

**A peer-reviewed version of this preprint was published in PeerJ on 5 December 2017.**

[View the peer-reviewed version](https://doi.org/10.7717/peerj.4116) (peerj.com/articles/4116), which is the preferred citable publication unless you specifically need to cite this preprint.

Dezecache G, Wilke C, Richi N, Neumann C, Zuberbühler K. 2017. Skin temperature and reproductive condition in wild female chimpanzees. PeerJ 5:e4116 <https://doi.org/10.7717/peerj.4116>

# Skin temperature and reproductive condition in wild female chimpanzees

**Guillaume Dezecache** <sup>Corresp., 1, 2</sup>, **Claudia Wilke** <sup>2, 3, 4</sup>, **Nathalie Richi** <sup>1, 2</sup>, **Christof Neumann** <sup>1</sup>, **Klaus Zuberbühler** <sup>1, 2, 3</sup>

<sup>1</sup> Institute of Biology, Université de Neuchâtel, Neuchâtel, Switzerland

<sup>2</sup> Budongo Conservation Field Station, Masindi, Uganda

<sup>3</sup> School of Psychology and Neuroscience, University of St. Andrews, Fife, United Kingdom

<sup>4</sup> Department of Psychology, University of York, York, United Kingdom

Corresponding Author: Guillaume Dezecache

Email address: guillaume.dezecache@gmail.com

Infrared thermal imaging has emerged as a valuable tool in veterinary medicine, in particular in evaluating reproductive processes. Here, we explored differences in skin temperature of cycling and pregnant wild chimpanzee females in Budongo Forest, Uganda. Based on previous literature, we predicted increased skin temperature when approaching peak fertility at the area of the reproductive organs of cycling females. For pregnant females, we made the same prediction, mainly because it has been argued that chimpanzee females have evolved mechanisms to conceal pregnancy, including exaggerated sexual swelling and sexually conspicuous vocal behaviour, and to encourage male mating behaviour in order to decrease their infanticidal tendencies by confusing paternity. Overall, we found only small changes in cycling females, with slight temperature increases towards the end of the swelling cycles but no overall increase in skin temperature between oestrous and non-oestrous phases. Interestingly, however, pregnant and cycling females had very similar skin temperatures. These results suggest that males cannot use skin temperature to discriminate between pregnant and non-pregnant/cycling females during maximal swelling, when ovulation is most likely to occur in cycling females. This pattern may be linked to the evolution of physiological means to conceal reproductive state in pregnant females.

# 1 Skin temperature and reproductive condition in wild female chimpanzees

2 Guillaume Dezecache<sup>1,2</sup>, Claudia Wilke<sup>2,3,4</sup>, Nathalie Richi<sup>1,2</sup>, Christof Neumann<sup>1</sup> & Klaus

3 Zuberbühler<sup>1,2,3</sup>

4 <sup>1</sup>Institute of Biology, University of Neuchâtel, Switzerland; <sup>2</sup>Budongo Conservation Field

