Thermal imaging reveals social monitoring during social feeding in wild chimpanzees

Claire Barrault1,2,†, Adrian Soldati1,2,3,†, Catherine Hobaiter2,3, Stephen Mugisha2, Delphine De Moor4, Klaus Zuberbühler1,2,3,† and Guillaume Dezecache2,5,†

1Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland
2Budongo Conservation Field Station, Masindi, Uganda
3School of Psychology and Neuroscience, University of St Andrews, St Andrews, UK
4Centre for Research in Animal Behaviour, University of Exeter, Exeter, UK
5Université Clermont Auvergne, LAPSCO CNRS, Clermont-Ferrand, France

Understanding the affective lives of animals has been a long-standing challenge in science. Recent technological progress in infrared thermal imaging has enabled researchers to monitor animals’ physiological states in real-time when exposed to ecologically relevant situations, such as feeding in the company of others. During social feeding, an individual’s physiological states are likely to vary with the nature of the resource and perceptions of competition. Previous findings in chimpanzees have indicated that events perceived as competitive cause decreases in nasal temperatures, whereas the opposite was observed for cooperative interactions. Here, we tested how food resources and audience structure impacted on how social feeding events were perceived by wild chimpanzees. Overall, we found that nasal temperatures were lower when meat was consumed as compared to figs, consistent with the idea that social feeding on more contested resources is perceived as more dangerous and stressful. Nasal temperatures were significantly affected by interactions between food type and audience composition, in particular the number of males, their dominance status, and their social bond status relative to the subject, while no effects for the presence of females were observed. Our findings suggest that male chimpanzees closely monitor and assess their social environment during competitive situations, and that infrared imaging provides an important complement to access psychological processes beyond observable social behaviours.

This article is part of the theme issue ‘Cognition, communication and social bonds in primates’.

1. Introduction

How are the affective lives of chimpanzees and other primates shaped by socio-ecological context? In recent decades, much has been learned about what information primates process when navigating their social environment [1], including information on others’ physical condition [2,3], rank [4,5], their own as well as others’ social relationships [6–8], and others’ knowledge states [9–12]. This understanding has been developed from studies using both systematic observations (e.g. [7]) and experiments (e.g. [3]), typically based on observable behavioural markers, such as gaze (e.g. [10,13]), vocalization (e.g. [9,13–15]) or movement (e.g. [8]).

Often however, primates and other animals do not show observable responses to key social events, despite evidence that events are perceived, processed and
often have future behavioural implications [1,16]. Primates continuously and closely monitor their social environment [17]. Affective responses play a crucial role in fostering social relationships (e.g. for emotional book-keeping; [18]; for the neuropeptide theory of social bonding; [19]), and in navigating social challenges, such as aggression or the threat thereof [8]. However, these important affective responses can be challenging to investigate, as they do not always include direct, easily observable, behavioural correlates.

Nevertheless, the role affective processes play in primate social lives has been gradually uncovered using methods such as hormonal profiling (e.g. oxytocin metabolites [20–23], corticosteroids [22,24–27] or pupillary dilatation [28]).

More recently, infrared thermography, a highly versatile technique increasingly used with both captive [16,29–36] and wild primates [37–40], has become part of the methodological toolkit [41]. Thermal imaging is particularly useful as it can offer a near real-time snapshot of the affective life of animals, providing an indirect measure of arousal [33,41]. More precisely, thermal imaging is a contact-free method that can assess the surface temperature of bodies through their wavelength and electromagnetic radiation [41–43]. Recent technological progress has made this technique sensitive to changes in peripheral blood flow [43,44], although other physiological processes, such as metabolic heat production, can also affect skin surface temperature [41]. Changes in blood flow are part of adaptive response mechanisms, measurable in temperature changes in the peripheral body parts, such as the perinasal area [30] or the tail [45]. Previous studies have demonstrated that situations likely to be perceived as stressful by an animal can lead to significant drops in nasal temperatures [30,36,39,44]. The general assumption is that changes in peripheral blood flow reflect changes in activity of the autonomic nervous system and that these changes can be used as a way to assess an animal’s ‘internal perspective’ (sensu [1,16]). For example, they have been used to show that chimpanzees respond to relevant social events, such as physical aggression seen in others [30,39], and/or participation in prosocial events, such as mutual grooming [39].

In the current study, we used thermal imaging to evaluate arousal levels in chimpanzees engaged in feeding while in the company of others, with the intention of uncovering whether individuals show otherwise non-observable responses to the presence of others, depending on the type of resource at stake, and the nature of their social relationship to those around them. Social monitoring is a putative function for well-documented audience effects [46,47] in which the presence of others impacts both cognitive and affective functions [48]. Audience effects have received substantial attention, both in the human and non-human animal literature (humans [48,49], primates [50–52], other species [53–55]). In humans, the presence of an audience considerably impacts our cognitive processes, such that the mere presence of others affects our attentional resources [48,56]. Audience effects also occur in non-human animals, and one hypothesis is that audiences which increase the risk of aggression or interference with one’s own activities lead to increased social monitoring and arousal [46,47,49].

