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

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Summary

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

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Main Text

Introduction

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

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

Notwithstanding the value of these approaches, blood and tissue sampling has some ethical and practical limitations, because it is invasive and requires capture and handling (or even sacrifice) of the animal. This creates a time lag from the event of interest to the sampling point [25] and acts as an additional stressor, directly affecting the physiological measures of interest [12,22,23] and potentially causing injury and infections. Time lags are also a problem for faecal sampling, a non-invasive method commonly used in field studies [23]. While useful for examining longer-term associations between stress physiology and dominance rank [12,13,24], the timing of defecation by the animal is beyond the experimenter's control and faecal glucocorticoids reflect stress levels several hours earlier [23,25], making it difficult to link them to specific events experienced by the animal. Assessing the impact of individual dominance encounters, which are typically brief and often happen in quick succession, requires measurements of physiological change that are not subject to time lags, and ideally are non-invasive.

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

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

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

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

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

Our main aim was to examine whether IRT reveals dynamic physiological changes occurring during dominance encounters. We tested three key hypotheses. First, in line with evidence across taxa that stress physiology is moderately repeatable within individuals [61], we predicted that head temperatures in pheasants would show consistent individual differences, potentially linked to other measurable characteristics such as sex and size. Alternatively, within-individual changes in temperature associated with different behavioural states (as seen in chickens [27]) might overwhelm between-individual differences, leading to low repeatability. Second, based on the suggestion that stress physiology covaries with behavioural differences such as proactive/reactive 'coping styles' [62], we hypothesised that individual differences in head temperature would predict the roles that individuals adopt in dominance encounters with their group mates, in terms of whether they are the aggressor or the recipient of aggression. Third, we predicted that during an aggressive encounter pheasants would show a drop in surface head temperature, reflecting a stress-induced hyperthermic response in which blood is redirected from the periphery to the body core [26]. We expected that SIH would occur in both aggressors and recipients, but that the response in recipients would be more pronounced and/or longer-lasting (as in [20,21,63]).

Methods

(a) Subjects and housing

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

(b) Procedure

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

(c) Video coding

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

(d) Thermal measurements

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

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

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

(e) Ethical note

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

(f) Statistical analysis

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

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

We then used two separate LMMs to model the temperature profile before (−5 to 0 s) and after (1 to 20 s) the moment of attack. These models included fixed effects of time, role (aggressor or recipient), average baseline temperature (mean of 30-s measurements for that pheasant), type of aggression (threat or peck), sex, tarsus length, body condition and group, and two random effects that allowed intercepts to vary both across individual pheasants and across the contests they were involved in. We modelled non-linear changes using polynomial terms for time and allowed this relationship to differ between aggressors and recipients by including a role × time interaction term, but these more complex terms were omitted where they did not significantly improve the fit of the model. We also checked whether there was any difference between aggressors and recipients in the timing of the highest and lowest temperatures during an encounter, using approximate two-sample Fisher–Pitman permutation tests in the package *coin* [71]. For visualisation and to check the robustness of our conclusions, we fitted a generalised additive mixed-effects model (GAMM) across the whole time sequence (−5 to 20 s) in the package *brms* [72], with smooth terms for the non-linear effect of time on temperature.

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

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

Results

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

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

An LMM with intercepts varying across individuals showed that maximum head temperature was positively associated with background temperature and dependent on behaviour (Table 3), with lower head temperatures when walking compared to resting (Fig. 2). Controlling for these effects, maximum head temperature showed low but highly significant repeatability within individual pheasants (between-individual variance $\alpha_{\alpha}^{2} = 0.159$, within-individual variance $\alpha_{\varepsilon}^{2} = 0.873$; repeatability $R_{\mathrm{M}} = 0.154$, 95% CI = 0.08–0.24; $\chi^{2}_{1} = 30.6$, $p < 0.001$). Inclusion of individual-level variables in the model (which reduced repeatability to $R_{\mathrm{M,adj}} = 0.116$, 95% CI = 0.05–0.20) showed that this was partly due to a sex difference, males having higher maximum head temperatures on average than females ($b \pm$ s.e. = 0.472 ± 0.158, $\chi^2_1 = 9.2$, $p = 0.002$; Fig. 2), whereas there was no relationship with morphological traits at release (tarsus length: $\chi^2_1 = 0.4$, $p = 0.520$; body condition: $\chi^2_1 = 1.0$, $p = 0.326$).

