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Hot-headed peckers: thermographic changes during aggression among juvenile pheasants (*Phasianus colchicus*)

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Summary

1 In group-living vertebrates, dominance status often covaries with physiological measurements (e.g.
2 glucocorticoid levels), but it is unclear how dominance is linked to dynamic changes in physiological
3 state over a shorter, behavioural timescale. In this observational study we recorded spontaneous
4 aggression among captive juvenile pheasants (*Phasianus colchicus*) alongside infrared thermographic
5 measurements of their external temperature, a non-invasive technique previously used to examine
6 stress responses in non-social contexts, where peripheral blood is redirected towards the body core.
7 We found low but highly significant repeatability in maximum head temperature, suggesting
8 individually consistent thermal profiles, and some indication of lower head temperatures in more
9 active behavioural states (e.g. walking compared to resting). These individual differences were partly
10 associated with sex, females being cooler on average than males, but unrelated to body size. During
11 pairwise aggressive encounters we observed a non-monotonic temperature change, with head
12 temperature dropping rapidly immediately prior to an attack and increasing rapidly afterwards, before
13 returning to baseline levels. This non-linear pattern was similar for birds in aggressor and recipient
14 roles, but aggressors were slightly hotter on average. Our findings show that aggressive interactions
15 induce rapid temperature changes in dominants and subordinates alike, and highlight infrared
16 thermography as a promising tool for investigating the physiological basis of pecking orders in
17 galliforms.

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Main Text

Introduction

18 Group-living animals often form dominance hierarchies in which some individuals consistently
19 outrank others [1], gaining preferential access to food, mates or other resources [2]. Since
20 Schjelderup-Ebbe's [3] pioneering observations on 'pecking orders' in domestic chickens (*Gallus*
21 *gallus domesticus*), there has been continued interest in how these hierarchies are formed and
22 maintained. Researchers have studied the role of pre-existing behavioural and physiological
23 differences between individuals [4,5], the reinforcement of previous contest outcomes [6] through
24 phenomena such as winner and loser effects [7–9] and bystander effects [10], and the impacts of
25 dominance interactions on physiology and cognition [11]. In social vertebrates, dominance status has
26 been linked to differences in circulating glucocorticoid levels [12] and even symptoms of chronic
27 psychosocial stress [13]. However, the precise relationship between stress physiology and dominance
28 status is variable and context-dependent [13–17]. Due to the complex, reciprocal links between
29 hormones and behaviour, it is often unclear to what extent physiological differences determine
30 dominance and *vice versa* [18].

31 One key issue is how organisms respond to their experiences in individual dominance encounters
32 [8]. Assays of blood and brain tissue after staged dyadic contests in the laboratory have shown that
33 winning and losing experiences may be associated with neuroendocrine changes in the hypothalamic-
34 pituitary-adrenocortical (HPA) system, involving serotonin and glucocorticoids [19]. In rainbow trout
35 (*Oncorhynchus mykiss*) and green anoles (*Anolis carolinensis*), for example, aggressive interactions
36 between males lead to elevated glucocorticoids in both winners and losers, but this increase tends to
37 be much longer-lasting for losers [20,21]. Experimental administration of exogenous glucocorticoids
38 appears to have differing effects depending on the length of exposure: acute doses tend to promote
39 aggression, while prolonged treatment may reduce it [18,19].

40 Notwithstanding the value of these approaches, blood and tissue sampling has some ethical and
41 practical limitations, because it is invasive and requires capture and handling (or even sacrifice) of
42 the animal. This creates a time lag from the event of interest to the sampling point [25] and acts as an
43 additional stressor, directly affecting the physiological measures of interest [12,22,23] and potentially
44 causing injury and infections. Time lags are also a problem for faecal sampling, a non-invasive
45 method commonly used in field studies [23]. While useful for examining longer-term associations
46 between stress physiology and dominance rank [12,13,24], the timing of defecation by the animal is

47 beyond the experimenter's control and faecal glucocorticoids reflect stress levels several hours earlier
48 [23,25], making it difficult to link them to specific events experienced by the animal. Assessing the
49 impact of individual dominance encounters, which are typically brief and often happen in quick
50 succession, requires measurements of physiological change that are not subject to time lags, and
51 ideally are non-invasive.

52 Changes in body temperature offer another potential route to examining immediate physiological
53 responses to stressors [25]. Stress-induced hyperthermia (SIH), also known as 'psychogenic fever', is
54 a common response in endothermic animals to perceived threats in which sympathetically mediated
55 vasoconstriction redirects peripheral blood flow towards the body core, raising core temperature
56 [26,27]. Humans, for instance, show SIH prior to exams [28,29]. In research on non-human animals,
57 where body temperature can be monitored using implanted devices [30], SIH has been found to
58 correlate with a faster heart rate [31] and increased glucocorticoid levels [19] in response to a
59 stressor. For instance, core body temperature, heart rate and plasma corticosterone increased in
60 laboratory mice (*Mus musculus*) when handled or injected [32–34], with some indication of a
61 stronger response in strains selectively bred for high aggression [33].

62 SIH can also be triggered by social stressors. Several studies have shown that social defeat leads
63 to increased core body temperature in laboratory rodents [35–37]. In captive male great tits (*Parus*
64 *major*), core body temperature (measured using a probe inserted down the throat) remained elevated
65 for 1 day after experiencing a social defeat, and defeated males also tended to avoid social interaction
66 with conspecifics during this period [38]. These studies induced social defeat using a resident–
67 intruder paradigm, whereby an 'intruding' individual is introduced to the home cage of a 'resident'
68 individual, with the latter almost always winning [39]. Such studies have focused on dyadic
69 interactions under enforced conditions. We know far less about physiological responses to the more
70 natural dominance interactions that occur spontaneously in larger groups. Implanted devices have
71 been used to detect heart-rate changes during aggression in free-roaming greylag geese (*Anser anser*)
72 [40], but, as with studies of core body temperature, the practical and ethical challenges associated
73 with invasive procedures limit their applicability [41].