In chimpanzees, social feeding carries an elevated risk of aggression owing to resource competition [57–61]. However, the perceived threat can vary dramatically from one feeding event to the next, in relation to changes in food patch size, monopolizability and desirability of food items, as well as nearby group members [56,62–64]. A particularly valuable food resource for chimpanzees is meat, usually the result of lengthy and socially coordinated hunting behaviour that can involve a considerable number of individuals jointly attacking a group of monkeys or other prey [65–68]. If successful, the carcass can be monopolized by one individual and defended against competitors, who may use various degrees of coercion to induce sharing [63], although meat may also be shared freely with social partners [7]. As a result, the acquisition and consumption of meat is probably socially more complex and associated with higher levels of competition than other, more commonly consumed and less easily monopolized foods, such as small- and medium-sized figs that can be harvested from large trees [68] and are typically of more moderate energetic value [69].

Chimpanzees, like many social animals, live in groups with individualized relationships, characterized by dominance, kinship, and social bonding [70,71]. As feeding typically takes place in the presence of others, the size and composition of the nearby audience is likely to impact how individuals perceive the social competition associated with a feeding event. In particular, we expect it to be impacted by the social context. For example, trying to retrieve a fruit near a dominant non-bonded group member is probably perceived as more stressful than doing so near a social partner [7,23,56,63], owing to differences in the risk of aggression. Importantly, these changes in stress response may not be easily directly observed, whether by human observers or conspecifics, from whom it may be advantageous to conceal them [72].

We used infrared thermography to assess how wild chimpanzees’ arousal changes during different types of feeding events (meat versus figs), in the presence of male and female group members, and with or without the presence of dominant individuals or social partners. Based on previous research with chimpanzees [30,31,37,39], we focused on temperature differences on the surface of the nose, a body part that reacts with measurable shifts in skin temperature in response to various types of external events [44], including perceived aggression [30,39]. We did not monitor nasal temperature across time (as locomotion is likely to affect skin temperature), but as single independent events. For this reason, we analysed relative differences across variables of interest, namely food type and audience composition. We predicted lower nasal temperatures for larger audiences, particularly when feeding on meat versus figs. More specifically, we predicted lower temperatures for large male audiences, who are not only competitors but also potential aggressors [73]. Similarly, we predicted lower temperatures in the presence of more dominant individuals. We predicted higher temperatures in the presence of social partners, who are less likely to aggress and more likely to support the subject during aggression, providing a potential social buffer in the context of competition. We expected the effects to be larger when feeding on meat as compared to figs. We control for the impact of mating competition as it is a social factor known to affect chimpanzee arousal levels [74,75] (in particular around nutritious food sources [76]).

2. Methods

(a) Field-site

Data collection were conducted in the Waibira community of the Budongo Central Forest Reserve, in north-western Uganda,
a moist, semi-deciduous tropical rain forest covering 428 km² at an altitude of 1100 m, between 1°35′ and 1°55′ N and 31°08′ and 31°42′ E [77]. Habituation of the Waibira community started in 2011 and most members of the community were well-habituated, including all adult males and all central adult females [78]. At the time of the study, the community was composed of approximately 100 named individuals. Some peripheral adult females and their dependent offspring, as well as some young infants remained unnamed (all are individually recognized and, when seen, interact socially with named individuals as part of the same community), giving an estimated total community size of around 120 individuals.

(b) Data collection

Data were collected between August 2018 and January 2019 by C.B. and S.M., using focal animal sampling [79] approximately during 07.00 to 17.00 focal follows for approximately 5.5 days a week. Focal animals were 19 adult individuals, nine females (15–37 years old) and 10 males (15–42 years old) (electronic supplementary material, table S1). The focal individuals were chosen because of their tolerance to the presence of observers within 10 m. Every day, one focal individual was chosen amongst the individuals encountered in the forest. No focal individual was followed for two consecutive days, and sampling time was balanced across individuals. Each focal individual was observed on average for approximately 13 h (range 9–15 h). Behavioural data were entered on a portable device (Runbo F1) using a custom built-in interface created with CYBERTRACKER (v. 3.389).

Thermal images were largely taken from focal individuals but, when this was impossible, they were opportunistically taken from other party members. ‘Subjects’ hereafter refers to individuals being photographed. Thermal images were taken using a TESTO thermal imager model 881–2. The camera sensor possesses a spectral range from 8 to 14 µm and a thermal sensitivity of less than 50 mK at 30°C. Emissivity was set at 0.98, the camera possesses a spectral range from 8 to 14 µm and a thermal sensitivity of less than 50 mK at 30°C. Emissivity was set at 0.98, a value used for chimpanzee thermal imaging [37,38]. A telephoto lens (9° × 7°/0.5 m) was attached to the camera at all times. Images were taken during feeding events from a distance of approximately 7 m (range 2–15 m) whenever possible to minimize the effect of distance on temperature reading [80], when subjects were feeding either on the ground or in trees (up to a maximum height of 2 m), and only when they were engaged in social feeding behaviour (i.e. feeding in the presence of at least one other subadult or adult individual within 10 m). Subjects were recorded when feeding on meat (Colobus guereza, Cercocebus mitis, Cephalophus natalensis), or on figs (here, largely on Ficus sur—a tree that produces large volumes of small figs distributed across its branches and trunk and of intermediate value, with respect to its level of sugar compared to other fig species [69]; and, infrequently, on Ficus exasperata).