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

We observed 85 pairwise aggressive encounters (21 threats and 64 pecks, with fighting never observed) in which one or both individuals could be identified from their numbered tags. A GLMM with a binomial error structure and intercepts varying across individuals showed that the role (aggressor or recipient) adopted in a given contest was unrelated to size (tarsus length at release: odds 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 = 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 the aggressor (odds ratio = 2.56, 95% CI = 0.63–13.48; $\chi^2_1 = 1.8$, $p = 0.186$). The average of an individual's baseline temperature measurements was very similar for aggressors (mean ± s.e. = 36.64 ± 0.08 °C) and recipients (36.49 ± 0.07 °C) and did not reliably predict whether they would be the aggressor in a given encounter (odds ratio = 1.32, 95% CI = 0.77–2.42; $\chi^2_1 = 1.05$, $p = 0.306$).

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

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

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

Temperature dropped significantly leading up to the moment of the attack (time −5 to 0 s; Table 4), but this drop did not differ between aggressors and recipients (LMM, role × time interaction term: $\chi^2_1 = 0.6$, $p = 0.435$). After an attack (time 1 to 20 s), temperature increased and then decreased (significant quadratic term; Table 5), but there was no clear difference between aggressors and recipients in this non-linear pattern (LMM, joint contribution of role × time and role × time^2 interaction terms: $\chi^2_2 = 2.4$, $p = 0.299$). Overall, across the 20 s following an attack, aggressors were 0.2 °C hotter than recipients and females were 0.4 °C cooler than males (Table 5).

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

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

Discussion

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

Baseline measurements

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

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

Aggression measurements

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

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

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

The temperature changes we recorded were rapid, with the biggest differences generally seen within 5 seconds either side of the moment of attack (Fig. 3). The fact that in our study the temperature drop began before the moment of attack suggests that there was some anticipation of the impending aggression, by both aggressors and recipients. On several occasions we observed that the aggressor and recipient were directly facing each other and the aggressor moved towards the recipient before delivering a peck or threat, in which case both birds would have been aware of the other's presence and potentially able to prepare for an imminent attack. We also observed some bursts of aggression (cf. [79,80]) in which a series of attacks spread quickly through the flock, in which case there may have been more general anticipatory responses to the occurrence of aggression nearby. After the attack, aggressors and recipients usually moved quickly away from each other, which perhaps explains why the post-stressor temperature changes were more rapid than those seen in chickens [45] and blue tits [47,49] during experimental procedures lasting a minute or more.

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

Limitations and future directions

Our study represents a first step towards characterising the short-term physiological responses to social competition, but there are of course some limitations. The main weakness is a lack of standardisation in our measurements: unlike some IRT studies using non-social stressors [49,50], we were unable to control physical parameters such as the distance and angle of the focal bird relative to the camera, which are known to influence thermographic measurements [82]. This issue is partly mitigated by the fact that our main analysis concerned within-individual changes in temperature over a brief period (25 s) in which both birds (aggressor and recipient) would have been in a similar part of the pen. There were also many varying aspects of the social context (e.g. aggression between other birds close by) that we did not attempt to control, which will have added statistical noise to our measurements compared to more standardised protocols (e.g. staged encounters in the resident–intruder paradigm). Given such limitations, it is promising that in this noisy environment we could still detect a clear thermographic response to aggressive encounters comparable to that seen for non-social stressors [45,49], but taking similar measurements in a more controlled setting would help to validate our findings. A more standardised protocol would also allow measurements to be collected over a longer period after the aggressive attack, to establish whether recipients have a slower return to their baseline surface temperature than aggressors, as observed for other physiological parameters [20,21,63].

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

There are a number of useful ways that future studies could build on our findings here. One obvious extension would be to collect thermographic measurements across a longer period spanning several weeks, as the dominance hierarchy develops. As well as enabling a clearer assessment of the individual repeatability of thermal profiles, this would reveal any changes as individuals ascend or descend in dominance rank. In our preliminary observations here we found that aggression was never met with retaliation and thus the aggressors were always victors, in line with evidence from chickens that ‘pair-flips’ are relatively rare [3,79]. Over a longer timescale, however, we would expect to see some dominance relationships being reversed. It would be particularly interesting to examine the thermographic changes during such dominance reversals, as arguably these should induce stronger physiological responses than encounters where the direction of dominance is maintained. Similarly, we might expect to see bigger thermographic changes when conflicts escalate to physical fighting, which was never observed in our study but is known to happen over longer periods [58]. Such effects might extend to individuals not directly involved in the dominance encounter, as has been reported for greylag geese using implanted heart-rate monitors [40]. By taking thermographic measurements from all flock members when such escalated interactions occur, it might be possible to detect physiological correlates of bystander effects. Another worthwhile follow-up study would be to conduct a more fine-grained analysis of the behavioural movements that occur during aggressive interactions. For example, it would be interesting to quantify the head movements of aggressors when attempting to peck recipients, and those of the recipients as they attempt to avoid being pecked, to examine whether the pattern of movement predicts individual changes in head temperature. Finally, as a complementary approach to all of these suggestions, it would be valuable to take thermographic measurements from interacting animals fitted with implanted devices, so that the data can be compared and validated against other, more established indicators of physiological arousal (e.g. heart rate [41] and core body temperature [26]).

