

1 **Heat stress inhibits cognitive performance in wild Western**
2 **Australian magpies (*Cracticus tibicen dorsalis*)**

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13
14 **Abstract**

15 Cognition enables animals to respond and adapt to environmental changes and has been
16 linked to fitness in multiple species. Identifying the potential impact of a warming climate
17 on cognition is therefore crucial. We quantified individual performance in an ecologically
18 relevant cognitive trait, associative learning, to investigate the relationship between heat
19 stress and cognition in wild Western Australian magpies (*Cracticus tibicen dorsalis*) over
20 two consecutive years. We found that heat stress had a significant negative effect on
21 performance in both years, with individual pass rates of 6% and 15% under heat stress,
22 compared to 82% and 76% under non-heat stress conditions. The long-term repeatability
23 of cognitive performance *within* temperature conditions was high (i.e. consistent fails
24 under heat stress and consistent passes under non-heat stress conditions between years),
25 but repeatability *between* conditions was low. This suggests that the observed effect could
26 not be attributed solely to natural fluctuation in cognitive performance. This study is one
27 of the first to reveal the negative influence of heat stress on cognitive performance in a
28 wild animal, drawing attention to the potential cognitive consequences of rising
29 temperatures.

30 **Keywords:** *associative learning, climate change, cognition, temperature, repeatability,*
31 *Passeriformes.*

32

33 **Introduction**

34 Cognition, defined as the mechanisms through which animals acquire, process, store and
35 act on information from the environment (Shettleworth 2001), underpins a number of
36 behaviours crucial to fitness (Sayol et al. 2016; Sol et al. 2005). Determining the factors
37 that influence cognition is therefore essential. Anthropogenic climate change is forecast
38 to increase global temperatures by 0.2°C per decade (Intergovernmental Panel on Climate
39 Change, 2018) and is predicted to become the single biggest threat to global biodiversity
40 and wildlife (Foden et al. 2013; Urban 2015). Until recently, the effect of rising
41 temperatures on cognition in wild animals had not been explored, despite evidence that
42 environmental conditions impact cognitive performance (Ashton et al. 2018a; Cauchoix
43 et al. 2020) and that cognition is linked to survival and reproductive success in a variety
44 of taxa (Keagy et al. 2009; Cole et al. 2012; Maille & Schradin 2016; Wetzel 2017;
45 Ashton et al. 2018b; Shaw et al. 2019; Sonnenberg et al. 2019). There is therefore an
46 urgent need for more research into the impact of environmental change on cognitive
47 performance (Soravia et al. 2021).

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

57 While evidence for a relationship between environmental variation and cognitive
58 performance is both compelling and important for our understanding of the potential
59 impacts of anthropogenic change on animal cognition, research into how heat stress may
60 impact animal cognition has thus far been confined to captive studies (Dayananda et al.
61 2017; Triki et al. 2017; Coomes et al. 2019; Danner et al. 2021). In captive cleaner fish
62 (*Labroides dimidiatus*), individuals were observed to be less adept at making strategic
63 decisions to maximise their food intake following an environmental disturbance that

64 increased water temperature (Triki et al. 2017). In captive zebra finches (*Taeniopygia*
65 *guttata*), the ability of females to discriminate between intraspecific and heterospecific
66 mating signals was impeded in hot conditions (Coomes et al. 2019). More recently, it was
67 found that detour-reaching task performance (an assay of inhibitory control) in captive
68 zebra finches was reduced when focal individuals were exposed to higher temperatures
69 (Danner et al. 2021). In addition, this study found that performance on a colour
70 association task was maintained at high temperatures, but birds were more likely to
71 overlook located food rewards at these temperatures, suggesting a cognitive decline
72 (Danner et al. 2021). Evidence for a temperature-cognition relationship has also been
73 identified in humans, whereby heat stress negatively influences cognitive performance
74 and increases the likelihood of lethal and sub-lethal workplace accidents (Ramsey et al.
75 1983; Hancock & Vasmatzidis, 2003). Combined, these findings support the hypothesis
76 that wild animals may suffer cognitive decline while experiencing heat stress.

77 Elevated temperatures can have both lethal (McKechnie et al. 2012) and sub-lethal
78 impacts on wild animals (Urban 2015; Conradie et al. 2019; Stillman 2019). The small
79 body size and diurnal activity of many bird species leaves them particularly vulnerable
80 to high temperatures (McKechnie & Wolf 2009; du Plessis et al. 2012; Gardner et al.
81 2016), leading to changes in behaviour, gut microbiome, thermoregulation, evaporative
82 water loss and survival (Smit et al. 2013; Nilsson et al. 2016; Conradie et al. 2019;
83 Davidson et al. 2020). These sub-lethal costs of heat exposure are likely to lead to rapid
84 population declines, particularly in arid regions (Conradie et al. 2019; Ridley et al. 2021).
85 There is also evidence for behaviour-thermoregulatory trade-offs in birds under hot
86 conditions, whereby vital foraging or reproductive behaviours trade-off against the
87 increasing need to dissipate heat through behaviours such as panting and wing splaying
88 (Cunningham et al. 2013; Edwards et al. 2015; Wiley & Ridley 2016; Cunningham et al.
89 2021). If cognitive processing experiences a similar trade-off with thermoregulation,
90 cognitive performance may decline as temperatures increase. Such trade-offs could
91 compound the physiological effects of heat stress on the brain, such as heat induced
92 neuroinflammation (Lee et al. 2015). Given the growing amount of evidence linking
93 cognitive traits to foraging behaviours (Shaw et al. 2015; Morand-Feron 2017; Rosati
94 2017), impairment of foraging behaviours as temperatures increase may be partially
95 induced by declines in cognitive performance.