Subjects had to be stationary for at least 1 min prior to taking images (to avoid the effects of locomotion on nasal temperature [30]), not exposed to direct sunlight, and when there was a direct and unobstructed line of sight. Once all of these conditions were met, we took as many pictures as possible (on average, one every 5 s). For each thermal image, we recorded the following information about adult and subadult individuals present within 10 m: the number of males and females, the number of social partners (defined below) and the dominance distance between the subject and the highest-ranking individual (defined below). Thermal data collection was interrupted as soon as the individual was not engaged in feeding or when the subject moved more than 5 m from the initial location. To control for environmental confounds, humidity (which affects emissivity) and ambient temperature (which affects surface temperature) were recorded every 15 min using a portable digital thermometer and hygrometer (HTC-1 LCD).

(c) Data analysis: measurement of infrared thermography data

Given that chimpanzee skin temperature can change rapidly (within about 10–20 s [37]) we considered two thermal images as statistically independent if they were separated by greater than 1 min. As the image angle can affect readings [81], we only included images if both eyes of the subject were clearly visible (maximum angle of 45°; figure 1). We extracted temperature measurements from the nasal area, using the TESTO IRSW analysis software (v. 4.0.5; figure 1). Because air flow entering and exiting the nose may create artefacts in temperature measurements, we manually drew a six-sided diamond-shaped polygon around the nasal area, avoiding the nostril area, and extracted the mean temperature. Intra-rater reliability was performed on n = 89 images (71% of the dataset used for analysis), which showed a high degree of agreement (intraclass correlation coefficient = 0.99).

(d) Data analysis: social correlates of thermal images

(i) Social partners and dyadic composite sociality index

The dyadic composite sociality index (DSI) is calculated as the sum of the duration of time a dyad spent grooming and a dyad spent in proximity, divided by the mean recorded duration of that behaviour, and then divided by the number of behaviours. We computed DSI for all dyads including a focal, based on positive social interactions that occurred between the two individuals. Both adults and subadults were considered as well as same-sex and mixed dyads. The DSI scores were calculated as described in [82], but using only grooming duration (with a distinction made between reciprocal and unidirectional grooming, the former being attributed to both individuals, with duration between the subject and the highest-ranking individual (defined below). Thermal data collection was interrupted as soon as the individual was not engaged in feeding or when the subject moved more than 5 m from the initial location. To control for environmental confounds, humidity (which affects emissivity) and ambient temperature (which affects surface temperature) were recorded every 15 min using a portable digital thermometer and hygrometer (HTC-1 LCD).

(c) Data analysis: measurement of infrared thermography data

Given that chimpanzee skin temperature can change rapidly (within about 10–20 s [37]) we considered two thermal images as statistically independent if they were separated by greater than 1 min. As the image angle can affect readings [81], we only included images if both eyes of the subject were clearly visible (maximum angle of 45°; figure 1). We extracted temperature measurements from the nasal area, using the TESTO IRSW analysis software (v. 4.0.5; figure 1). Because air flow entering and exiting the nose may create artefacts in temperature measurements, we manually drew a six-sided diamond-shaped polygon around the nasal area, avoiding the nostril area, and extracted the mean temperature. Intra-rater reliability was performed on n = 89 images (71% of the dataset used for analysis), which showed a high degree of agreement (intraclass correlation coefficient = 0.99).

(d) Data analysis: social correlates of thermal images

(i) Social partners and dyadic composite sociality index

The dyadic composite sociality index (DSI) is calculated as the sum of the duration of time a dyad spent grooming and a dyad spent in proximity, divided by the mean recorded duration of that behaviour, and then divided by the number of behaviours. We computed DSI for all dyads including a focal, based on positive social interactions that occurred between the two individuals. Both adults and subadults were considered as well as same-sex and mixed dyads. The DSI scores were calculated as described in [82], but using only grooming duration (with a distinction made between reciprocal and unidirectional grooming, the former being attributed to both individuals, with duration...
counted as double) and time spent in proximity (all individuals within 5 m of the focal were considered to be ‘in proximity’). DSI values ranged from 0 to infinity, with dyads with a DSI greater than 1 having a better than average social relationship relative to all recorded social relationships. For each of the subjects, we determined three social partners, corresponding to the three individuals with which the subject exhibited the highest DSI values (among the DSI values > 1) [79], excluding dependent offspring (see the electronic supplementary material, table S2). Number of social partners within 10 m was therefore defined as the number of individuals within 10 m to the subject that were among the top three social partners of the subject.

(ii) Dominance distance
We computed Elo ratings (dominance ranks) for all individuals based on unidirectional pant-grunts (a submission signal in chimpanzees [83]) collected ad libitum during the study period, using the ‘EloRating’ package (v. 0.46.11 [84,85]). The individual Elo ratings at the end of the study period were used as the dominance rank of the individual throughout the study period and applied to all recorded events. No obvious rank changes were observed during the study period, suggesting that the Elo-scores assigned to each individual were reliable estimates of their relative positions within the dominance hierarchy. We calculated dominance distance as the difference between the Elo rating of the highest-ranking individual within 10 m of the subject and the Elo rating of the subject. Positive values of dominance distance therefore indicate that the subjects were submissive to at least one individual in their audience, whereas negative dominance distance values indicated that the subject outranked all individuals in their audience.