5 Station, Masindi, Uganda; <sup>3</sup>School of Psychology and Neuroscience, University of St Andrews,

6 Scotland (UK); <sup>4</sup>Department of Psychology, University of York (UK)

7 Corresponding author: Guillaume Dezecache [guillaume.dezecache@gmail.com](mailto:guillaume.dezecache@gmail.com)

8

## 9 ABSTRACT

10 Infrared thermal imaging has emerged as a valuable tool in veterinary medicine, in particular in  
 11 evaluating reproductive processes. Here, we explored differences in skin temperature of cycling  
 12 and pregnant wild chimpanzee females in Budongo Forest, Uganda. Based on previous literature,  
 13 we predicted increased skin temperature when approaching peak fertility at the area of the  
 14 reproductive organs of cycling females. For pregnant females, we made the same prediction,  
 15 mainly because it has been argued that chimpanzee females have evolved mechanisms to conceal  
 16 pregnancy, including exaggerated sexual swelling and sexually conspicuous vocal behaviour,  
 17 and to encourage male mating behaviour in order to decrease their infanticidal tendencies by  
 18 confusing paternity. Overall, we found only small changes in cycling females, with slight  
 19 temperature increases towards the end of the swelling cycles but no overall increase in skin  
 20 temperature between oestrous and non-oestrous phases. Interestingly, however, pregnant and  
 21 cycling females had very similar skin temperatures. These results suggest that males cannot use  
 22 skin temperature to discriminate between pregnant and non-pregnant/cycling females during  
 23 maximal swelling, when ovulation is most likely to occur in cycling females. This pattern may  
 24 be linked to the evolution of physiological means to conceal reproductive state in pregnant  
 25 females.

26 **Keywords:** infra-red thermography, skin temperature, wild chimpanzees, oestrous cycle,  
 27 pregnancy

## 28 INTRODUCTION

29 Infrared thermal imaging (IRT) has emerged as a promising tool for studying animal behaviour.  
30 For instance, research employing this methodology has helped cast light on affective processing  
31 in a variety of species, including macaques (*Macaca mulatta*) (Nakayama et al. 2005; Kuraoka  
32 and Nakamura 2011; Ioannou et al. 2015), chimpanzees (*Pan troglodytes*) (Kano et al. 2016;  
33 Dezecache et al. 2017) or dogs (*Canis lupus familiaris*) (Travain et al. 2015; Riemer et al. 2016;  
34 Travain et al. 2016). In these studies, IRT was deployed to detect changes in emissivity of the  
35 skin caused by shifts in blood flow at body surface, a physiological process controlled by the  
36 autonomic nervous system (see Ioannou et al. 2014 for a comprehensive review). One important  
37 asset of this technique is its non-invasive character, since measurements can be made at a  
38 reasonable distance from free-ranging animals and without hindering ongoing natural social  
39 interactions.

40 Other strands of research have benefited from IRT as a non-invasive technique to study  
41 reproductive processes of wild animals (Cilulko et al. 2013). For example, and in qualitative  
42 assessment, Hilsberg-Merz 2008 showed that female Asian elephants (*Elephas maximus*) and  
43 Black rhinoceroses (*Diceros bicornis*) showed increased surface temperature in the area of their  
44 reproductive organs during oestrous, a pattern associated with increased attractiveness to males.  
45 In pigs, vulvar skin temperatures were higher during oestral compared to dioestral phases (Sykes  
46 et al. 2012), a pattern caused by increased blood flow towards the vulva due to oestrogen  
47 secretion in the ovarian follicles (Stelletta et al. 2013). Heightened temperature of the area of the  
48 reproductive organs and can be used as a tool to detect oestrous in cows, with vulva temperature  
49 peak around 24 hours before ovulation, followed by a slight decrease towards ovulation  
50 (Talukder et al. 2014).

Overall, most research using IRT has been performed on domestic and cattle animals, usually with the aim of enhancing veterinary diagnosis (Cilulko et al. 2013), and we are not aware of systematic use of this technology on wild animals. This is despite the fact that IRT may help to shed light on fundamental questions in behavioural ecology, including sexual behaviour in mammalian females.

Here, we were interested in the thermal signature of female chimpanzees (*Pan troglodytes*) throughout the swelling cycle, in order to test theories in female reproductive behaviour. In chimpanzees and other catarrhine species living in multi-male societies, females tend to develop exaggerated swellings of the anogenital area during the periovulatory phase of their oestrous cycles (Nunn 1999). There has been considerable debate on the biological function of exaggerated swellings, and particularly on whether swelling size, or tumescence, constitutes a reliable indicator of fertility. In chimpanzees, males show most interest in females during maximal tumescence (Wallis 1992; Deschner et al. 2004) when ovulation is most likely to occur (Deschner et al. 2004). Gradual increase in swelling size is caused by increased oestrogen concentrations, while its sudden decrease is caused by increased progesterone secretion (Graham et al. 1972; Emery and Whitten 2003; Emery Thompson 2005). However, swelling size is only a probabilistic indicator of fertility in chimpanzees, because maximal swelling can last up to 21 days with a mean of about 13 days and thus maximal tumescence may exceed the phase of peak fertility (Emery Thompson 2005).