74 While elevating core body temperature, SIH simultaneously results in a rapid drop (within
75 seconds) in surface body temperature [42,43]. In animals with exposed skin areas, such as the
76 periophthalmic ring in birds, this temperature drop can be detected through remote thermal imaging
77 using infrared cameras [44], as demonstrated in a series of studies on poultry [27,45,46], wild
78 passerines [47–49] and gamebirds [50]. A key advantage of infrared thermography (IRT) is that it
79 avoids the use of implants or other invasive probes needed to measure core body temperature, which
80 require capture, handling and other procedures that themselves are likely to induce a stress response

81 [51,52]. In primates, IRT has revealed rapid physiological responses to social stressors: nasal skin
82 temperature in captive rhesus macaques (*Macaca mulatta*) dropped within seconds of viewing a
83 video clip of an aggressively raging conspecific [53], while wild chimpanzees (*Pan troglodytes*)
84 showed changes in both nose temperature and ear temperature after hearing aggressive vocalisations
85 from a rival group [54]. In birds, studies using IRT to measure stress responses have focused
86 primarily on non-social stressors such as disease [55], heat [30], capture [27] and food removal [46].
87 General effects of group-level housing conditions (e.g. stocking density) have also been found [56],
88 but there have been no studies to our knowledge investigating responses to direct interactions with
89 conspecifics.

90 To address this gap, we recorded acts of aggressive dominance behaviour occurring naturally in
91 groups of captive-reared juvenile pheasants (*Phasianus colchicus*), alongside detailed infrared
92 thermographic measurements of their head temperature. Like other galliforms, juvenile pheasants
93 have areas of naturally bare skin around the eye and ear with a high density of blood vessels [57],
94 making them highly suitable for IRT studies. Pheasants are precocial, so in captivity a large number
95 of chicks can be hatched on the same day and reared under standardised conditions without their
96 parents [58], thereby eliminating differences in age and parental care. In the wild, pheasants exhibit
97 harem defence polygyny, with dominant males maintaining control of territories (and access to
98 females) over a prolonged period [58]. An individual adult male's social rank strongly influences his
99 mating success [59]. In captivity, pheasant chicks are aggressive towards one another and sexual
100 segregation emerges within the first few weeks of life, perhaps driven by female avoidance of
101 aggressive males [60].

102 Our main aim was to examine whether IRT reveals dynamic physiological changes occurring
103 during dominance encounters. We tested three key hypotheses. First, in line with evidence across
104 taxa that stress physiology is moderately repeatable within individuals [61], we predicted that head
105 temperatures in pheasants would show consistent individual differences, potentially linked to other
106 measurable characteristics such as sex and size. Alternatively, within-individual changes in
107 temperature associated with different behavioural states (as seen in chickens [27]) might overwhelm
108 between-individual differences, leading to low repeatability. Second, based on the suggestion that
109 stress physiology covaries with behavioural differences such as proactive/reactive 'coping styles'
110 [62], we hypothesised that individual differences in head temperature would predict the roles that
111 individuals adopt in dominance encounters with their group mates, in terms of whether they are the
112 aggressor or the recipient of aggression. Third, we predicted that during an aggressive encounter
113 pheasants would show a drop in surface head temperature, reflecting a stress-induced hyperthermic
114 response in which blood is redirected from the periphery to the body core [26]. We expected that SIH

115 would occur in both aggressors and recipients, but that the response in recipients would be more
116 pronounced and/or longer-lasting (as in [20,21,63]).

Methods

117 (a) Subjects and housing

118 We used 126 juvenile pheasants (*Phasianus colchicus*), aged 6–7 weeks at the time of our study, that
119 were being reared at the Rothamsted Research farm at North Wyke, Devon, UK. The birds were a
120 mix of full sibs, half-sibs and unrelated individuals that had hatched in artificial incubators from eggs
121 collected from pens of freely mating polygynandrous adults. On 24 May 2018, when they were 1 day
122 old, the chicks had been randomly allocated to four mixed-sex groups (three $n = 32$, one $n = 30$) and
123 housed in indoor pens (1 × 2 m floor area) that contained a heat lamp, feeder, drinker and assorted
124 branches. From 3 weeks old, each group could also access an outdoor run (12 × 4 m) with additional
125 food, water and perching locations. Age- and nutrient-specific food (Keeper’s Choice, Norfolk, UK)
126 and water were available *ad libitum* throughout rearing. Each pheasant bore a uniquely numbered
127 patagial tag for individual identification. At 9 weeks old (i.e. after our study), the birds were sexed
128 (via plumage traits), weighed (using a spring balance; precision = 5 g) and measured (tarsus length
129 and wing length, using callipers; precision = 0.1 mm) before being released into an open-topped
130 woodland pen covering approximately 4,000 m², as part of other studies into their ecology and
131 cognition. Mass at release was highly correlated with mass measured at 6 weeks ($r = 0.90$, $t_{124} = 23.1$,
132 $p < 0.001$), close to the point of our study.

133

134 (b) Procedure

135 On 5 and 13 July 2018, when they were 6–7 weeks old, the pheasants in each group were confined to
136 their indoor pen (after removal of the feeder) for up to 30 minutes as part of routine husbandry
137 procedures. Studies in other galliforms have shown that physiological stress responses are readily
138 detectable by this age [64,65]. We filmed each group once during this confinement period, using two
139 cameras fixed to a tripod positioned approximately 1 m outside the pen: a FLIR T530 thermal video
140 camera to record the birds’ external temperature, plus a Sony HDR CX625 video camera to identify
141 individuals from their numbered patagial tags (which were not visible in the infrared thermal
142 footage). The position of the tripod ensured that all thermal measurements were taken from a distance
143 of 1.0–2.3 m. Recordings from the two cameras were synchronised via hand waving to signal the
144 start of the observation period, which lasted for 13 minutes for each group.

145

146 **(c) Video coding**

147 All four videos were coded by one member of the research team (SK), who followed each bird over
148 the 13 minutes of footage to obtain two sets of behavioural observations. First, for the *baseline*
149 observations, every 30 s we recorded the bird's behavioural state, using the ethogram in Table 1.
150 Second, for the *aggression* observations, we identified any aggressive encounters with another bird.
151 For each encounter we noted the identities of both birds involved, the roles they played (aggressor or
152 recipient), the outcome (winner or loser) and the type of aggression (threat, peck or fight; Table 2).
153 The bird that initiated the aggressive encounter was classified as the 'aggressor', while the bird to
154 which the aggressive behaviour was directed was the 'recipient'. The bird that performed the last
155 aggressive act in the encounter was designated the 'winner', while if a bird retreated from its
156 opponent and did not retaliate it was designated the 'loser'. In all encounters we observed, the
157 aggressor 'won' and the recipient 'lost' (i.e. did not retaliate), so aggressor/recipient roles can be
158 considered synonymous with win/lose outcomes in our analysis.