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

109 A range of studies revealing a direct link between cognition and fitness have further
110 highlighted the importance of identifying factors that may adversely affect cognitive
111 performance. For instance, variation in tendencies to solve novel problems has been
112 positively correlated to reproductive measures such as clutch size (Cole et al. 2012), mating
113 success (Keagy et al. 2009), and survival of offspring to fledging (Wetzel 2017) across
114 various species. Another important cognitive skill, spatial memory, has been positively
115 correlated with reproductive success in male New Zealand robins (*Petroica australis*) (Shaw
116 et al. 2019), and survival in male African striped mice (*Rhabdomys pumilio*) (Maille &
117 Schradin 2016). Associative learning has been identified in numerous studies as a key
118 cognitive trait underpinning foraging, intraspecific competition and predator avoidance
119 behaviours (Shaw et al. 2015; Morand-Ferron 2017). In Western Australian magpies,
120 females with higher cognitive performance across multiple cognitive tasks (including
121 associative learning) raised more fledglings that survived to independence per year
122 (Ashton et al. 2018b). This cognition-fitness relationship suggests that heat-induced
123 declines in cognitive performance may have longer-term implications for the ability of
124 individuals to survive and reproduce.

125 In this study, we compared the intra-individual performance of wild Western Australian
126 magpies in an associative learning task when they were displaying heat stress behaviours
127 (panting and/or wing splaying) versus normal (no heat stress) behaviours in a paired

128 design, and identified a critical temperature point for rapid decline in cognitive
129 performance. We then compared repeatability of cognitive performance within and
130 between heat stress and non-heat stress conditions in order to determine the robustness
131 of observed patterns in cognitive performance.

132 **Methods**

133 *Study animals and site*

134

135 The Western Australian magpie is a sexually dichromatic medium-sized bird (250-370g)
136 that lives in cooperatively breeding groups ranging in size from 3 to 16 individuals, with
137 a lifespan of up to 25 years in the wild (Edwards et al. 2015; Ashton et al. 2018b). Western
138 Australian magpies are found throughout the southern half of Western Australia and are
139 common throughout the south-west of the state (Johnstone & Storr 2015). Summer
140 temperatures in this region are predicted to increase by 0.5°C – 1.2°C by 2030 and up to
141 1.1°C – 4.2°C by 2090 (Department of Primary Industries and Regional Development
142 2020).

143

144 Nine habituated magpie groups (group size range 4 - 16) located in Guildford (31°89'S,
145 115°96'E) and Crawley (31°98'S, 115°81'E), Perth, Western Australia were observed for
146 this study. Each group was habituated to the presence of humans (Pike et al. 2019), thus
147 allowing for close observation and individual presentation of cognitive tasks and has been
148 monitored since 2013 (Ashton 2017; Ashton et al. 2018b). The majority of individuals
149 were ringed to allow for individual identification and collection of life history information
150 (Pike et al. 2019; Ashton et al. 2018b).

151

152 *Experimental design*

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

160 Causally identical but visually distinct versions of the associative learning task have
161 been presented to the study population previously (Ashton et al. 2018b). To avoid
162 previous experience confounding performance, visually distinct shapes were used as
163 discrimination stimuli rather than colours, as used by Ashton et al. in previous
164 associative learning tasks (Ashton et al. 2018b). The shapes used in the two testing
165 periods and in each treatment condition of this study were visually distinct in order to
166 prevent any confounding effect of memory on performance (Ashton et al. 2018b). The
167 associative learning task required individuals to learn an association between a
168 particular shape on the lid of the task, and a food reward (small piece of mozzarella
169 cheese). The task consisted of a wooden foraging grid with two identical wells, each
170 covered by black wooden lids with distinct white shapes painted on them (Figure A1).
171 The food reward could be accessed by pecking one of two lids (the rewarded shape) on
172 the task. Test subjects did not need training due to previous experience with similar
173 cognitive tasks (Ashton et al. 2018b). Twelve shapes were used in the associative
174 learning task, arranged into sets of two that were always on the array together. Different
175 shapes were used in each of the two testing periods, as well as in each of the two
176 treatment conditions for each bird (resulting in a maximum of four tests per bird), so
177 that no individual was ever presented with the same shapes for multiple tests. Each
178 cognitive test included a maximum of 30 trials, each trial spaced a minute apart. The
179 same shape was rewarded throughout the duration of a test (set of maximum 30 trials).
180 Lids were swapped randomly between trials so that the rewarded shape was not always
181 on the same side of the array, ensuring the bird associated the shape with the food reward
182 and not the spatial location of the well. To control for olfactory cues, cheese was rubbed
183 around the inside of both wells prior to testing (*sensu* Ashton et al. 2018b). Following
184 the protocol of Shaw et al. (2015), the first trial of each test allowed the bird to peck at
185 both lids and explore both wells, to demonstrate that only one well contained a food
186 reward. Testing did not progress past this first trial until the focal bird explored both
187 wells. In all subsequent trials, the bird was only allowed to peck one of the lids before
188 the array was removed by the experimenter. During trials, the array was placed
189 approximately three metres away from the focal individual, with the experimenter
190 standing approximately 5m on the other side of the array in line with the middle of the
191 task so as to avoid any possible cueing to either of the two wells. The individual then

192 approached the task and pecked at one of the two wells. If the correct shape was pecked
193 first, the trial was passed, and the individual could obtain and consume the food reward.
194 If the incorrect shape was pecked first, the task was removed, and the individual did not
195 obtain the food reward. Testing was completed in relative isolation, with group members
196 other than the focal individual approximately 5 metres away from the task. This was
197 achieved through placement of the array behind an object (such as a tree or other plants)
198 that would effectively separate the focal individual from the rest of the group, or through
199 simply waiting until the focal bird moved sufficiently far away from the rest of the
200 group. This was easily achievable as magpies often forage over 10m away from each
201 other (Ashton et. al. 2018b). If another bird did approach the task of the individual being
202 tested, the test was paused until the individual being tested was once again isolated.
203 During each trial, air temperature was measured using an RS Pro RS42 digital
204 thermometer (in the shade, where testing occurred) and time of day was recorded. For
205 trials in 2019, we also recorded the ground temperature, each individual's body mass
206 and neophobia (the time it took for the individual to interact with the task, which was
207 used as a metric of motivation). Body mass, a measure of body condition, was measured
208 within 30 minutes of testing using a top-pan scale which the magpies had previously
209 been habituated to hop onto (Pike et al. 2019). In addition, during the 2019 testing
210 season, a FLIR T530 thermal imaging camera was used to capture images of individuals
211 within 30 minutes of completing testing. The FLIR ResearchIR software package was
212 then used to determine minimum eye-region surface temperature readings and the
213 number of pixels that made up the eye in each image. Model selection revealed that eye
214 temperature was not a superior measure for predicting heat induced cognitive decline
215 when compared to treatment condition and air and ground temperatures. We therefore
216 do not include eye temperature as a variable in the analyses presented (for more in-depth
217 discussion of the thermal imaging set-up and analysis used in this study, refer to
218 appendix 2). If an individual successfully pecked the rewarded shape in 10 out of 12
219 consecutive trials, they passed the test, as this represented a significant departure from
220 binomial probability (*sensu* Ashton et al. 2018b). If this was not achieved within 30
221 trials, the test was considered a fail. It was necessary to use binary (pass/fail) measures
222 with an upper limit of 30 trials, rather than continuous measures of cognitive
223 performance (as in previous studies where all individuals were tested until they passed

