, the shape set was randomly selected. For subsequent tests, only shape sets with which the individual had no previous experience were used. Individuals were tested once during heat stress and once during nonheat stress conditions during each year of testing. The order of testing (whether the individual underwent testing first in the heat or nonheat stress conditions) was randomized. In 2018, 17 individuals were tested (34 tests in total), and in 2019, 20 individuals were tested (40 tests in total). This totalled 74 tests across both years, of which 56 were the same 14 individuals tested in both conditions in both years. A total of 23 individuals were tested.

Heat stress and nonheat stress tests of the same individual were completed within 3 weeks of each other to control for potential differences in cognitive performance caused by seasonal shifts. All testing took place between 1000 and 1700 hours, when temperatures are at their maximum, between February and April (the nonbreeding season for this species) in 2018 and 2019.

Statistical Analyses

Investigation of factors influencing cognitive performance was conducted using the SPSS statistics package (version 27, IBM, Armonk, NY, U.S.A.). Analysis included a McNemar's test for paired nominal data to investigate paired intraindividual differences in test performance between heat stress and nonheat stress conditions. This was followed by model selection using generalized linear mixed models (GLMMs) to determine factors influencing the number of trials taken to pass the cognitive test. These models used a binomial distribution with a logit link function, treating trials taken to pass the test (with an upper limit of 30) as the response term. Individual and group identity were included as random terms in the analysis. Model predictors included sex, group size (adult group size, excluding juveniles, i.e. individuals below 3 years old), rewarded shape, heat condition (heat stress behaviours = 1, no heat stress behaviours = 0), time of testing, ground temperature, air temperature, testing order, body mass and neophobia. Model selection using Akaike information criterion values corrected for small sample size (AICc) was then conducted to determine which candidate models best explained variation in the data. Terms were

excluded from additive models if their confidence intervals intersected zero when tested alone, with the exception of terms included in interactions. To investigate a critical temperature point for rapid decline in cognitive performance, the model output for a binomial regression including air temperature as a predictor variable and pass/fail as the response variable was used. This identified an estimate for the point at which the probability of passing the associative learning test within 30 trials dropped below 50%, by dividing the estimate for the intercept of the regression by the estimate for the effect of air temperature.

Model Selection

We used AICc values to determine which terms best predicted data patterns by comparing a set of models that contained one or more terms. If multiple terms were highly correlated (e.g. air temperature and heat stress), the term with the lowest AICc as an individual predictor was used in further additive models (see Harrison et al., 2018). Models were selected based on their suitability as plausible biological hypotheses (Burnham & Anderson, 2002) and the AICc values for each were recorded and compared. Models were compared to a basic intercept model containing only the intercept and random terms. The model with the lowest AICc was considered the most parsimonious model, and terms contained within that model were considered significant if their parameter confidence intervals did not intersect zero, as per Grueber et al., (2011) and Symonds and Moussalli (2010). Following Harrison et al., (2018), where two models had a similar AICc value, the model with the simplest structure (fewer terms contributing to the AICc value) was considered more parsimonious. A top model set was then constructed using all the models with AICc values within five of the top model (Appendix 1, Table A1).

Repeatability in Cognitive Performance

Repeatability is defined as the fraction of total phenotypic variance that is explained by the variance among individuals, typically represented as a value from zero to one (Dingemanse & Dochtermann, 2013) and can be treated as a comparison of intra- and interindividual variation (Lessells & Boag, 1987; Morand-Ferron et al., 2015). Cognitive repeatability can be influenced by an individual's genetic, developmental and environmental circumstances (Cauchoix et al., 2018; Cole et al., 2011; Thornton & Lukas, 2012). Repeatability analyses were used to quantitatively confirm that observed differences in cognitive performance were indeed a result of heat stress and not simply the consequence of natural variation in cognitive performance. Decomposition of the variance components used to calculate repeatability gives an indication of whether repeatabilities were driven by intraindividual variation (i.e. consistency of intraindividual cognitive performance) or interindividual differences (Jenkins, 2011; Rudin et al., 2018; Stoffel et al., 2017).