(iii) Control for mating competition
We included the number of females in oestrus within 10 m of the subject as a proxy for mating competition.

(e) Statistical analysis: models
Statistical analyses were performed in R (v. 4.1.2 [86]) using R Studio (v. 2021.9.1.372 [87]). We built general linear mixed models (GLMM) using the ‘lme4’ function of the ‘lmer’ package (v. 1.1.27.1 [88]). Analyses were performed on n = 124 observations from 19 individuals (10 adult males, nine adult females), based on social feeding on ‘meat’ (here: meat of Colobus guereza, Ceropithecus mitis, Cephalophus natalensis) (n = 55 observations) or ‘figs’ (here: Ficus sur, Ficus exasperata) (n = 69 observations).

The dependent variable was nasal temperature, which was transformed to reduce skewness ([datapoint - min(of all data)]/range) of females in oestrus within 10 m as a proxy for mating competition. All predictors were scored. The predictors were: food type (meat or figs); number of males (within 10 m of the subject); number of females (within 10 m of the subject); number of social partners (number of top three social partners of subject within 10 m of the subject) and dominance distance (Elo rating of highest-ranking individual within 10 m of the subject minus Elo rating of subject). All predictors were z-scored. We also included three control variables: ambient temperature, expressed in °Celsius; ambient humidity, expressed in % of humidity in the air and number of females in oestrus within 10 m as a proxy for mating competition. All control variables were z-scored.

Colinearity checks were carried out using the function ‘vif’ of the package ‘car’ (v. 3.0.1, [89]). They indicate no colinearity issues (all variance inflation factors (VIFs) value below 1.9). Our sample size was within the range required for analysis using GLMM [90] (sample size ≥ 104 + no. predictors; sample size ≥ 115 in our case).

The full model comprised interactions between the predictor food type and all other predictors, as well as the two control variables and the identity of the subject as a random factor. We confirmed that the residuals were normally distributed and homogenous by inspecting a scatterplot and quantile-quantile plot of the residuals in function of the fitted values, and that no influential data points were present by excluding data points one at a time from the dataset and checking model estimates.

Before assessing the significance of the predictors, we tested our full model including all interactions against a null model (including only the control variables and random effect) using the function ‘Anova’ of the package ‘car’, to test whether the predictors improved model fit. We also reran the same full model, additionally including a random effect for thermal images taken within a 30 min time period, to ensure the results were robust to temporal auto-correlation. p-values were extracted using the function ‘Anova’ from the package ‘car’ (v. 3.0.1, [89]).

Figures were created using the packages ‘ggplot2’ (v. 3.3.5 [91]) and ‘ggpubr’ (v. 0.4.0 [92]).

3. Results
Our full model was a better fit than the null model (likelihood ratio test: $\chi^2 = 700.98$, $p < 0.0001$) and revealed a significant interaction between food type and the number of males within 10 m, the number of social partners within 10 m and the dominance distance to the highest-ranking individual within 10 m. We found no evidence for an effect of the interaction between food type and the number of females within 10 m, nor for an effect of the number of females independently after rerunning the model without the interaction term (table 1; electronic supplementary material, table S3). These results were robust to the inclusion of a random effect term for data points collected within the same 30 min time period (see the electronic supplementary material, table S4). Note also that, as expected, ambient temperature was a strong predictor of nasal temperature. We found no evidence for a significant effect of number of females in oestrus, used as a proxy for mating competition (table 1).

Nasal temperature while feeding on meat was lower for higher numbers of males within 10 m (figure 2a). The opposite pattern was found for figs, with higher nasal temperature for higher numbers of males within 10 m (figure 2a).

The model also revealed an interaction between food type and dominance distance. When feeding on meat, nasal temperature was lower for higher dominance distances to the highest-rankind individual within 10 m (figure 2b). We found no clear effect of dominance distance when feeding on figs.

Finally, the model showed an interaction between food type and the number of social partners within 10 m. The nasal temperature while feeding on meat was lower for fewer numbers of social bond partners present within 10 m. An opposite effect was observed for figs (figure 2c), although the effect should be treated with caution because of a limited number of data points for a larger number of social partners within 10 m.

Table 1 recapitulates the model results. Note that the values for the main terms are presented but, because of the presence of significant interactions, the interpretation of the individual main effects is limited to their effect, keeping the interacting effect at its average [93].

4. Discussion
In the human literature, audience effects are well documented, such that the mere presence of others is known to affect one’s attentional resources and level of arousal [48,49,53,56]. One
putative function of such audience effects is the ‘social monitoring’ of others to best prepare oneself for possible intrusion in one’s own activities [46,49], including potential aggression. Social feeding, because it carries an elevated risk of aggression, is an ideal context in which to evaluate this hypothesis in chimpanzees [57,94].