224 (Ashton et al. 2018b)) due to the time constraints of testing under heat stress versus non-
225 heat stress conditions.

226

227 Testing was completed using a paired design whereby the same individuals were tested
228 in both heat stress and non-heat stress conditions. An individual was considered heat
229 stressed if it displayed observable markers of heat dissipation (panting and/or wing
230 splaying) for at least 25% of the testing time (*sensu* duPlessis et al. 2012; Edwards et al.
231 2015). Heat stress behaviours were almost always exhibited at temperatures over 32°C,
232 a temperature previously determined to be a critical threshold for this species (Edwards
233 2014). During both test years, for the first test of each individual, the shape set was
234 randomly selected. For subsequent tests, only shape sets with which the individual had
235 no previous experience were used. Individuals were tested once during heat stress and
236 once during non-heat stress conditions during each year of testing. The order of testing
237 (whether the individual underwent testing first in the heat or non-heat stress conditions)
238 was randomised. In 2018, 17 individuals were tested (34 total tests), and in 2019, 20
239 individuals were tested (40 total tests). This totalled 74 tests across both years, of which
240 56 were the same 14 individuals tested in both conditions in both years. A total of 23
241 individuals were tested.

242 Heat stress and non-heat stress tests of the same individual were completed within three
243 weeks of each other to control for potential differences in cognitive performance caused
244 by seasonal shifts. All testing took place between 10am and 5pm, when temperatures
245 are at their maximum, between February and April (the non-breeding season for this
246 species) in 2018 and 2019.

247 *Statistical analyses*

248 Investigation of factors influencing cognitive performance was conducted using the
249 SPSS statistics package (IBM version 27, 2020). Analysis included a McNemar's test
250 for paired nominal data to investigate paired intra-individual differences in test
251 performance between heat stress and non-heat stress conditions. This was followed by
252 model selection using Generalised Linear Mixed Models (GLMMs) to determine factors
253 influencing the number of trials taken to pass the cognitive test. These models used a

254 binomial distribution with a logit link function, treating trials taken to pass the test, (with
255 an upper limit of 30) as the response term. Individual and group identity were included
256 as random terms in the analysis. Model predictors included sex, group size (adult group
257 size, excluding juveniles (individuals below 3 years old)), rewarded shape, heat condition
258 (heat stress behaviours = 1, no heat stress behaviours = 0), time of testing, ground
259 temperature, air temperature, testing order, body mass and neophobia. Model selection
260 using AICc values was then conducted to determine which candidate models best
261 explained variation in the data. Terms were excluded from additive models if their
262 confidence intervals intersected zero when tested alone, with the exception of terms
263 included in interactions. To investigate a critical temperature point for rapid decline in
264 cognitive performance, the model output for a binomial regression including air
265 temperature as a predictor variable and pass/fail as the response variable was used. This
266 identified an estimate for the point at which the probability of passing the associative
267 learning test within 30 trials dropped below 50%, through dividing the estimate for the
268 intercept of the regression by the estimate for the effect of air temperature.

269 *Model selection*

270 Akaike Information Criterion values corrected for small sample size (AICc) were used
271 to determine which terms best predicted data patterns by comparing a set of models
272 which contained one or more terms. If multiple terms were highly correlated (e.g. air
273 temperature and heat stress), the term with the lowest AICc as an individual predictor
274 was used in further additive models (*sensu* Harrison et al. 2018). Models were selected
275 based on their suitability as plausible biological hypotheses (Burnham & Anderson 2002)
276 and the AICc values for each were recorded and compared. Models were compared to a
277 basic intercept model containing only the intercept and random terms. The model with
278 the lowest AICc was considered the most parsimonious model, and terms contained
279 within that model were considered significant if their parameter confidence intervals did
280 not intersect 0, as per Grueber et al. (2011) and Symonds & Moussalli (2010). Following
281 Harrison et al. (2018), where two models have a similar AICc value, the model with the
282 simplest structure (fewer terms contributing to the AICc value) was considered more
283 parsimonious. A top model set was then constructed using all the models with AICc
284 values within five of the top model (Table A1).

285 *Statistical analysis of repeatability in cognitive performance*

286 Repeatability is defined as the fraction of total phenotypic variance that is explained by
287 the variance among individuals, typically represented as a value from zero to one
288 (Dingemanse & Dochtermann 2013) and can be treated as a comparison of intra- and
289 inter-individual variation (Lessels & Boag 1987; Morand-Ferron et al. 2015). Cognitive
290 repeatability can be influenced by an individual's genetic, developmental, and
291 environmental circumstances (Cole et al. 2011; Thornton & Lukas 2012; Cauchoix et al.
292 2018). Repeatability analyses were used to quantitatively confirm that observed
293 differences in cognitive performance were indeed a result of heat stress and not simply
294 the consequence of natural variation in cognitive performance. Decomposition of the
295 variance components used to calculate repeatability gives an indication of whether
296 repeatabilities were driven by intra-individual variation (i.e. consistency of intra-
297 individual cognitive performance) or inter-individual differences (Jenkins 2011; Stoffel
298 et al. 2017; Rudin et al. 2018).