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

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Authors' contributions

TWF and JRM conceived the study. All authors helped to design the methodology. SK collected the behavioural and thermographic data, while MAW and JRM collected the morphometric data. TWF 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 ± s.e.	χ^2‡	d.f.	*p*
intercept*	35.842 ± 0.312			
behavioural activity		**17.7**	**5**	**0.003**
resting	0.862 ± 0.285			
standing	0.606 ± 0.247			
preening	0.578 ± 0.292			
foraging	0.678 ± 0.284			
walking	0.303 ± 0.258			
background temperature†	**0.597 ± 0.218**	**7.6**	**1**	**0.006**
time held in pen	−0.002 ± 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 ± s.e.	χ^2‡	d.f.	*p*
intercept*	36.507 ± 0.212			
time	**−0.047 ± 0.017**	**7.7**	**1**	**0.006**
role (aggressor)	−0.042 ± 0.109	0.2	1	0.691
average baseline temperature†	0.135 ± 0.078	3.6	1	0.057
sex (female)	−0.344 ± 0.203	3.2	1	0.075
tarsus length†	−0.116 ± 0.127	0.9	1	0.353
body condition†	−0.102 ± 0.091	1.4	1	0.245
type of encounter (threat)	−0.189 ± 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 ± s.e.	χ^2‡	d.f.	p
intercept*	36.733 ± 0.174			
time				
linear	**0.051 ± 0.011**	**22.0**	**1**	**< 0.001**
quadratic	**−0.003 ± 0.001**	**29.2**	**1**	**< 0.001**
role (aggressor)	**0.186 ± 0.091**	**4.3**	**1**	**0.037**
average baseline temperature†	**0.123 ± 0.065**	**4.2**	**1**	**0.040**
sex (female)	**−0.424 ± 0.178**	**6.3**	**1**	**0.012**
tarsus length†	−0.136 ± 0.110	1.7	1	0.188
body condition†	−0.079 ± 0.077	1.3	1	0.255
type of encounter (threat)	−0.168 ± 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’)

†standardised before analysis (z-score method)

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

Figure and table captions

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

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

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.

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.

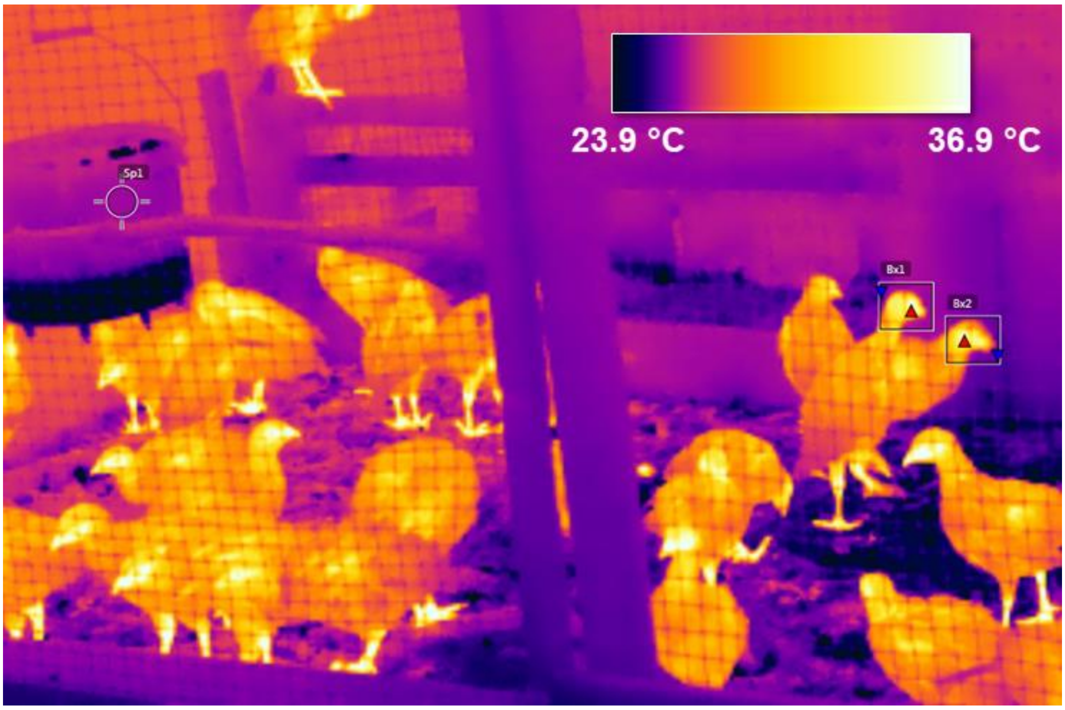
Table 5. Estimated fixed effects in an LMM predicting maximum head temperature (°C) of captive juvenile pheasants following an aggressive encounter (aggressive measurements, 1 to 20 s after the moment of attack), with random effects of individual pheasant (n = 53) and encounter (n = 77). Significant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