This has been interpreted as an evolved female strategy to prolong the period of sexual attractiveness and, by increasing the number of copulations with different males, confuse paternity (Nunn 1999; Alberts and Fitzpatrick 2012). Such a strategy is adaptive in species where males commit infanticide, as observed in several chimpanzee communities (Williams et al. 2008;

Goodall 1986; Nishida and Kawanaka 1985; Watts and Mitani 2000). In a first step, we were interested whether this seemingly strategically extended period of maximum tumescence, if compared to earlier phases, can be associated with a particular temperature profile. In a second step, we were interested in the temperature profiles of pregnant females, for which it has been suggested that they conceal gestation in an attempt to remain attractive to males (Wallis 1982). In particular, pregnant chimpanzee females continue to be sexually active, display sexual swellings despite being no longer able to conceive, in some instances even more so than cycling females (Wallis 1982). One functional explanation of this behavioural pattern is that, in doing so, pregnant females attempt to confuse paternity, which may lower the infanticidal tendencies of males once an infant is born.

To address these hypotheses, we investigated skin temperature of female chimpanzees in a wild group, the Sonso community of Budongo Forest, Uganda. To this end, we inspected the thermal patterns of pregnant and non-pregnant females to address the following predictions. First, for non-pregnant females we expected higher temperatures (particularly of the vulva) during estrous (when females show peak swelling sizes and when sexual proceptivity is higher (Wallis 1992)) compared to anoestral phases (when swelling is not maximally swollen and sexual proceptivity is comparably lower (Wallis 1992)). This was because, in farm animals, the skin temperature of the vulva is influenced by oestrogen secretion through increased blood. Related to this, we expected a gradual increase in skin temperature throughout the entire swelling cycle in the area of the reproductive organs, also because the ano-genital swelling relies on enhanced blood flow. Second, if pregnant females follow an evolved strategy to conceal their non-reproductive state when showing sexual tumescence, we predicted similarity in skin temperature at maximum tumescence between pregnant and non-pregnant females (when male mating efforts are typically

concentrated (Emery Thompson 2005)), compared to earlier swelling stages, when copulation is comparatively rare and ovulation unlikely.

## METHODS

**Study site** The study was carried out in the Budongo Forest Reserve, a moist semi-deciduous tropical forest in western Uganda, covering 428 km<sup>2</sup> at an altitude of 1,100 m, between 1°35' and 1°55'N and 31°08' and 31°42'E (Eggeling 1947). Data were collected from the Sonso community between November 2011 and May 2012, and between August 2013 and June 2014. Habituation of this community to humans began in 1990, with the majority of individuals (approximate *N* = 70) well habituated to human observers at the time of the study (Reynolds 2005). Permission to conduct the study was granted by the Ugandan Wildlife Authority (UWA) and the Uganda National Council for Science and Technology (UNCST). Ethics approval was given by the University of St Andrews' ethics committee.

**Materials** Surface skin temperature measurements were taken with a Testo (881-2) thermal imager, which operates between 8 and 14 μm with a thermal sensitivity of <80 mK at 30°C. Emissivity was set at 0.98, a value typically used for human skin (Steketee 1973). A telephoto lens was used for all images (9° x 7° / 0.5 m). The device emits no light or sound and is thus ideal for working with wild animals.

**Pregnancy status** We initially used HCG pregnancy tests (which respond to the presence of >25 mIU/ml human chorionic gonadotropin in the urine, a hormone produced by the placenta about one week after fertilisation), but later decided to estimate pregnancy status depending on the presence or absence of offspring 229 days after the recording was taken (assuming a mean gestation period of 229 days in chimpanzees (Reynolds 2005)). This was done because it was



119 only possible to perform one or two pregnancy tests for each individual, over a short time frame,  
120 so it is possible that some females may have been pregnant temporarily before or after testing.