299 Statistical analysis of repeatability of cognitive performance was carried out in R using
300 the rptR package (version 0.9.22, Nakagawa & Schielzeth 2010; Stoffel et al. 2017),
301 which generated a repeatability estimate using variance components obtained from
302 generalised linear mixed models. Repeatability estimates were calculated using 14
303 individuals which had completed two associative learning tests in each condition; one
304 heat stress test and one non-heat stress test in both 2018 and 2019, totalling 56 test
305 results. Repeatability estimates were generated for heat stress and non-heat stress
306 conditions separately. Between-condition repeatability estimates were also generated,
307 which included the total pool (both heat stress and non-heat stress conditions). A
308 generalised linear mixed model with a logit link function was used to calculate the
309 repeatability estimate, using data from the two cognitive test batteries. The generalised
310 linear mixed modelling process used a binary response variable (pass=1, fail=0), with
311 individual ID treated as a random factor. Group ID was not treated as a random factor
312 as it did not add any additional variance beyond individual ID. Uncertainty of the
313 repeatability estimate was quantified using parametric bootstrapping (N = 100), which
314 generated 95% confidence intervals and a p-value for the repeatability analysis (Rudin
315 et al. 2018). The number of replicates was chosen by increasing the number of replicates

316 until convergence (*sensu* Chernick 2007) and has also been identified as the lower limit
317 of replicates that is usually necessary (Pattengale et al. 2010). If the repeatability
318 estimate had confidence intervals that intersected 0, there was non-significant
319 repeatability for that condition. Repeatability estimates were considered significantly
320 different from each other if the 95% confidence intervals did not overlap. By using
321 individual ID as a random effect, this analysis identified the proportion of variance
322 accounted for by inter-individual differences (Rudin et al. 2018). However, inspection
323 of the individual variance components obtained from the generalised linear mixed
324 models used to calculate repeatability gave an indication of whether inter-individual or
325 intra-individual variance was driving the repeatability estimates (though these
326 differences between raw variance components could not be formally tested (*sensu*
327 Jenkins 2011; Rudin et al. 2018)).

328

329 **Results**

330 *Effect of heat stress on cognitive performance*

331 A total of 23 magpies from 9 different groups were tested, both when they were displaying
332 heat stress behaviours and when they were not. Recorded mean air temperatures for
333 cognitive tests ranged from a minimum of 21.8°C to a maximum of 44.1°C during the
334 February to April 2018 testing period, and from 22.2°C to 40.7°C during the 2019 testing
335 period.

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

339 During non-heat stress conditions, the average number of trials taken to pass was 20.14,
340 compared to 28.95 trials during heat stress conditions (Figure 1, Table 1). Adult group
341 size was negatively associated with the number of trials taken to pass, whereby magpies
342 from larger groups took significantly less trials to pass the associative learning test ($P <$
343 0.001 , Figure 2, Table 1). Neither sex, body mass or neophobia (measured as the time
344 taken to approach and peck at the array) influenced cognitive performance (see Table A1
345 for full model output). The order in which cognitive testing was completed (heat stress or

346 non-heat stress conditions first) and the shape that was rewarded also had no significant
347 impact on cognitive performance (Table A1). We also found no significant difference in
348 neophobia in heat stress and non-heat stress conditions (paired t-test, $T_{14} = -0.99$, $P =$
349 0.329).

350 In the 2019 test battery, the probability of passing the cognitive test remained steady from
351 24°C to 30°C before declining. The point at which the associative learning test pass rate
352 dropped to below 50% was at approximately 32°C , according to the output of a binomial
353 regression using air temperature as the predictor variable (Point estimate = 31.6, equation
354 = $20.55 - 0.65x$, $Z_{37} = -2.55$, $S.E. = 0.25$, $P = 0.01$). This suggests that $31\text{-}32^{\circ}\text{C}$ may be a
355 critical temperature for rapid cognitive decline in magpies. Below 31.83°C , 81% of
356 individuals passed the associative learning test, compared to only 14% of individuals
357 above this temperature. This temperature was also the same as the point at which heat
358 dissipation behaviours increased rapidly (approximately 32°C) (figure A2), and a
359 previously identified critical temperature point in magpies for heat dissipation and
360 foraging trade-offs (Edwards 2014).

361 *Repeatability of cognitive performance*
362 Intra-individual repeatability of performance in the associative learning task was very
363 high within both the heat stress condition and the non-heat stress condition ($R = 0.997$
364 and 0.952 , respectively, Table 2). Repeatability of cognitive performance was slightly
365 higher during heat stress, though this difference was not a significant deviation from
366 repeatability in the non-heat stress condition ($R = 0.997$, Table 2). Intra-individual
367 variance was lower than inter-individual variance within both conditions, but not between
368 conditions. This indicated there was very high intra-individual consistency within
369 conditions but low within-individual consistency between conditions (Table 2).

370

371

372 **Discussion**

373 This study provides some of the first empirical evidence that heat stress may negatively
374 affect cognitive performance in a wild animal. This is consistent with research on both
375 captive animals (Lee et al. 2015; Dayananda et al. 2017; Triki et al. 2017; Coomes et al.

376 2019; Danner et al. 2021) and humans (Ramsey et al. 1983; Hancock & Vasmatzidis
377 2003) and raises the possibility that heat-related declines in cognitive performance may
378 become a growing problem for many wild animals due to climate change. Repeatability
379 of cognitive performance was extremely high within heat conditions, but low between
380 conditions due to a consistently high pass rate in non-heat stress conditions and a
381 consistently low pass rate in heat stress conditions. This provides evidence that the
382 observed decline in cognitive performance was likely due to heat stress rather than natural
383 variation in performance in the associative learning task.