159
160 **(d) Thermal measurements**

161 At the same time points as the behavioural observations described above, we used the box selection
162 tool in *FLIR Tools* software version 5.13 (FLIR Systems, Inc. 2015) to pinpoint the maximum
163 temperature on the pheasant's head (Fig. 1).

164 *Baseline measurements.* Baseline measurements were taken at 30-s intervals throughout the 13-
165 min video, except when the bird was hidden from view or could not be reliably identified, or its head
166 was not at a lateral angle to the camera. We also excluded any measurements taken within 20 s of an
167 aggressive encounter involving that bird. At the same 30-s intervals we took spot measurements of a
168 suspended white plastic drinker filled with water (Fig. 1), which provided a stable background
169 reference temperature.

170 *Aggression measurements.* During aggressive encounters, we recorded the maximum head
171 temperature of both birds every second from 5 s before to 20 s after the aggressive behaviour
172 occurred, henceforth referred to as the moment of 'attack' (even if this involved no physical contact,
173 as in the case of threats). This period was chosen because previous literature suggests that thermal
174 values drop within 10–20 s after exposure to a stressor [49,53]. To reduce data overlap when
175 aggressive encounters occurred in bursts, we only included encounters for which a minimum of 20 s
176 had passed since that bird's last encounter.

177
178 **(e) Ethical note**

179 All work was approved by the University of Exeter Psychology Research Ethics Committee and
180 formed part of a larger research programme conducted under UK Home Office licence PPL 30/3204
181 (issued to JRM). Husbandry procedures adhered to the code of practice of the UK Department for
182 Environment, Food & Rural Affairs [66], with rearing densities lower than recommended. The
183 pheasants were held in their indoor pen for no longer than 30 min and no injuries were observed
184 during filming.

185

186 **(f) Statistical analysis**

187 All data processing and analysis was conducted in *R* version 3.6.3 [67]. Body condition at release
188 was calculated as mass (g) divided by tarsus length (mm) cubed. To analyse variation in the baseline
189 thermal measurements we fitted a linear mixed-effects model (LMM) in package *lme4* [68], with a
190 random effect that allowed varying intercepts across individual pheasants to account for the non-
191 independence of repeated measurements from the same individual; group was modelled as a fixed
192 effect rather than a random effect because there were only four replicates. We used the package *rptR*
193 [69] to calculate the repeatability (intra-class correlation coefficient) of maximum head temperature
194 within individuals and its associated confidence interval based on 1,000 bootstrapped samples,
195 controlling for behavioural activity, background temperature and time held in the pen. We then
196 averaged the readings for each individual and analysed whether this average baseline temperature,
197 alongside fixed effects of sex, tarsus length and body condition, predicted the role (aggressor or
198 recipient) adopted in a given encounter, using a generalised linear mixed-effects model (GLMM) in
199 *lme4* with a binomial error function and intercepts varying across individuals. Note that whereas
200 mass and tarsus length are highly correlated ($r = 0.81$, $t_{124} = 15.1$, $p < 0.001$), tarsus length and body
201 condition are not ($r = -0.12$, $t_{124} = -1.3$, $p = 0.192$), which allowed us to estimate their statistical
202 effects separately.

203 For the aggression thermal measurements, time was coded from -5 to 20 s, with 0 s representing
204 the moment of attack. There were a large number of missing values due to one or both individuals
205 briefly disappearing from view, so (following [49]) we used linear interpolation in the package *zoo*
206 [70] to infer the most parsimonious values between two or more recorded temperatures. For example,
207 if 36.2 °C was recorded at time 1 s and 36.8 °C at 4 s, we inferred the missing temperatures at 2 and 3
208 s to be 36.4 and 36.6 °C, respectively. Note that no missing values were replaced before the first or
209 after the last recorded temperature for a given individual in a given encounter.

210 We then used two separate LMMs to model the temperature profile before (-5 to 0 s) and after
211 (1 to 20 s) the moment of attack. These models included fixed effects of time, role (aggressor or
212 recipient), average baseline temperature (mean of 30-s measurements for that pheasant), type of

213 aggression (threat or peck), sex, tarsus length, body condition and group, and two random effects that
214 allowed intercepts to vary both across individual pheasants and across the contests they were
215 involved in. We modelled non-linear changes using polynomial terms for time and allowed this
216 relationship to differ between aggressors and recipients by including a role \times time interaction term,
217 but these more complex terms were omitted where they did not significantly improve the fit of the
218 model. We also checked whether there was any difference between aggressors and recipients in the
219 timing of the highest and lowest temperatures during an encounter, using approximate two-sample
220 Fisher–Pitman permutation tests in the package *coin* [71]. For visualisation and to check the
221 robustness of our conclusions, we fitted a generalised additive mixed-effects model (GAMM) across
222 the whole time sequence (-5 to 20 s) in the package *brms* [72], with smooth terms for the non-linear
223 effect of time on temperature.

224 For all mixed-effects models we used the package *DHARMA* [73] to generate diagnostic plots of
225 the residuals, which revealed no strong departures from the assumptions of normality and
226 homoscedasticity. The significance of fixed effects was computed using likelihood-ratio tests,
227 comparing the residual deviance of models including versus omitting that predictor. Continuous
228 predictors with a zero value outside the range of measurement (i.e. morphometric and temperature
229 variables) were standardised before analysis to aid interpretation.

230 The data files and associated R script are available as supplementary online material [74].

Results

231 (a) Baseline measurements: is head temperature individually repeatable?

232 We obtained 610 baseline head temperature measurements at 30-s intervals for 94 pheasants (1 to 18
233 measurements per pheasant; median = 6 measurements), excluding an additional 64 measurements
234 that occurred within 20 s of an aggressive encounter involving the focal pheasant. The maximum
235 temperature identified by *FLIR Tools* had an average value (mean \pm s.d.) across all measurements of
236 36.63 ± 1.04 °C (range 31.9–39.1 °C), compared to a background temperature (white plastic drinker
237 filled with water) of 25.82 ± 1.46 °C (range 23.2–27.5 °C).