To date, animal behaviour researchers were largely limited to the documentation of easily observable behaviours, such as shifts in gaze, or in relative position. Recently, infrared thermal imaging has gained prominence as an important new tool, providing a simple and non-invasive method to assess otherwise hidden physiological responses that can imply real-time cognitive processing of social interactions that would be undetectable with traditional methods [41,44].

We used infrared thermography to study the role of audience effects during feeding events in wild chimpanzees, with the hypothesis that chimpanzees passively monitor the audience when valuable resources are at stake. Our results revealed differences in nasal temperature related to the food resource, the audience size, and the audience composition (dominance and social partners). Specifically, nasal temperature of individuals feeding on meat were lower for contexts marked by higher competition, i.e. both when more males were present within 10 m, and when dominance distances between a lower-ranking subject and the most dominant individual in the party were large. These findings are consistent with elevated levels of stress when surrounded by dominant individuals and feeding on meat, a more easily monopolized and important resource [7,63]. Our results also suggest that social partners may have acted as a buffer (sensu [95]), with higher nasal temperature for individuals with more social partners within 10 m (relative to others with fewer social partners around) when feeding on meat.

This pattern of results is consistent with the findings of reduced temperature in peripheral areas of animals’ bodies (such as the nose, or the tail) owing to blood redirection away from areas vulnerable to significant blood loss [45] in social situations likely to be perceived as stressful [30,39,41,44]. These findings support the hypothesis that social feeding carries an elevated risk of physical aggression and stress that is likely to be mitigated by the presence of social partners [96] and the prospect of receiving coalitional support in case of escalation [8,97,98]. Interestingly, we found the opposite patterns of results for figs, with higher levels of nasal temperature for larger numbers of males present within 10 m, and for lower numbers of social partners present within 10 m. While figs are an important food resource [69,71], the small-sized Ficus sur (which accounted for the majority of observations of feeding on figs in our sample) represent a less competed-for and less monopolizable food resource than meat. In a large community such as Waibira, with an unusually large number of independent males, having more male and high-ranking individuals in a party could perhaps decrease the chance of aggression. The presence of so many males, and therefore of potential allies for whomever is threatened, makes any use of aggression a risky strategy. If this is the case, then when feeding on small-medium sized figs, a much more widely available and less easily monopolized food than meat and thus one less worth competing over, having more males and high-ranking individuals present could represent a lower risk environment than a smaller party with just one or two large dominant individuals present.

The presence of females in oestrus, a characteristic of the environment which is probably conducive to escalated risk of aggression [75], did not impact skin temperature. A possible reason is that there is a trade-off between mating and feeding in terms of time budget, such that feeding may be already reduced when mating opportunities are available (as seen in [99]) and mating opportunities thus had a reduced impact on the limited time left for feeding.

The mere presence of others can affect cognitive, behavioural and emotional responses (see [49] for a review). Several hypotheses have been discussed as to why this is the case. One hypothesis (referred to here as the ‘social monitoring’ hypothesis) is based on the arousal levels generated by the presence and proximity of others [53,100], among

| term                        | estimate | s.e.    | t-score | p-value |
|-----------------------------|----------|---------|---------|---------|
| intercept                   | −4.435   | 2.407   | −1.842  | 0.065   |
| food type                   | 0.222    | 0.222   | 1.019   | 0.308   |
| number of males             | 0.373    | 0.109   | 3.421   | 0.001   |
| number of females           | 0.068    | 0.150   | 0.451   | 0.652   |
| number of social partners   | −0.312   | 0.182   | −1.704  | 0.088   |
| ambient temperature         | 0.118    | 0.119   | 0.993   | 0.321   |
| ambient humidity            | −0.015   | 0.015   | −1.003  | 0.316   |
| number of oestrus females   | −0.085   | 0.083   | −1.023  | 0.306   |
| food type * number of males | −0.591   | 0.208   | −2.840  | 0.005   |
| food type * number of females| 0.056   | 0.190   | 0.303   | 0.762   |
| food type * number of social partners | 0.591 | 0.228 | 2.596 | 0.010 |
| food type * dominance distance | −0.380 | 0.171 | −2.221 | 0.026 |

a-scored to allow comparison of model estimates across predictors.

bNote that main effects have limited interpretative value when interactions are significant.
Figure 2. Interaction effect of food type and audience composition on nasal temperature (figs, grey circles; meat, black triangles). The fitted model lines (figs, light grey; meat, dark grey) are presented with 95% confidence bands for the fitted values (95%). (a) Interaction effect between the number of adult males within 10 m and food type on nasal temperature; (b) interaction effect between the dominance distance to the highest-ranking individual within 10 m (Elo rating of highest-ranking individual within 10 m of the subject — Elo rating of subject) and food type on nasal temperature; and (c) interaction effect between the number of social bond partners present within 10 m and food type on nasal temperature.

which are potential competitors for resources and/or individuals whose behaviour remains uncertain and can represent a physical threat to the subject [46,47], but who can also represent protection from non-social partners and provide social support [21,101]. In chimpanzees, social feeding can be characterized by an elevated risk of aggression [58], which makes monitoring of audience members and their social relationships particularly important. Audience effects are particularly expected for high-value food, such as meat, relative to more spatially dispersed, more abundant and less easily monopolized feeding sources, such as figs. This said, even in the absence of overt physical competition over food (as manifested by, for example, physical aggression or milder harassment, such as persistent begging gestures towards the individual in possession [63,102]), the physiological effects of arousal observed might also reflect an effect of the presence of others [48,53].