Statistical analysis of repeatability of cognitive performance was carried out in R using the rptR package (version 0.9.22, Nakagawa & Schielzeth, 2010; Stoffel et al., 2017), which generated a repeatability estimate using variance components obtained from GLMMs. Repeatability estimates were calculated using 14 individuals which had completed two associative learning tests in each condition, one heat stress test and one nonheat stress test in both 2018 and 2019, totalling 56 test results. Repeatability estimates were generated for heat stress and nonheat stress conditions separately. Between-condition repeatability estimates were also generated, which included the total pool (both heat stress and nonheat stress conditions). A GLMM with a logit link function was used to calculate the repeatability estimate, using data from the two cognitive test batteries. The GLMM process used a binary response variable (pass = 1, fail = 0), with individual ID treated as a random factor.

Group ID was not treated as a random factor as it did not add any additional variance beyond individual ID. Uncertainty of the repeatability estimate was quantified using parametric bootstrapping ($N = 100$), which generated 95% confidence intervals and a P value for the repeatability analysis (Rudin et al., 2018). The number of replicates was chosen by increasing the number of replicates until convergence (see Chernick, 2007) and has also been identified as the lower limit of replicates that is usually necessary (Pattengale et al., 2010). If the repeatability estimate had confidence intervals that intersected zero, there was nonsignificant repeatability for that condition. Repeatability estimates were considered significantly different from each other if the 95% confidence intervals did not overlap. By using individual ID as a random effect, this analysis identified the proportion of variance accounted for by interindividual differences (Rudin et al., 2018). However, inspection of the individual variance components obtained from the GLMMs used to calculate repeatability gave an indication of whether interindividual or intraindividual variance was driving the repeatability estimates (although these differences between raw variance components could not be formally tested; see Jenkins, 2011; Rudin et al., 2018).

Ethical Note

All birds involved in this study were wild animals, and hence could choose whether they took part in the cognitive testing. They were able to walk or fly away from the testing area and experimenter at any time if they desired. The cognitive task used in this experiment was designed to resemble natural ground foraging of these birds, and therefore was not uncomfortable or aversive to them. We had permission to conduct the study from the University of Western Australia Animal Ethics Committee (approval number RA/3/100/1656) under The Animal Welfare Act 2002 (WA).

RESULTS

Effect of Heat Stress on Cognitive Performance

A total of 23 magpies from nine different groups were tested, both when they were displaying heat stress behaviours and when they were not. Recorded mean air temperatures for cognitive tests ranged from 21.8 to 44.1 °C during the February to April 2018 testing period, and from 22.2 to 40.7 °C during the 2019 testing period.

Within-individual comparisons revealed individuals were significantly less likely to pass the cognitive test under heat stress than nonheat stress conditions (McNemar's related samples test: $P < 0.001$, $N = 23$).

During nonheat stress conditions, the average number of trials taken to pass was 20.14, compared to 28.95 trials during heat stress conditions (Fig. 1, Table 1). Adult group size was negatively associated with the number of trials taken to pass: magpies from larger groups took significantly fewer trials to pass the associative learning test ($P < 0.001$; Fig. 2, Table 1). Sex, body mass and neophobia (measured as the time taken to interact with the array) did not influence cognitive performance (see Appendix 1, Table A1 for full model output). The order in which cognitive testing was completed (heat stress or nonheat stress conditions first) and the shape that was rewarded also had no significant impact on cognitive performance (Appendix 1, Table A1). We also found no significant difference in neophobia in heat stress and nonheat stress conditions (paired t test: $t_{14} = -0.99$, $P = 0.329$).

In the 2019 test battery, the probability of passing the cognitive test remained steady from 24 to 30 °C before declining. The point at which the associative learning test pass rate dropped to below 50%
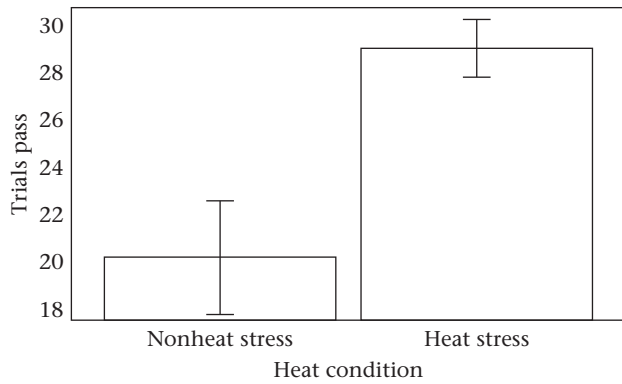
Figure 1. Average number of trials taken to pass the associative learning trial in nonheat stress and heat stress conditions ($N = 74$ associative learning experiments). Means were generated from the model output in Table 1. Error bars show 95% confidence intervals.