238 An LMM with intercepts varying across individuals showed that maximum head temperature
239 was positively associated with background temperature and dependent on behaviour (Table 3), with
240 lower head temperatures when walking compared to resting (Fig. 2). Controlling for these effects,
241 maximum head temperature showed low but highly significant repeatability within individual
242 pheasants (between-individual variance $\alpha_a^2 = 0.159$, within-individual variance $\alpha_e^2 = 0.873$;
243 repeatability $R_M = 0.154$, 95% CI = 0.08–0.24; $\chi^2_1 = 30.6$, $p < 0.001$). Inclusion of individual-level

244 variables in the model (which reduced repeatability to $R_{M,adj} = 0.116$, 95% CI = 0.05–0.20) showed
245 that this was partly due to a sex difference, males having higher maximum head temperatures on
246 average than females ($b \pm \text{s.e.} = 0.472 \pm 0.158$, $\chi^2_1 = 9.2$, $p = 0.002$; Fig. 2), whereas there was no
247 relationship with morphological traits at release (tarsus length: $\chi^2_1 = 0.4$, $p = 0.520$; body condition:
248 $\chi^2_1 = 1.0$, $p = 0.326$).

249

250 **(b) Does average baseline temperature predict aggressor and recipient roles?**

251 We observed 85 pairwise aggressive encounters (21 threats and 64 pecks, with fighting never
252 observed) in which one or both individuals could be identified from their numbered tags. A GLMM
253 with a binomial error structure and intercepts varying across individuals showed that the role
254 (aggressor or recipient) adopted in a given contest was unrelated to size (tarsus length at release: odds
255 ratio = 1.78, 95% CI = 0.72–4.63; $\chi^2_1 = 1.6$, $p = 0.200$), body condition (odds ratio = 1.17, 95% CI =
256 0.58–2.30; $\chi^2_1 = 0.2$, $p = 0.628$) or sex, with males ($n = 34$) and females ($n = 21$) equally likely to be
257 the aggressor (odds ratio = 2.56, 95% CI = 0.63–13.48; $\chi^2_1 = 1.8$, $p = 0.186$). The average of an
258 individual's baseline temperature measurements was very similar for aggressors (mean $\pm \text{s.e.} = 36.64$
259 ± 0.08 °C) and recipients (36.49 ± 0.07 °C) and did not reliably predict whether they would be the
260 aggressor in a given encounter (odds ratio = 1.32, 95% CI = 0.77–2.42; $\chi^2_1 = 1.05$, $p = 0.306$).

261

262 **(c) Aggression measurements: does head temperature change during an aggressive encounter?**

263 There were 82 pairwise aggressive encounters, involving 55 individually identified pheasants (34
264 males, 21 females), for which we could measure the maximum head temperature of either the
265 aggressor ($n = 23$), the recipient ($n = 40$) or both ($n = 19$) at some point during the encounter. These
266 encounters gave a total of $n = 906$ temperature measurements, which we increased to $n = 1,850$ using
267 linear interpolation at 1-s intervals between two or more observed values.

268 The temperature profile during an aggressive encounter showed a strongly non-linear pattern,
269 showing a slight drop prior to the attack and then increasing sharply afterwards, before falling back
270 down towards the baseline (Fig. 3). The lowest recorded temperature was very similar for aggressors
271 (mean $\pm \text{s.e.} = 35.67 \pm 0.11$ °C) and recipients (35.67 ± 0.06 °C) and occurred at a similar time point
272 for both roles (permutation test: $z = 0.24$, $p = 0.817$). Likewise, the highest recorded temperature was
273 very similar for aggressors (37.67 ± 0.10 °C) and recipients (37.45 ± 0.09 °C) and there was no clear
274 difference in its timing ($z = 0.19$, $p = 0.857$).

275 Temperature dropped significantly leading up to the moment of the attack (time -5 to 0 s;
276 Table 4), but this drop did not differ between aggressors and recipients (LMM, role \times time interaction
277 term: $\chi^2_1 = 0.6$, $p = 0.435$). After an attack (time 1 to 20 s), temperature increased and then decreased

278 (significant quadratic term; Table 5), but there was no clear difference between aggressors and
279 recipients in this non-linear pattern (LMM, joint contribution of role \times time and role \times time²
280 interaction terms: $\chi^2_2 = 2.4$, $p = 0.299$). Overall, across the 20 s following an attack, aggressors were
281 0.2 °C hotter than recipients and females were 0.4 °C cooler than males (Table 5).

282 To check the consistency of our results, we also modelled temperature changes across the
283 whole time course of the encounter (time -5 to 20 s) using smooth terms rather than a polynomial
284 function (Fig. 3). Our conclusions from this approach were the same: the smooth term was clearly
285 non-linear (GAMM: estimated variance parameter = 1.42, 95% CI 0.54–2.87) and gave a
286 substantially better fit than a linear term (Δ elpd-LOO = 29.6), but separating this smooth term
287 between aggressors and recipients did not improve the model (Δ elpd-LOO = 1.4) [74].

288 As a further check on the robustness of our results, we repeated the analysis on a reduced data
289 set ($n = 906$) with the interpolated points removed. The effect estimates from this analysis were very
290 similar to those from our original analysis (full results in supplementary online material [75]); in
291 particular, maximum head temperature dropped significantly leading up to the moment of attack ($b \pm$
292 s.e. = -0.058 ± 0.025 , $\chi^2_1 = 5.4$, $p = 0.021$; Supplementary Table S1), while after the attack it rose
293 and then fell (linear term: 0.063 ± 0.021 , $\chi^2_1 = 8.7$, $p = 0.003$; quadratic term: -0.003 ± 0.001 , $\chi^2_1 =$
294 8.3 , $p = 0.004$; Supplementary Table S2).

Discussion

295 In this study we monitored thermographic changes in captive flocks of juvenile pheasants while they
296 engaged in spontaneous aggressive interactions during a brief period of confinement. We found that
297 head temperature dropped sharply in the few seconds prior to an attack, followed by an increase and
298 then a more gradual decline back down towards baseline levels. Aggressors were on average slightly
299 hotter than recipients, but the changes in temperature were similar for both roles. These findings are
300 based on a novel application of infrared thermography, which is an increasingly popular technique to
301 study stress-induced hyperthermia in birds and other endotherms [27,44–48,50,53,54,56]. The ability
302 to measure such physiological responses without any physical contact with the animals makes IRT
303 potentially applicable to a wide range of systems, giving a clear advantage over other techniques that
304 rely on implanted or wearable devices [26,41]. Previous avian IRT work has largely focused on the
305 responses to acute non-social stressors [27,46] or long-term exposure to adverse health or welfare
306 conditions [30,55,56], overlooking immediate short-term responses to the social interactions that
307 establish and maintain dominance hierarchies. To the best of our knowledge, our study is the first to

308 show detectable changes in body surface temperature during individual aggressive events occurring
309 spontaneously in a group setting.