While discussion remains over the exact source of body surface temperature shifts [41], some consensus exists over the valid use of infrared thermography to infer shifts in blood flow caused by the activation of the autonomic nervous system [44], with a decrease in nasal temperature when individuals are exposed to stressful events [30,36,39,44]. Although it is tempting to interpret the observed differences in temperature as reflecting absolute levels of arousal, no time series were collected here, preventing interpretation of our data as indicating shifts in skin temperature relative to a known baseline or changes occurring after a specific stimulus (unlike in e.g. [30,37]). We therefore interpret skin temperature profiles strictly as ‘relative’ differences across various audience sizes and composition, with lower nasal temperature indicating relatively lower blood flow in peripheral regions of the body, a pattern typically associated with the experience of negative emotions [44].

While our findings are strongly suggestive, they remain—like much of the thermal imaging field—preliminary. We would benefit substantially from much larger datasets that allow analysis both within individuals, and between a larger number of individuals with a greater range of social relationships. In future work, longitudinal comparisons may provide a means to explore variation in coping-style across individuals, a fundamental aspect of how other species (including humans) vary in their individual responses to stressful events [103,104]. Future studies could also include complimentary physiological measurements (such as hormonal profiles, e.g. [30]) that could support and enrich our understanding of the effects being observed (e.g. help identify the physiological source of changes in arousal, for example the potential involvement of the hypothalamus–pituitary–adrenal axis, as in [30]).

In summary, our study shows that wild chimpanzees are affected by the presence of audience in stressful situations, such as when feeding over potentially contested resources, and that audience effects in non-human apes include nuanced monitoring of their day-to-day social landscape.

Ethics. The study adhered to the ASAB guidelines for the treatment of animals during behavioural studies [105]. A minimum distance of 7 m was maintained between the observer and the focal animal, though habituated chimpanzees would sometimes approach closer. The study was approved by the Uganda Wildlife Authority (UWA/COD/96/5), the Uganda National Council for Science and Technology (NS 637), and the research ethics committees of the Universities of Neuchâtel (38/2019-B) and St Andrews (N. 171).

Data accessibility. Data are available at osf.io/c5pku. Data are also provided in the electronic supplementary material [106].

Authors’ contributions. C.B.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; A.S.: conceptualization, formal analysis, investigation, methodology, software, supervision, validation, visualization, writing—original draft, writing—review and editing; S.M.: investigation, methodology, resources, supervision, writing—original draft, writing—review and editing; C.H.: funding acquisition, methodology, resources, supervision, writing—original draft, writing—review and editing; D.D.M.: formal analysis, methodology, software, validation, visualization, writing—original draft, writing—review and editing; K.Z.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing—review and editing; G.D.: conceptualization, methodology, resources, supervision, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.
References

1. Cheney DL, Seyfarth RM. 2018 How monkeys see the world: inside the mind of another species. Chicago, IL: University of Chicago Press.

2. Benitez ME, Pappano DJ, Beehner JC, Bergman TJ. 2017 Evidence for mutual assessment in a wild primate. Sci. Rep. 7, 2952. (doi:10.1038/s41598-017-02993-w)

3. Kitchen DM, Cheney DL, Engh AL, Fischer J, Moscovec LR, Seyfarth RM. 2013 Male baboon responses to experimental manipulations of loud ‘hawoh calls’: testing an honest signal of fighting ability. Behav. Ecol. Sociobiol. 67, 1825–1835. (doi:10.1007/s00265-013-1592-9)

4. Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM. 2003 Hierarchical classification by rank and kinship in baboons. Science 302, 1234–1236. (doi:10.1126/science.1087513)

5. Fischer J, Kitchen DM, Seyfarth RM, Cheney DL. 2004 Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. Behav. Ecol. Sociobiol. 56, 140–148. (doi:10.1007/s00265-003-0739-4)

6. Bergman TJ, Sheehan MJ. 2013 Social knowledge and signals in primates. Am. J. Primatol. 75, 683–694. (doi:10.1002/ajp.22103)

7. Samuni L, Preis A, Mundry R, Deschner T, Crockford C. 2012 Social bonds facilitate cooperative food sharing in wild chimpanzees. Proc. R. Soc. B 285, 20121643. (doi:10.1098/rspb.2012.1643)

8. Wittig RM, Crockford C, Langgerbraber KE, Zuberbühler K. 2014 Triadic social interactions operate across time: a field experiment with wild chimpanzees. Proc. R. Soc. B 281, 20133155. (doi:10.1098/rspb.2013.3155)

9. Crockford C, Wittig RM, Mundry R, Zuberbühler K. 2012 Wild chimpanzees inform ignorant group members of danger. Curr. Biol. 22, 142–146. (doi:10.1016/j.cub.2011.11.055)

10. Crockford C, Wittig RM, Zuberbühler K. 2017 Vocalizing in chimpanzees is influenced by social-cognitive processes. Sci. Adv. 3, e1701742. (doi:10.1126/sciadv.1701742)