Figure 2. Relationship between adult group size and number of trials taken to pass the cognitive test. Data were gathered from 74 associative learning tests on 23 individuals from nine groups. The regression line is represented by the solid line and SEs are represented by the shaded areas.

was at approximately 32 °C, according to the output of a binomial regression using air temperature as the predictor variable (point estimate = 31.6, equation = $20.55 - 0.65x$, $Z_{37} = -2.55$, SE = 0.25, $P = 0.01$). This suggests that $31 - 32$ °C may be a critical temperature for rapid cognitive decline in magpies. Below 31.83 °C, 81% of individuals passed the associative learning test, compared to only 14% of individuals above this temperature. This temperature was also the same as the point at which heat dissipation behaviours increased rapidly (approximately 32 °C; Appendix 1, Fig. A2) and a previously identified critical temperature point in magpies for heat dissipation and foraging trade-offs (Edwards, 2014).

Repeatability of Cognitive Performance

Intraindividual repeatability of performance in the associative learning task was very high within both the heat stress and the nonheat stress condition (Table 2). It was slightly higher during heat stress, although this difference was not significant (Table 2). Intraindividual variance was lower than interindividual variance within both conditions, but not between conditions. This indicated intraindividual consistency was high within conditions but low between conditions (Table 2).

DISCUSSION

This study provides some of the first empirical evidence that heat stress may negatively affect cognitive performance in a wild animal. This is consistent with research on both captive animals (Coomes et al., 2019; Danner et al., 2021; Lee et al., 2015;
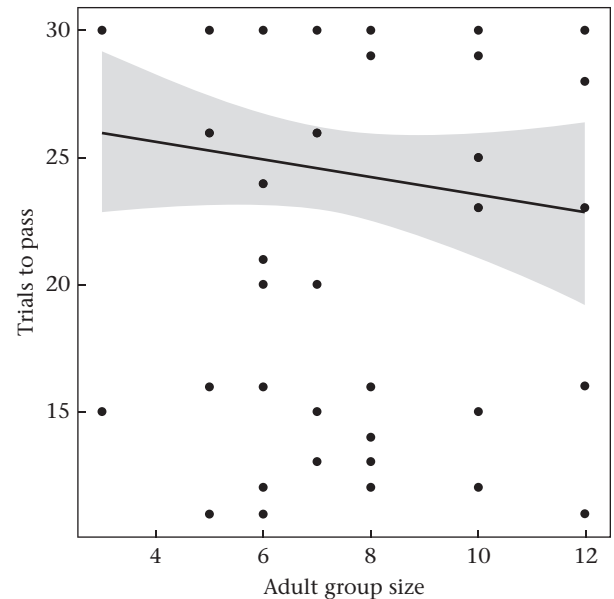
Table 1
Top model set for trials taken to pass

Top Model set		AIC	ΔAIC
Heat condition + Adult group size		496.12	0.00
Basic intercept		754.18	258.06
Parameter	Estimate	SE	CI
Adult group size	- 0.38	0.09	-0.56−0.20
Heat condition			
Nonheat stress	-2.86	0.19	-3.23−2.49
Heat stress	0	—	—

Data are based on 74 associative learning tests completed on 23 magpies, including 37 tests in heat stress conditions and 37 tests in nonheat stress conditions. Outputs were generated using model selection from binomial GLMM analysis. The top model set includes models within 5 AIC of the best model. CI = 95% confidence intervals. For a full set of models tested see Appendix 1, Table A1.