121 ***Thermography data collection*** Data collection took place between 07:00 and 16:30 local time.  
122 On a given morning, a focal female individual was selected and followed throughout the day,  
123 with surrounding individuals sampled ad libitum. Although we considered all females during  
124 data collection, we later excluded 64 images of females that still had a dependent infant (defined  
125 as having an infant below 4 years old of age) and that did therefore not qualify as being either  
126 potentially receptive or pregnant. All sampled individuals were sufficiently tolerant to observer  
127 presence within 10m. Each body part (face, ears, nose, hands and feet, and swelling/genitals) was  
128 sampled only once every half hour with females contributing differently to the dataset (see Table  
129 1). For an image to be taken, the focal had to be within a distance of 15m (range: less than 1m–  
130 15m) and less than 5m above ground. They had to be in unobstructed view, in dry conditions  
131 (water alters the temperature and emissivity of skin) and not exposed to direct sunlight. Readings  
132 were taken from body parts that were exposed and free of fur. For each image, we estimated the  
133 distance to the focal individual (in metres). Ambient temperature and humidity were collected  
134 using an electronic recorder, as these may affect infra-red readings. Swelling size was  
135 determined by experienced field assistants from stage 0 (absence of tumescence) to stage 4  
136 (maximum tumescence) as judged by the degree of wrinkling (Furuichi 1987); (adapted for  
137 chimpanzees: Townsend et al., 2008). Importantly, the field assistants were blind to the aims and  
138 hypotheses of the study.

139 ***Image analysis*** Thermal images were analysed using the Testo IRTSoft analysis software. A  
140 polygon image selection tool was used on each image to select specific body parts of interest for  
141 subsequent thermal analysis. For each selected region of interest, we obtained the mean

142 temperature (see Figure 1 for examples). Two coders (GD and CW) performed the image  
143 analysis.

144 **Statistical analysis** We used a linear mixed model with Gaussian error structure and maximum  
145 likelihood estimation to assess how swelling stage and pregnancy affected skin temperature of  
146 female chimpanzees. In our initial model we fitted the two-way interaction between swelling  
147 stage and reproductive state. This also allowed us to specifically address the possibility that  
148 variation in temperature between swelling stages may show different patterns in pregnant and  
149 cycling females. In addition, we controlled for ambient temperature, humidity and distance  
150 between camera and subject. Because some images allowed simultaneous measurement of  
151 several body parts, we fitted image ID nested in subject ID as random intercept. In this way, we  
152 also accounted for multiple measurements of the same female. Furthermore, we fitted body part  
153 as random intercept. In addition, we allowed the effects of swelling stage and pregnancy state on  
154 surface temperature to vary between body parts by incorporating random slopes for these  
155 variables (Barr et al. 2013). Ideally, we would have incorporated similar random slopes for  
156 female ID, thereby allowing between subject variation in the effects of swelling and pregnancy  
157 on temperature. Unfortunately, we had to forego this step because the resulting model structure  
158 was too complex for our data set. Before model fitting, we inspected distributions of variables  
159 and transformed them to achieve symmetric distributions. In addition, we scaled all numeric  
160 variables to mean=0 and standard deviation=1 (Schiele 2010). We checked for homogeneity  
161 and normality of model residuals visually and calculated variance inflation factors (Fox and  
162 Weisberg 2010). Neither check indicated serious deviations from modelling assumptions. We  
163 then calculated Cook's distance as a measure for the influence of each single individual in our  
164 data set on our model results. Here we found a number of individuals with substantial influence

on our results. Specifically, Cook's distance for all four females in our data set that were pregnant during the study exceeded the critical threshold (c.f. Nieuwenhuis et al. 2012). Furthermore, we tested full models against our null models (see below) in a leave-one-out fashion to assess the potential influence of single females: we fitted the full and null model with a data set from which one female was excluded per turn. Here, one female (OK – see Table 1) led to the full model not being significant ( $p > 0.05$ ). Despite the consistency in the direction of this effect, the interaction must be interpreted with some caution, as their statistical significance hinges on one individual. However, the signs of our major result concerning the differences between pregnant and non-pregnant females remained consistent, regardless of which female we excluded.