310

311 *Baseline measurements*

312 Our baseline temperature measurements, taken every 30 s, showed low but highly significant
313 repeatability within individual pheasants. This was partly attributable to a sex difference (females
314 were on average 0.4–0.5 °C cooler than males), but even after accounting for this effect there were
315 consistent individual differences in maximum head temperature, which may reflect underlying
316 differences in metabolic rate [76] and potentially stress physiology [47,61]. An interesting avenue for
317 future work would be to explore the extent to which these differences are linked to genotype, by
318 comparing the temperature profiles of related and unrelated individuals. We did not find evidence
319 that temperature differences were related to behavioural role: average baseline temperature did not
320 predict whether an individual would be the aggressor or the recipient in a given dominance
321 encounter. More extensive observations of these pheasants would be needed to establish whether any
322 behavioural differences are linked to repeatable differences in physiology, as has been suggested
323 elsewhere [62,77]. Furthermore, given that our measurements were taken from a single 13-minute
324 period for each group of pheasants, it is unclear whether the observed temperature differences would
325 persist over a longer timescale, or are more reflective of transient differences in state on a particular
326 day. It would be interesting to investigate this by collecting equivalent measurements across multiple
327 days.

328 Despite the significant repeatability, we also found that maximum head temperature varied
329 within individuals depending on their behavioural state, as reported previously in chickens [27].
330 Temperatures appeared to be lowest in more active states such as walking and foraging compared to
331 resting, perhaps because greater activity redirects more peripheral blood towards the muscle tissue
332 where it is needed. This finding is consistent with human studies showing that skin surface
333 temperature falls with increasing exercise intensity, mediated by cutaneous vasoconstriction [78].

334

335 *Aggression measurements*

336 During aggressive encounters with another pheasant, our per-second measurements revealed a rapid
337 change in maximum head temperature both before and after the moment of attack. In the 5 seconds
338 leading up to an attack, we observed a drop in surface temperature that likely reflects cutaneous
339 vasoconstriction and the redirection of peripheral blood towards the body core, causing a concurrent
340 increase in core body temperature [26]. This physiological change is consistent with the core
341 hyperthermic response to social defeat seen in laboratory studies of rodents [35–37] and passerines

342 [38], commonly measured using implanted devices or invasive probes. Here, however, we detected a
343 thermal response non-invasively during spontaneous, brief and acute dominance encounters between
344 group mates, which were unlike the more severe and asymmetric aggression artificially induced by
345 the resident–intruder paradigm, where a larger or highly aggressive resident individual delivers
346 attacks on a smaller or submissive intruder placed within its home cage [39].

347 Having dropped prior to the attack, maximum head temperature increased to a peak, then
348 steadily decreased towards baseline levels over the 20 s afterwards. This non-linear pattern is
349 remarkably similar in shape (though on a shorter timescale) to that observed in two different avian
350 IRT studies involving a handling stressor. Domestic chickens showed an initial drop of 1.3–2.2 °C in
351 wattle and comb temperature when put in a ‘side-pinned’ hold (presumed to be a severe acute
352 stressor), followed by a significant increase above baseline more than 10 minutes after release [45].
353 In wild blue tits (*Cyanistes caeruleus*), mean eye region surface temperature dropped by around 1 °C
354 within 10 s of being suddenly trapped inside a box, then increased to a peak around 1 °C above
355 baseline when they were captured, held in the hand and blood sampled by an experimenter, followed
356 by a decline back towards the baseline lasting for 1–2 minutes after capture [49]. The reason for this
357 temperature peak after the initial drop is unclear, but it may be linked to the mechanisms that re-
358 establish homeostasis after stress-induced hyperthermia [26]. Intriguingly, a temperature peak was
359 not observed in chickens that were cradled rather than side-pinned [45], nor in blue tits that were
360 trapped but not handled or blood-sampled [47]. The fact that we observed such a peak in freely
361 interacting pheasants shows that transfer of heat from the experimenter’s hands (cf. [49]) or a specific
362 mode of handling cannot be the explanation in this case. An alternative possibility is that the post-
363 drop peak is a response to more intense stressors [45,49], which would support the notion that
364 dominance interactions are a highly salient, albeit short-lived, stimulus for these group-living birds. It
365 is also possible that the temperature changes we observed were linked to rapid head movements by
366 both birds, as the aggressor attempted to peck the recipient and the recipient attempted to avoid being
367 pecked. More research is needed to identify the particular circumstances that induce this
368 characteristic non-linear pattern and to understand the physiological mechanisms driving it.

369 The temperature changes we recorded were rapid, with the biggest differences generally seen
370 within 5 seconds either side of the moment of attack (Fig. 3). The fact that in our study the
371 temperature drop began before the moment of attack suggests that there was some anticipation of the
372 impending aggression, by both aggressors and recipients. On several occasions we observed that the
373 aggressor and recipient were directly facing each other and the aggressor moved towards the
374 recipient before delivering a peck or threat, in which case both birds would have been aware of the
375 other’s presence and potentially able to prepare for an imminent attack. We also observed some

376 bursts of aggression (cf. [79,80]) in which a series of attacks spread quickly through the flock, in
377 which case there may have been more general anticipatory responses to the occurrence of aggression
378 nearby. After the attack, aggressors and recipients usually moved quickly away from each other,
379 which perhaps explains why the post-stressor temperature changes were more rapid than those seen
380 in chickens [45] and blue tits [47,49] during experimental procedures lasting a minute or more.