Dayananda & Webb, 2017; Triki et al., 2017) and humans (Hancock & Vasmatzidis, 2003; Ramsey et al., 1983) and raises the possibility that heat-related declines in cognitive performance may become a growing problem for many wild animals due to climate change. Repeatability of cognitive performance was extremely high within heat conditions, but low between conditions due to a consistently high pass rate in nonheat stress conditions and a consistently low pass rate in heat stress conditions. This provides evidence that the observed decline in cognitive performance was likely to be due to heat stress rather than natural variation in performance in the associative learning task.

Performance in the associative learning task declined sharply when temperatures exceeded approximately 32 °C, the same as a previously identified critical temperature point at which a trade-off between heat dissipation and foraging effort occurs in magpies (Edwards, 2014). This temperature (32 °C) may therefore represent the upper critical thermal limit for this species, above which heat stress increases rapidly and investment in offsetting heat is required (Speakman & Król, 2010) at the cost of other behaviours (Edwards et al., 2015). This trade-off may also explain the decrease in cognitive performance observed in magpies above this critical limit. As climate change accelerates (Intergovernmental Panel on Climate Change, 2018), it is likely that the critical temperature threshold of magpies (and other species) will be exceeded with increasing regularity, leading to persistent reduction in cognitive performance. Despite evidence that some species can adapt their thermal tolerance to more extreme temperatures (Bennett et al., 2021; Muñoz et al., 2014), it is widely acknowledged that global warming is most likely progressing at a rate too rapid for such adaptation in most species (Bennett et al., 2021; Colwell et al., 2008). Unless they are able to move to cooler areas, many species are therefore likely to experience temperatures out of their thermal breadth increasingly frequently in the coming years. The decline in an animal's ability to learn to associate stimuli correctly could potentially impact foraging effort, behavioural response, predator detection, adaptation to anthropogenic changes and parental investment (Cunningham et al., 2013; Edwards et al., 2015; Lee & Thornton 2021; Soravia et al., 2021; Wiley & Ridley, 2016). In

Table 2
Repeatability estimates of cognitive performance

Heat condition	Intraindividual variance	Interindividual variance	Repeatability estimate	95% CI	P
Heat stress	15.08	4077.41	0.996	0.891, 0.998	<0.001
Nonheat stress	5.93	117.78	0.952	0.891, 0.998	0.006
Between condition	4.132	0.142	0.033	0.00, 0.244	0.373

Estimates are across two associative learning test batteries. Each cognitive test battery included one test on 14 individuals, totalling 28 cognitive tests. The 95% confidence intervals (CI), SE and P values were generated using parametric bootstrapping ($N = 100$).

2018 and 2019, the number of days in southwest Western Australia with maximum temperatures equalling or exceeding 32 °C was 53 and 69, respectively (Bureau of Meteorology, 2021). Mean and maximum temperatures in this region are predicted to continue to increase (Department of Primary Industries and Regional Development, 2020). Therefore, a 32 °C upper thermal limit would likely see heat-induced cognitive impairment become increasingly common in Western Australian magpies in the future.

Understanding the consequences of heat-induced declines in cognitive performance allows for more accurate predictions of how species may be influenced by climate change (McKechnie et al., 2012). If short-term heat-induced cognitive declines become more frequent and severe, then the future fitness and population dynamics of numerous species may be under threat (McKechnie et al., 2012; McKechnie & Wolf, 2009). One potentially harmful implication of heat-induced cognitive decline in magpies is likely to be reduced reproductive success. Previous research has found that female magpies with greater cognitive performance produce more fledglings surviving to independence per year (Ashton et al., 2018b). Heat stress has also been shown to decrease time spent foraging in magpies (Edwards et al., 2015). This may be partially generated by heat-induced cognitive decline, particularly through reductions in associative learning, as empirical evidence shows that associative learning is tied to foraging efficiency (Raine & Chittka, 2008) and identifying variation in food quality (Morand-Ferron, 2017). As temperatures increase, the resulting cognitive decline may lead to reductions in the level of energy intake and parental care, and therefore declines in reproductive success. Similar consequences of heat-induced cognitive decline are likely to occur in a range of species that may be of higher conservation concern than Western Australian magpies (currently listed as 'least concern', International Union for Conservation of Nature, 2018). Our study therefore highlights the importance of considering the effects of cognitive impairment due to heat stress when predicting how rising temperatures may affect threatened species.