384 Performance in the associative learning task declined sharply when temperatures
385 exceeded approximately 32°C, the same as a previously identified critical temperature
386 point at which a trade-off between heat dissipation and foraging effort occurs in magpies
387 (Edwards 2014). This temperature (32°C) may therefore represent the upper critical
388 thermal limit for this species, above which heat stress increases rapidly and investment in
389 offsetting heat is required (Speakman & Krol 2010) at the cost of other behaviours
390 (Edwards et al. 2015). Such a trade-off may also explain the decrease in cognitive
391 performance observed in magpies above this critical limit. As climate change accelerates
392 (IPCC 2018), it is likely that the critical temperature threshold of magpies (and other
393 species), will be exceeded with increasing regularity, leading to persistent reduction in
394 cognitive performance. Despite evidence that some species can adapt their thermal
395 tolerance to more extreme temperatures (Muñoz et al. 2014; Bennett et al. 2021), it is
396 widely acknowledged that global warming is most likely progressing at a rate too rapid
397 for such adaptation in most species (Colwell et al. 2008; Bennett et al. 2021). Unless they
398 are able to move to cooler areas, many species are therefore likely to experience
399 temperatures out of their thermal breadth increasingly frequently in the coming years.
400 The decline in an animal's ability to learn to associate stimuli correctly could potentially
401 impact foraging effort, behavioural response, predator detection, adaptation to
402 anthropogenic changes and parental investment in young (Cunningham et al. 2013;
403 Edwards et al. 2015; Wiley & Ridley 2016; Lee & Thornton 2021; Soravia et al. 2021).
404 In 2018 and 2019 respectively, the number of days in south-west Western Australia with
405 maximum temperatures equalling or exceeding 32°C was 53 and 69 respectively (Bureau
406 of Meteorology, 2021). Mean and maximum temperatures in this region are predicted to
407 continue to increase in coming years (Department of Primary Industries and Regional

408 Development 2020). Therefore, a 32°C upper thermal limit would likely see heat-induced
409 cognitive impairment become increasingly common in Western Australian magpies in
410 the next decade and beyond.

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

431 The mechanisms behind the observed reduction in cognitive abilities resulting from
432 increased temperature are little explored (Soravia et al. 2021). While our study found no
433 significant difference in time taken to approach the associative learning task (neophobia)
434 in the heat versus non-heat stress conditions, we cannot completely rule out an effect of
435 motivation on performance in the task. Indeed, previous work (Edwards et al. 2015) on
436 this population found evidence that foraging effort was significantly reduced when birds
437 were exhibiting heat stress behaviours. It is possible that individuals in this study may
438 have been similarly affected and therefore were less motivated to search for food or
439 interact with the task when under heat-stress conditions. However, the fact that all

440 individuals that were presented with the task completed testing and continued returning
441 to the task (either by passing or reaching the upper limit of 30 trials) regardless of the
442 temperature condition, suggests that motivation alone does not explain the difference in
443 cognitive performance between the two conditions. In order to more confidently rule out
444 the potential effects of motivation on cognitive performance, future studies should
445 incorporate measures such as foraging efficiency and time spent interacting with the task
446 into analyses. A ‘motivation test’ similar to that used in Danner et. al. (2021), whereby
447 birds are presented with a food dish after completion of cognitive testing and the time
448 taken to approach the food dish is measured, could also be utilised to investigate
449 motivation levels of individuals. Another possible explanation for the decline in
450 performance under heat stress conditions is that individual birds may revert to randomly
451 selecting wells under heat stress, however this change in sampling technique in itself is
452 evidence of cognitive decline under heat stress, as random sampling is a less effective
453 sampling method than directed choice in contexts where certain stimuli are consistently
454 associated with rewards. Accordingly, our results point towards a direct effect of heat
455 stress on cognitive performance.

456 Laboratory studies investigating the physiological mechanisms behind heat-induced
457 cognitive impairment suggest that inflammation of the brain may be largely responsible
458 for cognitive impairment under heat stress (Trollor et al. 2011; Chauhan et al. 2012;
459 Sartori et al. 2012; Lee et al. 2015). Many studies have shown stressors, including heat
460 stress, to be a significant cause of inflammation both in the brain and systemically (Trollor
461 et al. 2011; Cohen et al. 2012; Lee et al. 2015). Despite inflammation usually being a
462 protective response of the body involved in healing, continuous increases in inflammation
463 can cause significant tissue damage (Sartori et al. 2012). Such persistent inflammation
464 has been strongly linked to cognitive deficits in humans and various species of captive
465 non-human animals (Cohen et al. 2012; Sartori et al. 2012; Lee et al. 2015). While the
466 physiological mechanisms behind cognitive impairment are not yet known, these studies
467 suggest that inflammation arising as a result of heat stress might play a role. If heat-
468 induced inflammation influences attentional processes, this presents a potential
469 explanation for our observed cognitive decline. Cognitive decline may also have occurred
470 as a result of heat stress conditions impairing the motor function of individuals. Although
471 we have no evidence of heat stress impacting lid-pecking behaviour, and we observed no

472 obvious differences in the lid-pecking behaviour of birds between conditions, we cannot
473 rule out the possibility that heat stress may have affected other motor functions that led
474 to the observed cognitive decline. In future work, understanding the physiological
475 mechanisms behind cognitive impairment will be important to more accurately predict
476 factors that will adversely affect cognition in wild animals (Soravia et al. 2021).

477 High cognitive repeatability within conditions and low cognitive repeatability between
478 conditions strongly indicates that heat stress is the factor decreasing cognitive
479 performance in wild magpies. Cognitive repeatability *within* both the heat stressed and
480 non-heat stress conditions was very high, due to high intra-individual consistency - with
481 intra-individual variance lower than inter-individual variance within both conditions.
482 Observations of consistent fails in heat stress conditions and consistent passes in non-
483 heat stress conditions support this. Cognitive repeatability *between* conditions was not
484 statistically significant, most likely due to a decrease in intra-individual consistency, as
485 most individuals passed in non-heat stress conditions but failed during heat stress.