381 We predicted that the recipients of aggressive behaviour would show a stronger thermographic
382 response than the aggressors, based on the expectation that being threatened or physically attacked
383 would be a more ‘stressful’ experience than choosing to deliver that aggression. Yet there was
384 limited evidence to support this prediction. The maximum head temperature of recipients was 0.2 °C
385 lower than that of aggressors across the 20 s following an attack, but although this difference was
386 significant, the predominant pattern was that recipients and aggressors showed the same, strongly
387 non-linear change in temperature. This finding indicates that, rather than acting as a stressor for one
388 party but not the other, directed aggressive interactions may in fact induce similar physiological
389 responses in the aggressor and the recipient, at least in the short term. Numerous other studies
390 support this interpretation, suggesting that the vertebrate neuroendocrine ‘stress’ response (via the
391 sympatho-adrenomedullary and HPA systems) actually reflects metabolic and cardiovascular
392 demands associated with behavioural activity, rather than the rewarding or aversive nature of the
393 triggering stimulus [63,81]. For example, glucocorticoid levels were elevated in both the winners and
394 losers of aggressive conflicts in rainbow trout [20], green anoles [21] and laboratory rats (*Rattus*
395 *norvegicus*) [63], while winning and losing rats also showed similar peak responses in heart rate,
396 blood pressure and core body temperature [63]. The main difference between winners and losers
397 observed in these studies was in the speed of return to baseline (pre-conflict) values, with losers
398 showing more prolonged elevation of physiological parameters [20,21,63]. In the pheasants we did
399 not find such a difference between aggressors and recipients, although this may reflect the relatively
400 mild nature of the social defeats that were inflicted in our set-up, compared to those in experimental
401 rodent studies. To allow a proper comparison, it would be interesting to take IRT measurements from
402 animals involved in aggressive encounters under more controlled conditions (e.g. the resident–
403 intruder paradigm) and follow them over a longer period of time (e.g. up to an hour afterwards).

404

405 *Limitations and future directions*

406 Our study represents a first step towards characterising the short-term physiological responses to
407 social competition, but there are of course some limitations. The main weakness is a lack of
408 standardisation in our measurements: unlike some IRT studies using non-social stressors [49,50], we
409 were unable to control physical parameters such as the distance and angle of the focal bird relative to

410 the camera, which are known to influence thermographic measurements [82]. This issue is partly
411 mitigated by the fact that our main analysis concerned within-individual changes in temperature over
412 a brief period (25 s) in which both birds (aggressor and recipient) would have been in a similar part
413 of the pen. There were also many varying aspects of the social context (e.g. aggression between other
414 birds close by) that we did not attempt to control, which will have added statistical noise to our
415 measurements compared to more standardised protocols (e.g. staged encounters in the resident–
416 intruder paradigm). Given such limitations, it is promising that in this noisy environment we could
417 still detect a clear thermographic response to aggressive encounters comparable to that seen for non-
418 social stressors [45,49], but taking similar measurements in a more controlled setting would help to
419 validate our findings. A more standardised protocol would also allow measurements to be collected
420 over a longer period after the aggressive attack, to establish whether recipients have a slower return
421 to their baseline surface temperature than aggressors, as observed for other physiological parameters
422 [20,21,63].

423 At the same time, the lack of experimental control is an important strength of our study, lending
424 our results greater ecological validity. The acts of aggression we observed arose spontaneously
425 among familiar, same-aged birds that had been reared together since hatching, as is standard practice
426 in the gamebird industry [83]. Captive pheasants are aggressive towards one another within the first
427 few weeks of life [60] and dominance relationships can continue to change as males move into
428 adulthood [84], so the behaviour we recorded likely represents the early emergence of a dominance
429 hierarchy that can ultimately shape their sexual success [59]. In contrast, the resident–intruder
430 paradigm commonly used in rodent studies of aggression is a more controlled but contrived setting,
431 where the intruder is forcibly exposed to an aggressive resident, with the odds stacked heavily against
432 the former [39]. Another strength is that the birds in our study engaged in aggressive behaviour while
433 surrounded by their flock mates, potentially allowing bystander effects [10] to operate. Detailed
434 analysis of dominance hierarchies in other galliforms suggests that they are acutely sensitive to
435 interactions between other individuals in the flock, and that this affects hierarchy formation [79]. For
436 these reasons, although the resident–intruder paradigm has clearly provided valuable insights into the
437 physiological consequences of social defeat, we suggest that it sheds less light on the establishment
438 and maintenance of dominance in groups of freely interacting individuals.

439 There are a number of useful ways that future studies could build on our findings here. One
440 obvious extension would be to collect thermographic measurements across a longer period spanning
441 several weeks, as the dominance hierarchy develops. As well as enabling a clearer assessment of the
442 individual repeatability of thermal profiles, this would reveal any changes as individuals ascend or
443 descend in dominance rank. In our preliminary observations here we found that aggression was never

444 met with retaliation and thus the aggressors were always victors, in line with evidence from chickens
445 that ‘pair-flips’ are relatively rare [3,79]. Over a longer timescale, however, we would expect to see
446 some dominance relationships being reversed. It would be particularly interesting to examine the
447 thermographic changes during such dominance reversals, as arguably these should induce stronger
448 physiological responses than encounters where the direction of dominance is maintained. Similarly,
449 we might expect to see bigger thermographic changes when conflicts escalate to physical fighting,
450 which was never observed in our study but is known to happen over longer periods [58]. Such effects
451 might extend to individuals not directly involved in the dominance encounter, as has been reported
452 for greylag geese using implanted heart-rate monitors [40]. By taking thermographic measurements
453 from all flock members when such escalated interactions occur, it might be possible to detect
454 physiological correlates of bystander effects. Another worthwhile follow-up study would be to
455 conduct a more fine-grained analysis of the behavioural movements that occur during aggressive
456 interactions. For example, it would be interesting to quantify the head movements of aggressors when
457 attempting to peck recipients, and those of the recipients as they attempt to avoid being pecked, to
458 examine whether the pattern of movement predicts individual changes in head temperature. Finally,
459 as a complementary approach to all of these suggestions, it would be valuable to take thermographic
460 measurements from interacting animals fitted with implanted devices, so that the data can be
461 compared and validated against other, more established indicators of physiological arousal (e.g. heart
462 rate [41] and core body temperature [26]).

463 A century has passed since Schjelderup-Ebbe’s landmark paper on pecking orders in chickens
464 [3]. Alongside his pioneering behavioural observations he made several intriguing comments about
465 the birds’ emotional state in the face of social challenges, referring to their “anger”, “fear” and
466 “courage” (translation of [3] by M. Schleidt & W.M. Schleidt), despite not having any data on
467 physiological variables, let alone cognitive or emotional appraisal. A proliferation of sampling
468 techniques in recent decades has provided many windows on the physiological response to aggressive
469 conflict and other stressors [25]. Our data on groups of freely interacting individuals suggest that
470 infrared thermography can offer additional valuable insights into the mechanisms driving the
471 formation of animal dominance hierarchies.

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Authors' contributions

478 TWF and JRM conceived the study. All authors helped to design the methodology. SK collected the
 479 behavioural and thermographic data, while MAW and JRM collected the morphometric data. TWF
 480 and SK analysed the data. SK and TWF wrote the manuscript with input from all other authors.