The mechanisms behind the observed reduction in cognitive abilities resulting from increased temperature are little explored (Soravia et al., 2021). While our study found no significant difference in time taken to approach the associative learning task (neophobia) in the heat versus nonheat stress conditions, we cannot completely rule out an effect of motivation on performance in the task. Indeed, previous work (Edwards et al., 2015) on this population found evidence that foraging effort was significantly reduced when birds were exhibiting heat stress behaviours. It is possible that individuals in this study may have been similarly affected and therefore were less motivated to search for food or interact with the task when under heat-stress conditions. However, the fact that all individuals that were presented with the task completed testing and continued returning to the task (either by passing the task or reaching the upper limit of 30 trials) regardless of the temperature condition, suggests that motivation alone does not explain the difference in cognitive performance between the two conditions. To rule out the potential effects of motivation on cognitive performance more confidently, future studies should incorporate measures such as foraging efficiency and time spent interacting with the task into analyses. A 'motivation test' similar to that used in

Danner et al. (2021), in which birds are presented with a food dish after completion of cognitive testing and the time taken to approach the food dish is measured, could also be utilized to investigate motivation levels of individuals. Another possible explanation for the decline in performance under heat stress conditions is that individual birds may revert to randomly selecting wells under heat stress; however, this change in sampling technique is evidence of cognitive decline under heat stress, as random sampling is a less effective sampling method than directed choice in contexts where certain stimuli are consistently associated with rewards. Accordingly, our results point towards a direct effect of heat stress on cognitive performance.

Laboratory studies investigating the physiological mechanisms behind heat-induced cognitive impairment suggest that inflammation of the brain may be largely responsible for cognitive impairment under heat stress (Chauhan et al., 2012; Lee et al., 2015; Sartori et al., 2012; Trollor et al., 2011). Many studies have shown stressors, including heat stress, to be a significant cause of inflammation both in the brain and systemically (Cohen et al., 2012; Lee et al., 2015; Trollor et al., 2011). Despite inflammation usually being a protective response of the body involved in healing, continuous increases in inflammation can cause significant tissue damage (Sartori et al., 2012). Such persistent inflammation has been strongly linked to cognitive deficits in humans and various species of captive nonhuman animals (Cohen et al., 2012; Lee et al., 2015; Sartori et al., 2012). While the physiological mechanisms behind cognitive impairment are not yet known, these studies suggest that inflammation arising as a result of heat stress might play a role. If heat-induced inflammation influences attentional processes, this presents a potential explanation for our observed cognitive decline. Cognitive decline may also have occurred as a result of heat stress conditions impairing the motor function of individuals. Although we have no evidence of heat stress impacting lid-pecking behaviour, and we observed no obvious differences in this behaviour between conditions, we cannot rule out the possibility that heat stress may have affected other motor functions that led to the observed cognitive decline. In future work, understanding the physiological mechanisms behind cognitive impairment will be important to more accurately predict factors that will adversely affect cognition in wild animals (Soravia et al., 2021).

High cognitive repeatability within conditions and low cognitive repeatability between conditions strongly indicates that heat stress is the factor decreasing cognitive performance in wild magpies. Cognitive repeatability within both the heat stress and nonheat stress conditions was very high, due to high intraindividual consistency, with intraindividual variance lower than interindividual variance within both conditions. Observations of consistent fails in heat stress conditions and consistent passes in nonheat stress conditions support this. Cognitive repeatability between conditions was not statistically significant, most likely due to a decrease in intraindividual consistency, as most individuals passed in nonheat stress conditions but failed during heat stress.

Although estimates of cognitive repeatability appeared to support the relationship between heat stress and cognition, the analysis had two potential limitations. First, only long-term cognitive

repeatability estimates were calculated using results from test batteries in February—April 2018 and 2019. Short-term repeated measures are expected to produce better estimates of repeatability because the internal and external states of individuals are similar (Cauchoix et al., 2018; Thornton & Lukas, 2012). Second, our repeatability analysis is also constrained by the binomial nature of the data (pass or fail of the cognitive test), which may inflate repeatability estimates. However, the repeatability estimates generated in this study are in a similar range to previous short-term repeatability estimates of magpie associative learning performance ($R = 0.97$; Ashton et al., 2018b) that were not generated using a binomial response term.