To test the significance of our full model, we built an informed null model, which contained the random effect structure as described above and the three control fixed effects (ambient temperature, humidity, distance). We then tested our full model against this null model using a likelihood ratio test (LRT, Dobson and Barnett 2008). Similarly, we tested the interaction by comparing the model including the interaction (i.e. the full model) against a model without the interaction (swelling stage and reproductive state as main effects only). We calculated marginal and conditional  $R^2$  following Nakagawa and Schielzeth 2013 and Johnson 2014, using the MuMIn package (Bartoń 2016). We fitted all models in R 3.3.0 (Team 2016), using the lme4 package (v. 1.1-12, (Bates et al. 2015)).

## RESULTS

From the existing literature, we predicted an increase in temperature throughout the swelling cycle in non-pregnant chimpanzees, with a peak temperature at full tumescence, in particular at

187 the area of the reproductive organs, when females are in oestrous. Second, and following the  
188 hypothesis that chimpanzees have evolved physiological and behavioural strategies to conceal  
189 pregnancy, we predicted pregnant females to show similar patterns of skin temperature changes  
190 at peak tumescence when the probability of conception is at its highest for non-pregnant females.

191 To address the two predictions, we assessed skin temperature associated with swelling and  
192 reproductive state, at various body parts, controlling for ambient temperature, humidity and  
193 recording distance.

194 Our full model (containing swelling stage and reproductive state and their interaction plus the  
195 control terms: distance, humidity and ambient temperature) was significantly different from the  
196 null model (containing the control terms only) (LRT:  $\chi^2_9 = 19.48$ ,  $p = 0.0214$ ,  $R^2_m = 0.33$ ,  $R^2_c =$   
197  $0.90$ , Table 2). Concerning our variables of interest, reproductive state and swelling stage, we  
198 found that the model containing the interaction between the two was significantly different from  
199 a model from which the interaction term was removed (LRT:  $\chi^2_4 = 9.72$ ,  $p = 0.0455$ ).

200 Our results indicate that, overall, body temperature was more variable in pregnant than non-  
201 pregnant females. Generally, pregnant females had lower surface temperatures than cycling  
202 females when deflated and during smaller swelling stages (stages 0 – 2, Figure 2), of less than  
203  $1^\circ\text{C}$  overall. This pattern changed later in the cycle, with pregnant females having higher skin  
204 temperature compared to cycling females (stage 3, Figure 2), again with a magnitude of less than  
205  $1^\circ\text{C}$ . During maximum tumescence (swelling stage 4), temperatures of cycling and pregnant  
206 females appeared most similar compared to all other swelling stages. This was true for all body  
207 parts measured (Figures 3 and 4).

Finally, and contrary to our predictions, we did not find a clear increase in temperature throughout the swelling cycle (Figure 2), at the area of the reproductive organs and elsewhere (Figure 3). There was a modest increase in body temperature between stages 1-2 and stages 3-4, in both pregnant and cycling females, in particular around (but yet no restricted to) the vulvar area (Figure 3). Yet, we did not find a clear difference between the surface temperature at maximal swelling (where female proceptivity is higher (Wallis 1992)) and reduced swelling stages. Finally, skin temperature seems comparable or even slightly higher during detumescence than at maximum tumescence.