11. Krupenye C, Call J. 2019 Theory of mind in animals: current and future directions. Wiley Interdiscip. Rev. Cogn. Sci. e1503. (doi:10.1002/wics.1503)

12. Girard-Buttoz C, Surbeck M, Samuni L, Tkaczynski P, Boesch C, Fruth B, Wittig RM, Hohmann G, Crockford C. 2020 Information transfer efficiency differs in wild chimpanzees and bonobos, but not social cognition. Proc. R. Soc. B 287, 20200523. (doi:10.1098/rspb.2020.0523)

13. Schel AM, Townsend SW, Machanda Z, Zuberbühler K, Slocombe KE. 2013 Chimpanzee alarm call production meets key criteria for intentionality. PLoS ONE 8, e76674. (doi:10.1371/journal.pone.0076674)

14. Slocombe KE, Keller T, Turman L, Townsend SW, Papworth S, Seulibs P, Zuberbühler K. 2010 Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. Behav. Ecol. Sociobiol. 64, 1959–1966. (doi:10.1007/s00265-010-1006-0)

15. Fedurek P, Slocombe KE. 2013 The social function of food-associated calls in male chimpanzees. Am. J. Primatol. 75, 726–739. (doi:10.1002/ajp.22122)

16. Brügger RK, Willems EP, Burkart JM. 2021 Do marmosets understand others’ conversations? A thermography approach. Sci. Adv. 7, eabf8790. (doi:10.1126/sciadv.abf8790)

17. Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB. 2012 The evolution of primate societies. Chicago, IL: University of Chicago Press.

18. Schino G, Aureli F. 2010 Primate reciprocity and its cognitive requirements. Evol. Anthropol. Issues News Rev. 19, 130–135. (doi:10.1002/evan.20270)

19. Dunbar RIM. 2010 The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. Neurosci. Biobehav. Rev. 34, 260–268. (doi:10.1016/j.neubiorev.2008.07.001)

20. Crockford C, Deschner T, Ziegler TE, Wittig RM. 2014 Endogenous peripheral oxytocin measures can give insight into the dynamics of social relationships: a review. Front. Behav. Neurosci. 8, 68. (doi:10.3389/fnbeh.2014.00686)

21. Samuni L, Preis A, Mundry R, Deschner T, Crockford C, Wittig RM. 2017 Oxytocin reactivity during intergroup conflict in wild chimpanzees. Proc. Natl Acad. Sci. USA 114, 268–273. (doi:10.1073/pnas.1618612114)

22. Samuni L, Preis A, Deschner T, Wittig RM, Crockford C. 2019 Cortisol and oxytocin show independent activity during chimpanzee intergroup conflict. Psychoneuroendocrinology 104, 165–173. (doi:10.1016/j.psyneuen.2019.02.007)

23. Wittig RM, Crockford C, Deschner T, Langgerbraber KE, Ziegler TE, Zuberbühler K. 2014 Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. Proc. R. Soc. B 281, 20133096. (doi:10.1098/rspb.2013.3096)

24. Girard-Buttoz C et al. 2021 Early maternal loss leads to short- but not long-term effects on diurnal cortisol slopes in wild chimpanzees. eLife 10, e64134. (doi:10.7554/eLife.64134)

25. Abbott DH et al. 2003 Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. Horm. Behav. 43, 67–82. (doi:10.1016/S0017-9707(02)00037-5)

26. Rincon AV, Heistermann M, Schülke O, Ostner J. 2020 Testosterone and cortisol are negatively associated with ritualized bonding behavior in male macaques. Psychoneuroendocrinology 120, 104774. (doi:10.1016/j.psyneuen.2020.104774)

27. Tkaczynski PJ et al. 2020 Patterns of urinary cortisol levels during ontogeny appear population specific rather than species specific in wild chimpanzees and bonobos. J. Hum. Evol. 147, 102869. (doi:10.1016/j.jhevol.2020.102869)

28. Kret ME, Tomonaga M, Matusawa T. 2014 Chimpanzees and humans mimic pupal size of conspecifics. PLoS ONE 9, e104886. (doi:10.1371/journal.pone.0104886)

29. Ermatinger FA, Brügger RK, Burkart JM. 2019 The use of infrared thermography to investigate emotions in common marmosets. Physiol. Behav. 211, 112672. (doi:10.1016/j.physbeh.2019.112672)

30. Kano F, Hirata S, Deschner T, Behringer V, Call J. 2016 Nasal temperature drop in response to a playback of conspecific fights in chimpanzees: a thermo-imaging study. Physiol. Behav. 155, 83–94. (doi:10.1016/j.physbeh.2015.11.029)

31. Sato Y, Kano F, Hirata S. 2018 Cutting-edge infrared thermography as a new tool to explore animal emotions. Jpn J. Anim. Psychol. 68, 1–15.