Finally, we also identified a positive association between adult group size and cognitive performance in both years of testing, whereby individuals from larger groups performed better in the associative learning task under both heat stress and nonheat stress conditions. This confirms the findings of Ashton et al. (2018b) and lends additional support to the idea that living in large, dynamic social groups drives elevated cognitive performance (Ashton et al., 2018a; see also Dunbar & Shultz, 2007). In social species such as Western Australian magpies, the challenges associated with tracking and responding to others' actions in contexts such as competitive interactions, offspring rearing and territory defence may generate challenges that favour the development and evolution of elevated cognitive performance (Ashton et al., 2018a). Through identifying an association between group size and cognitive performance our study provides further evidence that the social environment may influence the expression of cognitive phenotypes (Ashton et al., 2018a, 2019; Dunbar & Shultz, 2007; Humphrey, 1976).

Conclusion

Our study identified a relationship between elevated temperatures and cognitive impairment in magpies, suggesting that anthropogenic climate change may have a significant impact on the ability of wild birds to process, retain and act on environmental information. This represents important empirical evidence of heat-induced cognitive impairment in a wild animal: an essential step in understanding how environmental change is likely to influence animal cognition and, potentially, fitness. Long-term studies of cognitive trends in relation to environmental factors would be invaluable as an avenue for future research.

Author Contributions

Grace Blackburn: conceptualization, formal analysis, investigation, data curation, writing − original draft, writing − review & editing, visualization. **Ethan Broom:** conceptualization, formal analysis, investigation, data curation, writing − original draft, writing − review & editing, visualization. **Benjamin Ashton:** conceptualization, methodology, validation, formal analysis, investigation, writing − original draft, writing − review & editing, supervision, project administration. **Alex Thornton:** conceptualization, methodology, writing − review & editing. **Amanda Ridley:** conceptualization, methodology, validation, formal analysis, investigation, resources, writing − original draft, writing − review & editing, supervision, project administration.

Data Availability

The data used in this study are available in figshare (see Blackburn et al., 2022).

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Appendix 1

Table A1
Full model set for factors affecting trials to pass

Model	AICc	ΔAICc
Heat condition + Adult group size	**496.12**	**0**
Heat condition	507.10	10.98
Air temperature	624.34	128.22
Baited shape	727.16	231.04
Adult group size	747.19	251.07
Time	750.96	254.84
Trial order	751.61	255.49
Sex	753.94	257.82
Basic	754.18	258.06
Body mass[1]	350.07	—
Ground temperature[1]	290.72	—
Neophobia[2]	291.16	—

Candidate models were generated using model selection from a binomial GLMM analysis ($N = 74$). Group ID and Individual ID were included as random terms. Additive models were conducted only when the two terms did not correlate and if a single term was nonsignificant, it was not included in subsequent additive models. The model within 5 AICc values of the best model is in bold.

[1] Body mass and ground temperature were only recorded in 40 of the 74 cognitive tests. As such, analysis of these predictor variables was completed on the subset of tests that contained these data. The AICc value for body mass and ground temperature has therefore been compared against a basic intercept model with an AICc of 343.46 from $N = 40$ data points instead of the basic intercept model used for the other predictor variables.

[2] Neophobia was only recorded in 35 of the 74 cognitive tests. The AICc value for neophobia has therefore been compared against a basic intercept model with an AICc of 287.99 from $N = 35$ data points instead of the basic intercept model used for the other predictor variables.