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Tables

Table 1. Ethogram used to classify behavioural states of captive juvenile pheasants at 30-s time intervals, adapted from [85,86].

Behaviour	Description
Resting	Body flush with substrate, wings tucked and head either upright or relaxed. Eyes open or closed.
Standing	Balanced upright on both feet with legs extended. No body movement but head may be moving. Head upright or relaxed and eyes open or closed.
Walking	Making more than one step with feet in one direction. Head upright.
Exploratory pecking	Using beak to peck other pheasants gently, without aggression.
Aggression	Threatening, pecking or fighting with other pheasants (see Table 2).
Preening	Using beak to clean wings and feathers. Also includes feather ruffling and wing stretching.
Foraging	Head lowered, with beak pecking or scratching at the floor.
Other	Other behaviours not covered by any of the above descriptions.

Table 2. Ethogram used to classify the types of aggressive encounter between captive juvenile pheasants, in order of increasing intensity. Adapted from [87].

Behaviour	Description
Threat	Bird raises head and neck rapidly, stares at opponent and appears ready to deliver an aggressive peck. Usually face to face with opponent.
Peck	Rapid downward stabbing motion with the beak, directed towards the head of another bird.
Fight	Birds stand directly in front of each other, necks and heads raised at the same level, and deliver vigorous kicks to the opponent.

Table 3. Estimated fixed effects in an LMM predicting maximum head temperature (°C) of captive juvenile pheasants measured every 30 s (baseline measurements), with random effects of individual pheasant ($n = 94$). Significant effects are shown in bold.

Fixed effect	Estimate \pm s.e.	χ^2_{\ddagger}	d.f.	p
intercept*	35.842 \pm 0.312			
behavioural activity		17.7	5	0.003
resting	0.862 \pm 0.285			
standing	0.606 \pm 0.247			
preening	0.578 \pm 0.292			
foraging	0.678 \pm 0.284			
walking	0.303 \pm 0.258			
background temperature†	0.597 \pm 0.218	7.6	1	0.006
time held in pen	-0.002 \pm 0.014	< 0.1	1	0.848
group		18.1	3	< 0.001

*predicted maximum head temperature for a pheasant engaged in ‘other’ activities at the start of the observation session at the average background temperature

†standardised before analysis (z-score method)

‡change in deviance from a likelihood-ratio test comparing models that include or omit that predictor

Table 4. Estimated fixed effects in an LMM predicting maximum head temperature (°C) of captive juvenile pheasants leading up to an aggressive encounter (aggressive measurements, -5 to 0 s prior to the moment of attack), with random effects of individual pheasant ($n = 52$) and encounter ($n = 71$). Significant effects are shown in bold.

Fixed effect	Estimate \pm s.e.	χ^2_{\ddagger}	d.f.	p
intercept*	36.507 \pm 0.212			
time	-0.047 \pm 0.017	7.7	1	0.006
role (aggressor)	-0.042 \pm 0.109	0.2	1	0.691
average baseline temperature†	0.135 \pm 0.078	3.6	1	0.057
sex (female)	-0.344 \pm 0.203	3.2	1	0.075
tarsus length†	-0.116 \pm 0.127	0.9	1	0.353
body condition†	-0.102 \pm 0.091	1.4	1	0.245
type of encounter (threat)	-0.189 \pm 0.165	1.3	1	0.254
group		0.8	3	0.842

*predicted maximum head temperature at time 0 (moment of attack) for a male pheasant (‘recipient’) of average size and with average baseline temperature, being pecked by another pheasant (‘aggressor’)

†standardised before analysis (z-score method)

‡change in deviance from a likelihood-ratio test comparing models that include or omit that predictor

Table 5. Estimated fixed effects in an LMM predicting maximum head temperature (°C) of captive juvenile pheasants following an aggressive encounter (aggressive measurements, 1 to 20 s after the moment of attack), with random effects of individual pheasant ($n = 53$) and encounter ($n = 77$). Significant effects are shown in bold.

Fixed effect	Estimate \pm s.e.	χ^2_{\ddagger}	d.f.	p
intercept*	36.733 \pm 0.174			
time				
linear	0.051 \pm 0.011	22.0	1	< 0.001
quadratic	-0.003 \pm 0.001	29.2	1	< 0.001
role (aggressor)	0.186 \pm 0.091	4.3	1	0.037
average baseline temperature\ddagger	0.123 \pm 0.065	4.2	1	0.040
sex (female)	-0.424 \pm 0.178	6.3	1	0.012
tarsus length \ddagger	-0.136 \pm 0.110	1.7	1	0.188
body condition \ddagger	-0.079 \pm 0.077	1.3	1	0.255
type of encounter (threat)	-0.168 \pm 0.116	1.7	1	0.194
group		0.7	3	0.872

*predicted maximum head temperature at time 0 (moment of attack) for a male pheasant ('recipient') of average size and with average baseline temperature, being pecked by another pheasant ('aggressor')

\ddagger standardised before analysis (z-score method)

\ddagger change in deviance from a likelihood-ratio test comparing models that include or omit that predictor

Figure and table captions

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Figure 1. Infrared thermographic image taken from *FLIR Tools*, showing an aggressive encounter between two juvenile pheasants (middle right of the image). The scale at the top indicates the colour-coding of temperatures, while the red, upwards-pointing triangles automatically pinpoint the maximum temperature within a selection box drawn manually around each pheasant's head. Here, the aggressor on the left (*Bx1*), with a maximum head temperature of 37.5 °C, has just delivered an aggressive peck to the recipient on the right (*Bx2*), who has a maximum head temperature of 35.7 °C. The background reference temperature is 26.5 °C, taken from a white plastic drinker filled with water (*Sp1*), suspended above the pen floor (top left of image).

Figure 2. Boxplots showing the distribution (median, interquartile range and outliers) of maximum head temperatures (averaged within individuals) of male and female captive juvenile pheasants engaged in different behavioural activities.

Figure 3. Change in head temperatures during an aggressive encounter between captive juvenile pheasants in aggressor and recipient roles. Lines are conditional smooths with 95% uncertainty intervals, generated from a GAMM using the package *brms*. Boxplots show the distribution (median, interquartile range and outliers) of the times (averaged within individuals within encounters) at which the minimum (bottom) and maximum (top) temperatures occurred and their observed values (right).