32. Chotard H, Ioannou S, Davila-Ross M. 2018 Infrared thermal imaging: positive and negative emotions modify the skin temperatures of monkey and ape faces. Am. J. Primatol. 80, e22863. (doi:10.1002/ajp.22863)

33. Ioannou S, Chotard H, Davila-Ross M. 2015 No strings attached: physiological monitoring of threes monkeys (Macaca mulatta) with thermal imaging. Front. Behav. Neurosci. 9, 160. (doi:10.3389/fnbeh.2015.00160)

34. Ross SR, Lake BR, Fultz A, Hopper LM. 2021 An evaluation of thermal imaging as a welfare monitoring tool for captive chimpanzees. Primates 62, 919–927.
82. De Moor D, Roos C, Ostner J, Schülke O. 2020 Female Assamese macaques bias their affiliation to paternal and maternal kin. Behav. Ecol. 31, 493–507. (doi:10.1093/beheco/art213)
83. Fedurek P, Tkaczynski PJ, Hobaiter C, Zuberbühler K, Wittig RM, Crockford C. 2021 The function of chimpanzee greeting calls is modulated by their acoustic variation. Anim. Behav. 174, 279–289. (doi:10.1016/j.anbehav.2021.02.002)
84. Neumann C, Kulik L. 2020 EloRating: animal dominance hierarchies by Elo rating. See https://CRAN.R-project.org/package=EloRating.
85. Neumann C, Duboscq J, Dubuc C, Ginting A, Irwan AM, Agil M, Widdig A, Engelhardt A. 2011 Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Anim. Behav. 82, 911–921. (doi:10.1016/j.anbehav.2011.07.016)
86. R Core Team. 2019 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
87. R Studio Team. 2019 RStudio: integrated development environment for R. Boston, MA: R Studio Inc.
88. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. (doi:10.18637/jss.v067.i01)
89. Fox J, Weisberg S, Price B, Adler D, Bates D, Bauboy G, Bolker B. 2019 car: Companion to Applied Regression. See https://cran.r-project.org/web/packages/car/index.html.
90. Field A. 2013 Discovering statistics using IBM SPSS statistics. Los Angeles, CA: Sage Publications.
91. Wickham H. 2009 Elegant graphics for data analysis. Media 35, 10–1007.
92. Kassambara A. In press. ggplot2 based publication ready plots. See https://rpkgs.datanovia.com/ggpubr/index.html.
93. Underwood AJ. 1997 Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge, UK: Cambridge University Press.
94. Muller MN, Mitani JC. 2005 Conflict and cooperation in wild chimpanzees. Adv. Study Behav. 35, 275–331. (doi:10.1016/S0065-3454(05)35007-8)
95. Kikusui T, Winslow JT, Mori Y. 2006 Social buffering: relief from stress and anxiety. Phil. Trans. R. Soc. B 361, 2215–2228. (doi:10.1098/rstb.2006.1941)
96. Wittig RM, Crockford C, Weltring A, Langergraber KE, Deschner T, Zuberbühler K. 2016 Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. Nat. Commun. 7, 1–8. (doi:10.1038/ncomms13361)
97. Gilby VC, Brent LT, Wroblewski EE, Rudicell RS, Hahn BH, Goodall J, Pusey AE. 2013 Fitness benefits of coalitional aggression in male chimpanzees. Behav. Ecol. Sociobiol. 67, 373–381. (doi:10.1007/s00265-012-1457-6)
98. Newton-Fisher NE. 2006 Female coalitions against male aggression in wild chimpanzees of the Budongo Forest. Int. J. Primatol. 27, 1589–1599. (doi:10.1007/s10764-006-9087-3)
99. Georgiev RA, Russell AF, Emery Thompson M, Otali E, Muller MN, Wangham RW. 2014 The foraging costs of mating effort in male chimpanzees (Pan troglodytes schweinfurthii). Int. J. Primatol. 35, 725–745. (doi:10.1007/s10764-014-9788-y)
100. Ioannou S, Morris P, Mercer H, Baker M, Gallee V, Reddy V. 2014 Proximity and gaze influences facial temperature: a thermal infrared imaging study. Front. Psychol. 5, 845. (doi:10.3389/fpsyg.2014.00845)
101. Samuni L, Crockford C, Wittig RM. 2021 Group-level cooperation in chimpanzees is shaped by strong social ties. Nat. Commun. 12, 1–10. (doi:10.1038/s41467-020-20709-9)
102. Hobaiter C, Leavens DA, Byrne RW. 2014 Deictic gesturing in wild chimpanzees (Pan troglodytes)? Some possible cases. J. Comp. Psychol. 128, 82. (doi:10.1037/a0033757)
103. Sapolsky RM. 2004 Why zebras don’t get ulcers: the acclaimed guide to stress, stress-related diseases, and coping. New York, NY: Holt Paperbacks.
104. Beasley M, Thompson T, Davidson J. 2003 Resilience in response to life stress: the effects of coping style and cognitive hardness. Personal. Individ. Differ. 34, 77–95. (doi:10.1016/j.paid.2002.08.002)
105. No authorship indicated. 2018 Guidelines for the treatment of animals in behavioural research and teaching. Anim. Behav. 135, i–x. (doi:10.1016/j.anbehav.2017.10.001)
106. Barrau C, Soldati A, Hobaiter C, Mugisha S, De Moor D, Zuberbühler K, Dezecache G. 2022 Data from: Thermal imaging reveals social monitoring during social feeding in wild chimpanzees. Figshare. (doi:10.6084/m9.figshare.c.6060627)