Figure A1. Associative learning task showing the square/triangle shape pairing. Other shape combinations used were circle/cross, oval/rectangle, diamond/crescent, heart/pentagon and semicircle/trapezium.
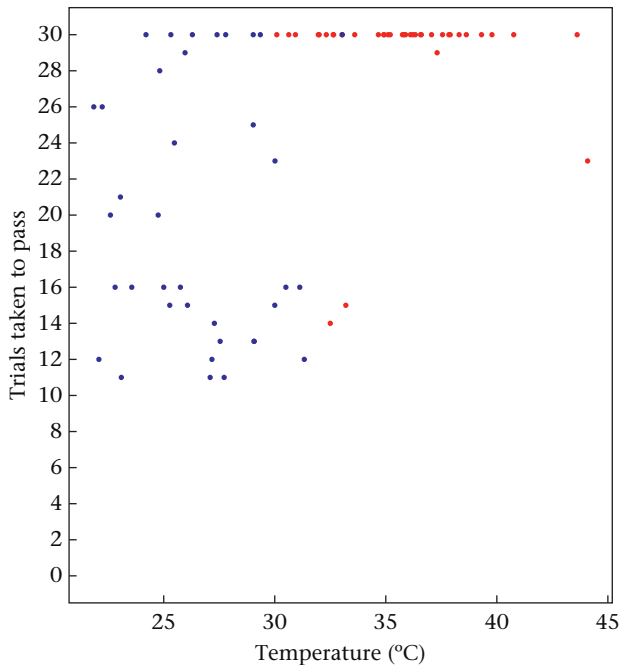
Figure A2. Relationship between air temperature and number of trials taken to pass the cognitive test. Red points indicate tests where individuals were showing heat stress behaviours at least 25% of the time; blue points indicate tests where individuals were not exhibiting heat stress behaviours.

Appendix 2

Thermal imaging

The application of thermal imaging technology to quantify eye surface temperatures in wild magpies and relate this to heat stress was investigated in the 2019 test battery. Thermal imaging is a relatively new practice, allowing the body surface temperatures of free-moving animals to be determined noninvasively (Jerem et al., 2018). Thermal imaging of the eye region in birds has been shown to be a useful measure of stress levels under fluctuating environmental conditions, with one study revealing it to be a better measure than environmental temperature in predicting baseline corticosterone levels (Busnardo et al., 2010; Jerem et al., 2019). Thermal imaging may therefore be a suitable method to quantitatively predict heat stress during hot conditions. If magpie eye temperatures increase with air temperature in cooler conditions but not in hotter conditions, this may suggest physiological heat stress is generating changes in relative eye temperatures (Herborn et al., 2018). Through this application, thermal imaging may provide a superior quantitative method for predicting heat stress and heat-induced cognitive decline in comparison to observation of heat dissipation behaviour.

During cognitive testing, where possible, individuals had their image captured by a FLIR T530 thermal imaging camera within 30 min of completing testing. Thermal images were captured approximately 1−2 m from the focal individual and were only taken when the individual was not in direct sunlight, as per Jerem et al. (2019). Minimum eye region surface temperature readings and the number of pixels that made up the eye in the image were gathered using the FLIR ResearchIR software package (version 4.40.9.30, FLIR Systems, Inc., 2015). Minimum temperature readings were taken as motion blurring would confound the cooler eye temperatures with the neighbouring hotter areas in heat stress conditions, resulting in overestimation of eye temperature being more likely than underestimation (see Jerem et al., 2018). Head position (above or below shoulders), head angle (facing ahead or towards the ground), head tilt (side on, towards or away from the camera) and side of head (left or right) were also recorded, as these factors can influence eye temperature readings (Herborn et al., 2015; 2018).

Statistical analysis of thermal images

Analysis of factors predicting eye temperature was investigated in SPSS using linear mixed models (version 25, IBM, Armonk, NY, U.S.A.). Two separate analyses were used, one for images associated with cognitive testing when mean air temperature was above 32 °C (N images = 44), and one for testing when mean air temperature was below 32 °C (N images = 31). This separation was made because 32 °C is the temperature at which heat dissipation behaviours increase exponentially in magpies (Edwards et al., 2015). In both analyses, minimum eye surface temperature was the dependent variable. Individual ID, group ID and cognitive test ID were included as random effects, as some individuals had more than one thermal image captured per cognitive test. Air and ground temperature at the time of thermal imaging, number of pixels in the eye in the thermal image, head tilt, head angle and side of head were included as predictors during model selection. Head position was not considered, as only one level was observed. Model selection was used in the analysis as described above; however, the dependent variable was normally distributed and therefore AICc values were used. Only one predictor term could be fitted to each model to avoid overparameterization.