## DISCUSSION

Our aim was to assess whether skin temperature may reveal the reproductive state of female chimpanzees, using IRT, a well-developed technique in veterinary medicine, with yet little application so far in the field of behavioural ecology. In this study, we compared wild female chimpanzees throughout their swelling cycle and predicted that, (i) cycling females should show higher skin temperature when oestral than when anoestral, as well as an increase in skin temperature (with maximal temperature at the end of the swelling cycle, particularly at the area of the reproductive organs), following what had been found in the literature (Hilsberg-Merz 2008; Scolari 2011; Sykes et al. 2012; Talukder et al. 2014). We also predicted that (ii) pregnant females should match the temperature patterns exhibited by cycling females, despite their different hormonal state, at maximum swelling (stage 4) when male efforts are concentrated. This second prediction is based on the hypothesis that pregnant females will indeed have evolved gestation concealing strategies, as they incur an adaptive advantage in concealing pregnancy, to enhance the benefits of paternity confusion by promiscuous mating as long as possible.

Regarding prediction (i), our results showed slightly higher temperatures of the anogenital regions when transitioning from stages 1-2 to 3-4 (Figure 2), a pattern which may appear consistent with what as previously been found in other mammal species when approaching the periovulatory period (Hilsberg-Merz 2008; Scolari 2011; Sykes et al. 2012; Stelletta et al. 2013; Talukder et al. 2014). However, this pattern was true for most body parts considered, not solely for the anogenital region (Figure 3). Although it is hard to directly compare our results to previous studies using IRT because of definitions and study timeframes, we find that our estimated differences are similar or somewhat smaller in magnitude (about 1°C) to other studies (Scolari 2011; Sykes et al. 2012). In human and non-human female primates, skin colour and tone can change during the fertile period (Roberts et al. 2004; Dubuc et al. 2009), and such variation may be perceived by males (Higham et al. 2011). Consequently, the thermal signature associated with fertility may not be restricted to the periovulatory area but may also be visible within the facial and limbs regions. However, we did not find any difference in skin temperature between measures taken from anoestral and oestral stages in cycling females. This is inconsistent with the existing literature, and casts some doubt on the possibility that fertility is associated with a general thermal signature in female chimpanzees.

Regarding our second prediction, we found smaller changes in skin temperature in non-pregnant (cycling) compared to pregnant females. Crucially, for stage 4, we observed more similar skin temperatures between pregnant and non-pregnant females, compared to the other swelling stages (Figure 2), a pattern true for all body parts considered (Figure 3). Our data may therefore appear consistent with the prediction that, during gestation, chimpanzee females seek to approximate behavioural and physiological cues that characterise non-pregnant females. This could be part of an evolved strategy to remain sexually attractive to adult males and so to confuse paternity and

lower infanticide risk after parturition. It is also worth mentioning that pregnant females appear to show less clear transition in swelling stage patterns from swelling stages 1 to 4 if compared to cycling females. Instead, swelling sizes appear to change more erratically, and hence a probably simpler means for males would be to attend to gradation of swelling changes. Sexual swellings during pregnancy have also been reported in other non-human primates, such as sooty mangabeys (*Cercocebus torquatus atys*) (Gordon et al. 1991) or Barbary macaques (*Macaca sylvanus*) (Möhle et al. 2005), but in these species the swelling patterns between pregnant and non-pregnant females also seem to differ. Whether males are responsive to non-monotonic changes in swelling and, if so, whether this affects their mating behaviour and future infanticidal tendencies would be worth exploring.

It is also worth mentioning that other cues may help males approximate fertility during females' sexual swelling cycle. Olfactory signals are notably likely to play a role in helping males detect fertility in females (Michael and Zumpe 1982). In humans (*Homo sapiens*), female body odour close to ovulation is preferred by males (Gildersleeve et al. 2012), a pattern also present in some non-human primates (Ziegler et al. 1993; Converse et al. 1995; Clarke et al. 2009); however so far there is no evidence of this in chimpanzees (Fox 1982). Visual signals may also play a role. In human and non-human female primates, skin colour and tone can change during the fertile period (Roberts et al. 2004; Dubuc et al. 2009), and such variation may be perceived by males (Higham et al. 2011). Finally, female sexual behaviour itself can reveal the most fertile period of the swelling cycle (e.g., Engelhardt et al. 2005). Future studies should also investigate whether cycling vs. pregnant females may show difference in those behaviours.