486 Though estimates of cognitive repeatability appeared to support the relationship between
487 heat stress and cognition, the analysis possessed two potential limitations. Firstly, only
488 long-term cognitive repeatability estimates were calculated using results from test
489 batteries in February-April 2018 and February-April 2019. It is expected that short-term
490 repeated measures produce better estimates of repeatability because the internal and
491 external states of individuals are similar (Thornton & Lukas 2012; Cauchoix et al. 2018).
492 Our repeatability analysis is also constrained by the binomial nature of the data (pass or
493 fail of the cognitive test), which may inflate repeatability estimates. However, the
494 repeatability estimates generated in this study are in a similar range to previous short-
495 term repeatability estimates of magpie associative learning performance ($R = 0.97$;
496 Ashton et al. 2018b) that were not generated using a binomial response term.

497 Finally, we also identified a positive association between adult group size and cognitive
498 performance in both years of testing, whereby individuals from larger groups performed
499 better in the associative learning task under both heat stress and non-heat stress
500 conditions. This confirms the findings of Ashton et al. (2018b) and lends additional
501 support to the idea that living in large, dynamic social groups drives elevated cognitive
502 performance (Ashton et al. 2018a; see also Dunbar & Schultz 2007). In social species

503 such as Western Australian magpies, the challenges associated with tracking and
504 responding to others' actions in contexts such as competitive interactions, offspring
505 rearing and territory defence may generate challenges that favour the development and
506 evolution of elevated cognitive performance (Ashton et al. 2018a). Through identifying
507 an association between group size and cognitive performance our study provides further
508 evidence that the social environment may influence the expression of cognitive
509 phenotypes (Humphrey 1976; Dunbar & Schultz 2007; Ashton et al. 2018a; Ashton et al.
510 2019).

511

512 **Conclusion**

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

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921 Tables. figures and appendix: next page

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942 **Table 1:** Top model set for trials taken to pass.

Top Models¹	AIC	ΔAIC	
Heat condition + Adult group size	496.12	0.00	
<i>Basic intercept</i>	754.18	258.06	
Parameter	Estimate	S. E	C.I
Adult group size	- 0.38	0.09	-0.56 – -0.20
Heat condition			
Non-heat stress	-2.86	0.19	-3.23 – -2.49
Heat stress	0	-	-

943 ¹Data is based on 74 associative learning tests completed on 23 magpies, including 37
 944 tests in heat stress conditions and 37 tests in non-heat stress conditions. Outputs were
 945 generated using model selection from binomial GLMM analysis. The top model set
 946 includes models within 5 AIC of the best model. C.I = 95% confidence intervals. For a
 947 full set of models tested refer to Table A1.

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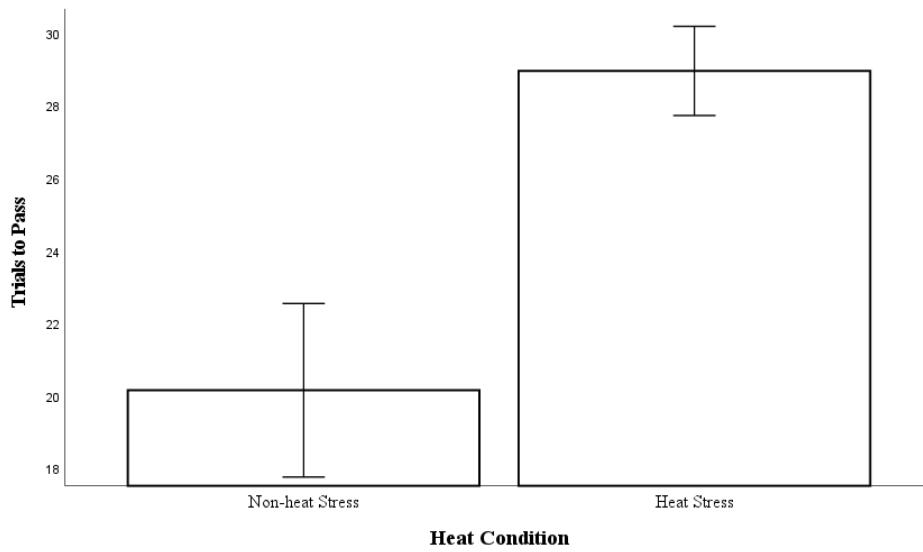
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950 **Table 2:** Repeatability estimates of cognitive performance¹

Heat condition	Intra-individual variance	Inter- individual variance	Repeatability estimate	95% C.I	<i>P</i>
Heat stress	15.08	4077.41	0.996	0.891, 0.998	<0.001
Non-heat 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

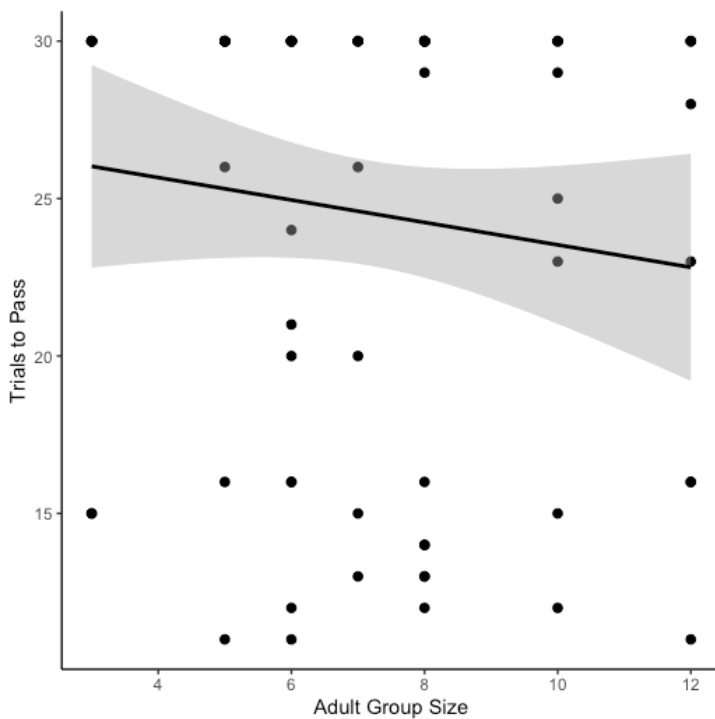
951 ¹ Estimates are across two associative learning test batteries. Each cognitive test battery
 952 included one test on 14 individuals, totaling 28 cognitive tests. 95% confidence
 953 intervals standard error and P-values were generated using parametric bootstrapping
 954 (N=100). C.I = 95% confidence intervals.