The importance of eye surface temperature as a predictor of pass rate in the associative learning task was also investigated. As eye temperature readings were only available for some cognitive tests (N = 27), this was completed in a separate analysis to the primary investigation of factors influencing pass rate in the cognitive test. The same variables were used as random terms and predictors, aside from the addition of eye surface temperature as a predictor term.

Ground and air temperature significantly predicted eye temperature in images taken from tests with mean air temperatures below 32 °C (Table A2) but did not predict eye temperature during conditions above 32 °C (Table A3). This suggests there is a nonlinear relationship between air and ground temperature readings and eye temperature, with a positive association in cooler conditions but not hot conditions.

Although both temperature readings significantly influenced eye temperature below 32 °C but not above 32 °C, ground temperature was a better predictor in both heat conditions (Table A2). Head angle, tilt and position, side of head and number of pixels in the eye had no significant effect on eye temperature in tests above or below 32 °C (Tables A2, A3).

Model selection revealed that eye temperature did not perform as well as condition, air temperature or ground temperature in predicting probability to pass the test (Tables A2−A4). Therefore, eye temperatures gathered using thermal imaging technology were not a superior method for predicting heat-induced cognitive decline compared to observations of heat dissipation behaviours.

Table A2
Top and full model sets for factors affecting eye surface temperature for thermal images captured in tests with a mean air temperature below 32 °C.

	AICc	ΔAICc	Effect, SE	CI
Top model set				
Ground temperature	122.50	0.00	0.47, 0.13	0.21, 0.74
Air temperature	124.49	1.99	0.49, 0.15	0.17, 0.81
Basic model	131.54	8.96		
Full model set				
No. pixels in eye	139.87	17.37		
Head tilt	127.80	5.30		
Side of head	129.22	6.78		
Head angle	129.54	7.04		

N images = 31. Model selection was achieved through linear mixed modelling, using individual ID, group ID and test ID as random terms. CI = 95% confidence intervals.

Table A3
Top and full model sets of factors affecting eye surface temperature for thermal images captured in 2019 tests with a mean air temperature above 32 °C

	AICc	ΔAICc	Estimate, SE	CI
Top model set				
Head tilt[1]	171.22	0	Away: 1.21, 1.10	-1.01, 3.44
			Side: -0.74, 0.70	-0.74, 2.08
Head angle[1]	173.02	1.80	Down: 0.84, 0.75	-0.67, 2.36
Basic model	175.55	4.33		
Full model set				
No. pixels in eye	181.56	10.34		
Side of head	174.16	2.94		
Ground temperature	178.05	6.83		
Air temperature	177.90	66.68		

N images = 44. Model selection was achieved through linear mixed modelling, individual ID, group ID and test ID as random terms. CI = 95% confidence intervals.

[1] These models were not considered further as confidence interval parameters intercepted zero.

Table A4
Top and full model set of factors affecting probability of passing the associative learning test for tests in 2019 which recorded body surface temperatures using thermal imaging technology

	AICc	ΔAICc	Estimate, SE	CI
Top model set				
Heat condition	25.43	0	3.97, 0.014	1.45, 5.94
Basic model	37.89	13.27		
Full model set				
Basic model	37.89	12.46		
Adult group size	38.03	12.60		
Baited shape	44.88	19.45		
Body mass	38.93	13.50		
Bill temperature	30.77	5.34		
Heat condition	25.43	0		
Eye temperature	33.99	8.56		
Ground temperature	28.25	7.95		
Leg temperature	34.18	8.75		
Neophobia[1]	32.81	—		
Sex	39.64	14.21		
Trial order	41.20	16.77		

N tests = 22. Outputs were generated using model selection from binomial GLMM analyses. Top model set includes models within five corrected quasi information criterion values (QICc) of the best model. Group and individual IDs were included as random terms. Top model set is in bold. CI = 95% confidence intervals.

[1] Neophobia was only recorded in 19 of the 22 tests included in this model selection process. Analysis of neophobia was completed on only this subset of tests. The QICc value for neophobia has therefore been compared against a basic intercept model with a QICc of 33.84 instead of the basic intercept model used for the other predictor variables.