We see a number of limitations to this research. First, we did not find a clear increase in skin temperature when comparing the oestrous and the anoestral stages. Second, only four pregnant

females contributed to our dataset, so it would be important to replicate these findings with a larger sample of pregnant females. Third, we did not collect any hormonal data and were therefore unable to determine the point of likely ovulation. A validation study clearly is necessary, and seems largely feasible in captive settings, where hormonal measurements can be more easily collected. Fourth and finally, we had no behavioural data to show that males are directly responsive to changes in skin temperature, and can be deceived by pregnant females who may have similar skin temperature profiles as fertile individuals. Nevertheless, we consider this a likely possibility, mainly because shifts in blood flow, and their corresponding changes in skin temperature, may affect skin colouration in the face and elsewhere, which can be perceived by recipients (Hiramatsu et al. 2017).

In sum, our data appear consistent with the prediction that, during gestation, chimpanzee females not only approximate behavioural and visual cues that characterise non-pregnant females, but also physiological cues. However, we offer inconclusive evidence of a thermal pattern associated with fertility, as skin temperature indeed seems to increase throughout the swelling cycle, but with no clear differences in skin temperature compared to when females are anoestral. Our research yet offers a tentative exploration of changes in skin temperature associated with fertility and pregnancy in wild female chimpanzees, which future research can build on, using a technology, which has not or seldom been used to tackle fundamental questions in the field of behavioural ecology.

## ETHICAL STATEMENT



297 The research was supported by a Fyssen fellowship awarded to GD, and has received funding  
298 from the European Union's Seventh Framework Programme for research, technological  
299 development and demonstration under grant agreement no 283871.

300 The authors declare no conflict of interest.

301 Permission to conduct the study was granted by the Ugandan Wildlife Authority (UWA) and the  
302 Uganda National Council for Science and Technology (UNCST). Ethics approval was given by  
303 the University of St Andrews' ethics committee.

304 Informed consent: non-applicable

## 305 **ACKNOWLEDGMENTS**

306 We thank UWA and UNCST for permission to conduct the study. Our gratitude goes to Geoffrey  
307 Muhanguzi, Caroline Asiimwe, Geresomu Muhumuza, Bosco Chandia and Sam Adué for their  
308 support in the field. We further thank Cat Hobaiter, Roman Wittig, Dave Perrett, William  
309 Paterson, Dominic McCafferty, Ross Whitehead, Amanda Hahn and Brittany Fallon for helpful  
310 discussions. We are grateful to the Royal Zoological Society of Scotland for providing core  
311 funding to the Budongo Conservation Field Station.

## 312 **REFERENCES**

- 313 Alberts SC, Fitzpatrick CL (2012) Paternal care and the evolution of exaggerated sexual swellings in  
314 primates. *Behav Ecol* 23:699–706. doi: 10.1093/beheco/ars052
- 315 Barr DJ, Levy R, Scheepers C, Tily HJ (2013) Random effects structure for confirmatory hypothesis  
316 testing: Keep it maximal. *J Mem Lang* 68:255–278.
- 317 Bartoń K (2016) MuMIn: Multi-Model Inference.
- 318 Bates D, Mächler M, Bolker B, Walker S (2014) Fitting Linear Mixed-Effects Models using lme4.