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966 **Figure 1.** Average number of trials taken to pass the associative learning trial in non-
967 heat stress and heat stress treatments ($N=74$ associative learning experiments). Means
968 generated from model output in Table 1. Error bars show 95% confidence intervals.

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980 **Figure 2.** Relationship between adult group size and number of trials taken to pass the
981 cognitive test. Data were gathered from 74 associative learning tests on 23 individuals
982 from 9 groups.

983 **Appendix 1**

984

985 **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	-

986

987 ¹ Candidate models generated using model selection from a binomial GLMM analysis
 988 ($N = 74$). Group ID and Individual ID were included as random terms. Additive models
 989 were conducted only when the two terms did not correlate and if a single term was non-
 990 significant, it was not included in subsequent additive models. Models within 5 AICc
 991 values of the best model are in bold. Body mass and ground temperature was only
 992 recorded in 40 of the 74 cognitive tests. As such, analysis of these predictor variables
 993 was completed on the subset of tests which contained these data. The AICc value for
 994 body mass and ground temperature has therefore been compared against a basic
 995 intercept model with an AICc of 343.46 from $N = 40$ data points instead of the basic
 996 intercept model used for the other predictor variables

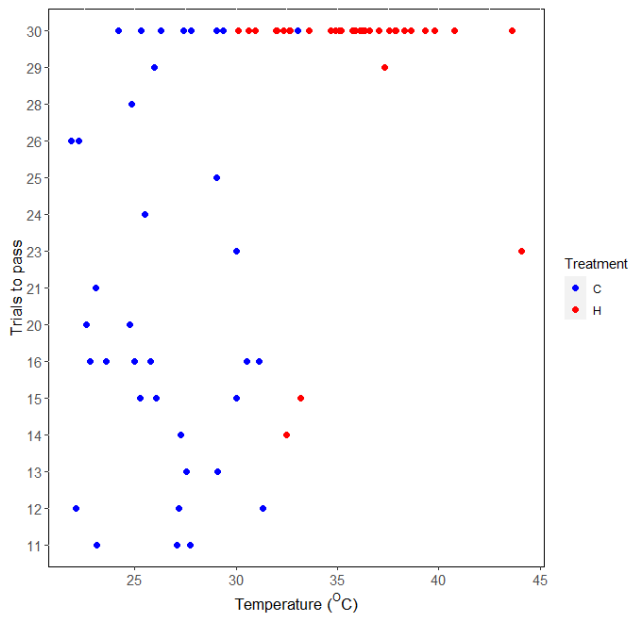
997 ²Neophobia was only recorded in 35 of the 74 cognitive tests. The AICc value for
 998 neophobia has therefore been compared against a basic intercept model with an AICc of
 999 287.99 from $N = 35$ data points instead of the basic intercept model used for the other
 1000 predictor variables.

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1016 **Figure A1:** Associative learning task showing the square/triangle shape pairing. Other
1017 shape combinations used were; circle/cross, oval/rectangle, diamond/crescent, heart/
1018 pentagon, & semicircle/trapezium.

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1032 **Figure A2:** Relationship between air temperature and number of trials taken to pass the
1033 cognitive test. (Red points indicate tests were individuals were showing heat stress
1034 behaviours at least 25% of the time, blue points indicate individuals were not exhibiting
1035 heat stress behaviours).

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1037 **Appendix 2**

1038 *Thermal imaging*

1039 The application of thermal imaging technology to quantify eye surface temperatures in
1040 wild magpies and relate this to heat stress was investigated in the 2019 test battery.

1041 Thermal imaging is a relatively new practice, allowing the body surface temperatures
1042 of free-moving animals to be determined non-invasively (Jerem et al. 2018). Thermal
1043 imaging of the eye-region in birds has previously been revealed to be a useful measure
1044 of stress levels under fluctuating environmental conditions, with one study revealing it
1045 to be a better measure than environmental temperature in predicting baseline
1046 corticosterone levels (Jerem et al. 2019; Busnardo et al. 2010). Thermal imaging may
1047 therefore be a suitable method to quantitatively predict heat stress during hot
1048 conditions. If magpie eye temperatures increase with air temperature in cooler
1049 conditions but not in hotter conditions, this may suggest physiological heat stress is
1050 generating changes in relative eye temperatures (Herborn et al. 2018). Through this
1051 application, thermal imaging may provide a superior quantitative method for predicting
1052 heat stress and heat-induced cognitive decline in comparison to observation of heat
1053 dissipation behaviour.

1054 During cognitive testing, where possible, individuals had their image captured by a
1055 FLIR T530 thermal imaging camera within 30 minutes of completing testing. Thermal
1056 images were captured approximately one to two metres from the focal individual and
1057 were only taken when the individual was not in direct sunlight, as per Jerem et al.
1058 (2019). Minimum eye-region surface temperature readings and the number of pixels
1059 that made up the eye in the image were gathered using the FLIR ResearchIR software
1060 package (version 4.40.9.30). Minimum temperature readings were taken as motion
1061 blurring would confound the cooler eye temperatures with the neighbouring hotter areas
1062 in heat stress conditions, resulting in overestimation of eye temperature being more
1063 likely than underestimation (*sensu* Jerem et al. 2018). Head position (above or below

1064 shoulders), head angle (facing ahead or towards the ground), head tilt (side on, toward
1065 or away from the camera) and side of head (left or right) were also recorded, as these
1066 factors can influence eye temperature readings (Herbon et al. 2018; Herborn et al.
1067 2015).