Figures

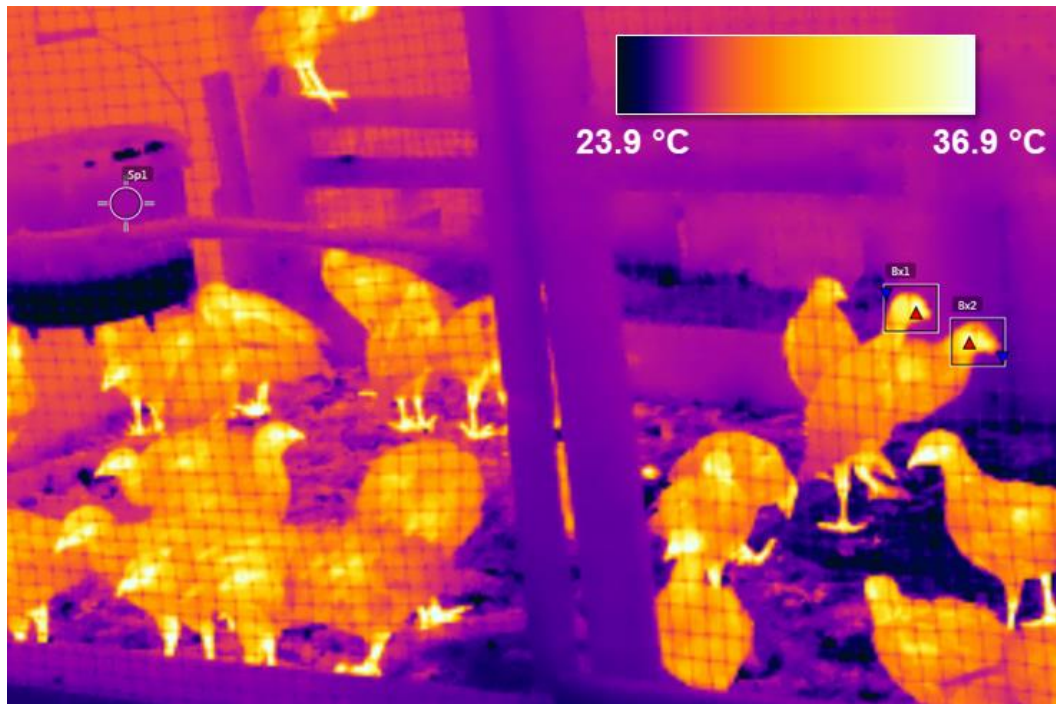


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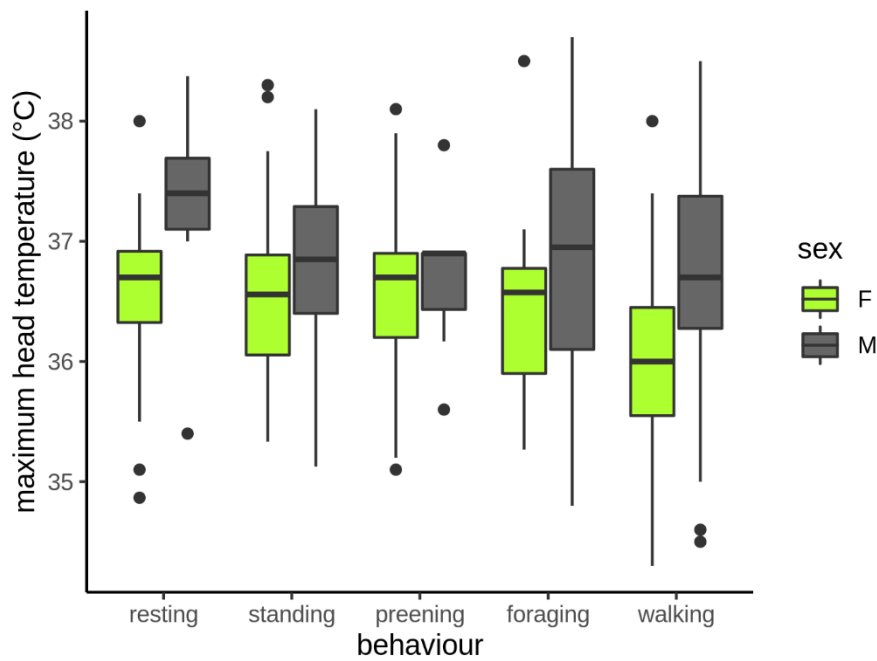


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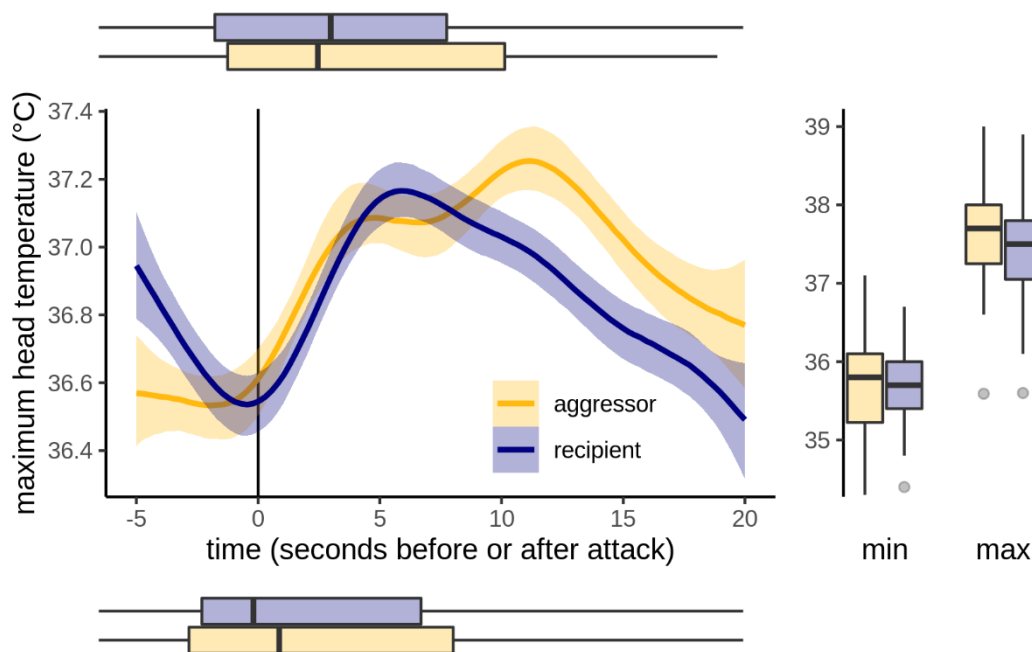


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