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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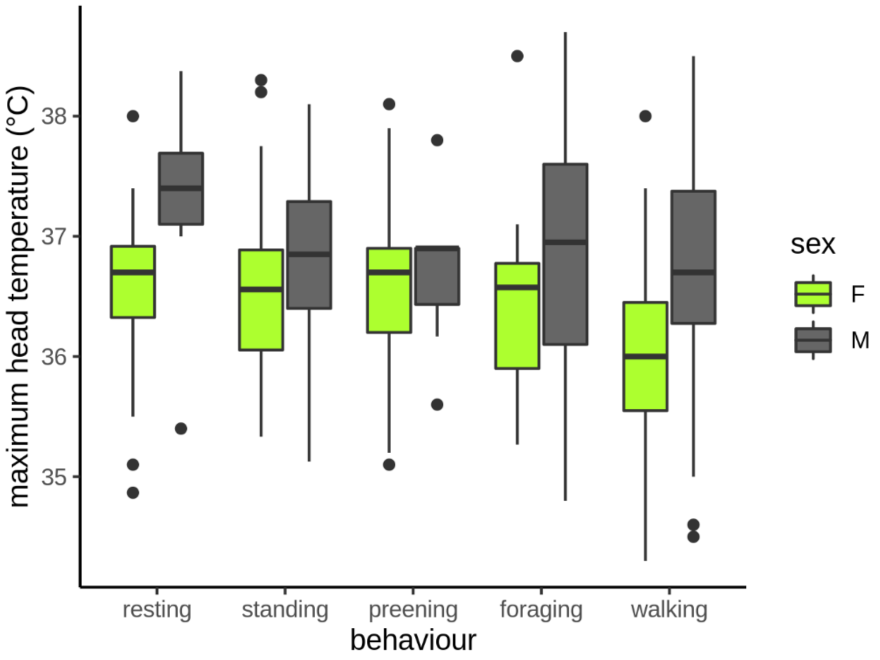

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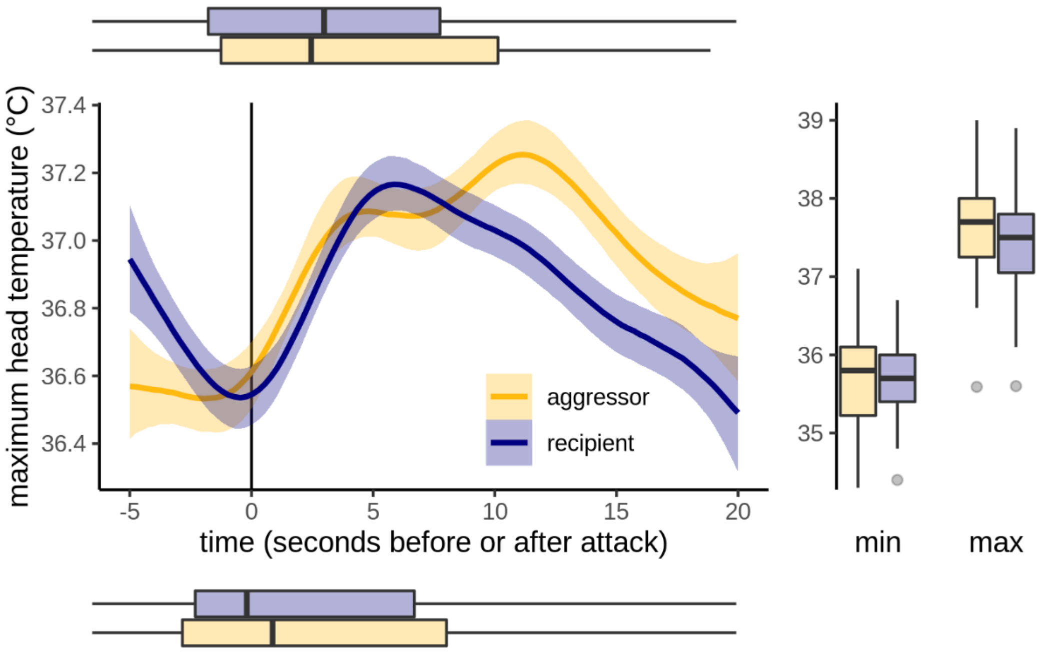

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