1068 *Statistical analysis of thermal images*

1069 Analysis of factors predicting eye temperature was investigated in SPSS using linear
1070 mixed models (IBM version 25, 2019). Two separate analyses were used, one for
1071 images associated with cognitive testing when mean air temperatures were above 32°C
1072 (N images = 44), and one for testing when mean air temperature was below 32°C (N
1073 images = 31). This separation was made because 32°C is the temperature at which heat
1074 dissipation behaviours increase exponentially in magpies (Edwards et al. 2015). In both
1075 analyses, minimum eye surface temperature was the dependent variable. Individual ID,
1076 group ID and cognitive test ID were included as random effects, as some individuals
1077 had more than one thermal image captured per cognitive test. Air and ground
1078 temperature at the time of thermal imaging, number of pixels in the eye in the thermal
1079 image, head tilt, head angle and side of head were included as predictors during model
1080 selection. Head position was not considered, as only one level was observed. Model
1081 selection was used in the analysis as described above, however the dependent variable
1082 was normally distributed, therefore Akaike's Information Criterion (AICc) values were
1083 used. Only one predictor term could be fitted to each model to avoid
1084 overparameterization.

1085 The importance of eye surface temperature as a predictor of pass rate in the associative
1086 learning task was also investigated. As eye temperature readings were only available
1087 for some cognitive tests ($N = 27$), this was completed in a separate analysis to the
1088 primary investigation of factors influencing pass rate in the cognitive test. The same
1089 variables were used as random terms and predictors, aside from the addition of eye
1090 surface temperature as a predictor term.

1091 Ground and air temperature significantly predicted eye temperature in images taken
1092 from tests with mean air temperatures below 32°C (Table A2) but did not predict eye
1093 temperature during conditions above 32°C (Table A3). This suggests there is a non-
1094 linear relationship between air and ground temperature readings and eye temperature,

1095 whereby there is a positive association in cooler conditions but not hot conditions.
 1096 Though both temperature readings significantly influence eye temperature below 32°C
 1097 but not above 32°C, ground temperature is a superior predictor in both heat conditions
 1098 (Table A2). Head angle, tilt and position, side of head and number of pixels in the eye
 1099 had no significant effect on eye temperature in tests above or below 32°C (Table A2,
 1100 Table A3).

1101 Model selection revealed that eye temperature did not perform as well as condition, air
 1102 temperature or ground temperature in predicting probability to pass the test (Table A4).
 1103 Therefore, eye temperatures gathered using thermal imaging technology were not a
 1104 superior method for predicting heat-induced cognitive decline compared to
 1105 observations of heat dissipation behaviours.

1106

1107 **Table A2:** Top model set and complete candidate model set of the terms affecting eye
 1108 surface temperature for thermal images captured in tests with a mean air temperature
 1109 below 32°C (N images = 31).

Top Model Set	AICc	ΔAICc	Effect +- S.E	C.I
Ground temperature	122.50	0.00	0.47, 0.13	0.21, 0.74
Air	124.49	1.99	0.49, 0.15	0.17, 0.81
temperature				
<i>Basic model</i>	131.54	8.96		
Complete 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		

1110 Model selection was achieved through linear mixed modelling, using individual ID,
 1111 group ID and test ID as random terms.

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1114 **Table A3:** Top model set and complete model set of the terms eye surface temperature
 1115 for thermal images captured in 2019 tests with a mean air temperature above 32°C (*N*
 1116 images = 44).

Top Model Set	AICc	ΔAICc	Estimate +- S.E	C.I
Head tilt ¹	171.22	0	Away: 1.21, 1.10 Side: -0.74, 0.70	-1.01, 3.44 -0.74, 2.08
Head angle ¹	173.02	1.80	Down: 0.84, 0.75	-0.67, 2.36
<i>Basic model</i>	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		

1117

1118 Model selection was achieved through linear mixed modelling, using individual ID,
 1119 group ID and test ID as random terms. ¹These models were not considered further as
 1120 confidence interval parameters intercepted zero.

1121

1122 **Table A4:** Top model set and complete model set of terms affecting probability to pass
 1123 the associative learning test for 2019 tests which recorded body surface temperatures
 1124 using thermal imaging technology (*N* = 22).

Top Model Set	AICc	ΔAICc	Estimate +- S.E	C.I
Heat condition	25.43	0	3.97, 0.014	1.45, 5.94
<i>Basic model</i>	37.89	13.27		
Full model set				
Basic	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

1125 Outputs were generated using model selection from binomial GLMM analyses. Top
1126 model set includes models within five Corrected Quasi Information Criterion values
1127 (QICc) of the best model. Group and individual identity were included as random terms.
1128 Top model set is in bold.

1129 ¹ Neophobia was only recorded in 19 in of the 22 tests included in this model selection
1130 process. Analysis of neophobia was completed on only this subset of tests. The QICc
1131 value for neophobia has therefore been compared against a basic intercept model with a
1132 QICc of 33.84 instead of the basic intercept model used for the other predictor
1133 variables.

1134

1135 Eye temperatures increased with air and ground temperatures during non-heat stress
1136 conditions but not conditions above 32C. This suggests the association between
1137 physiological stress and eye temperatures identified in Jerem et al. [1,2] was present, as
1138 relative eye temperatures were negatively associated with the likelihood of heat stress.
1139 In homeothermic animals such as magpies, stress-induced hyperthermia leads to
1140 increased core temperature and the diversion of blood away from the body surface to
1141 regions with the highest metabolic need, thus decreasing body surface temperatures
1142 [3,6,7]. Therefore, during hotter temperatures, eye temperature readings may plateau as
1143 air and ground temperatures increase due to the diversion of blood away from the eye
1144 surface. Through this mechanism, trends in eye surface temperatures would be expected
1145 to be useful as an indicator of heat stress and in turn, cognitive performance [1,2].
1146 However, eye temperature readings were inferior predictors of heat-induced cognitive

1147 decline compared to heat dissipation behaviours and air and ground temperatures. As
1148 eye temperature readings are similar in both heat stress and non-heat stress conditions,
1149 they are not able to appropriately reflect the distinction between the two states and
1150 therefore cannot predict the changes in cognitive performance effectively. Therefore,
1151 thermal imaging may not be preferable to behavioural measures when quantifying heat
1152 stress.