- 319 Cilulko J, Janiszewski P, Bogdaszewski M, Szczypińska E (2013) Infrared thermal imaging in studies of  
320 wild animals. *Eur J Wildl Res* 59:17–23.
- 321 Clarke PMR, Barrett L, Henzi SP (2009) What role do olfactory cues play in chacma baboon mating? *Am J*  
322 *Primatol* 71:493–502. doi: 10.1002/ajp.20678
- 323 Converse LJ, Carlson AA, Ziegler TE, Snowdon CT (1995) Communication of ovulatory state to mates by  
324 female pygmy marmosets, *Cebuella pygmaea*. *Anim Behav* 49:615–621. doi: 10.1016/0003-  
325 3472(95)80194-4
- 326 Deschner T, Heistermann M, Hodges K, Boesch C (2004) Female sexual swelling size, timing of ovulation,  
327 and male behavior in wild West African chimpanzees. *Horm Behav* 46:204–215.
- 328 Dezechache G, Zuberbühler K, Davila-Ross M, Dahl CD (2017) Skin temperature changes in wild  
329 chimpanzees upon hearing vocalizations of conspecifics. *Open Sci* 4:160816. doi:  
330 10.1098/rsos.160816
- 331 Dobson AJ, Barnett A (2008) An introduction to generalized linear models. CRC press
- 332 Dubuc C, Brent LJ, Accamando AK, et al (2009) Sexual skin color contains information about the timing of  
333 the fertile phase in free-ranging *Macaca mulatta*. *Int J Primatol* 30:777–789.
- 334 Eggeling WJ (1947) Observations on the ecology of the Budongo rain forest, Uganda. *J Ecol* 20–87.
- 335 Emery MA, Whitten PL (2003) Size of sexual swellings reflects ovarian function in chimpanzees (*Pan*  
336 *troglodytes*). *Behav Ecol Sociobiol* 54:340–351.
- 337 Emery Thompson M (2005) Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes*  
338 *schweinfurthii*): methodological considerations and the role of hormones in sex and conception.  
339 *Am J Primatol* 67:137–158.
- 340 Engelhardt A, Hodges JK, Niemitz C, Heistermann M (2005) Female sexual behavior, but not sex skin  
341 swelling, reliably indicates the timing of the fertile phase in wild long-tailed macaques (*Macaca*  
342 *fascicularis*). *Horm Behav* 47:195–204.
- 343 Fox GJ (1982) Potentials for Pheromones in Chimpanzee Vaginal Fatty Acids. *Folia Primatol* (Basel)  
344 37:255–266. doi: 10.1159/000156036
- 345 Fox J, Weisberg S (2010) An R companion to applied regression. Sage
- 346 Furuichi T (1987) Sexual swelling, receptivity, and grouping of wild pygmy chimpanzee females at  
347 Wamba, Zaire. *Primates* 28:309–318.
- 348 Gildersleeve KA, Haselton MG, Larson CM, Pillsworth EG (2012) Body odor attractiveness as a cue of  
349 impending ovulation in women: Evidence from a study using hormone-confirmed ovulation.  
350 *Horm Behav* 61:157–166. doi: 10.1016/j.yhbeh.2011.11.005
- 351 Goodall J (1986) The chimpanzees of Gombe: Patterns of behavior.

- 352 Gordon TP, Gust DA, Busse CD, Wilson ME (1991) Hormones and sexual behavior associated with  
353 postconception perineal swelling in the sooty mangabey (*Cercocebus torquatus atys*). *Int J*  
354 *Primatol* 12:585–597. doi: 10.1007/BF02547671
- 355 Graham CE, Collins DC, Robinson H, Preedy JRK (1972) Urinary levels of estrogens and pregnanediol and  
356 plasma levels of progesterone during the menstrual cycle of the chimpanzee: relationship to the  
357 sexual swelling. *Endocrinology* 91:13–24.
- 358 Higham JP, Hughes KD, Brent LJN, et al (2011) Familiarity affects the assessment of female facial signals  
359 of fertility by free-ranging male rhesus macaques. *Proc R Soc Lond B Biol Sci* rspb20110052. doi:  
360 10.1098/rspb.2011.0052
- 361 Hilsberg-Merz S (2008) Infrared thermography in zoo and wild animals. *Zoo Wild Anim Med Curr Ther*  
362 20–32.
- 363 Hiramatsu C, Melin AD, Allen WL, et al (2017) Experimental evidence that primate trichromacy is well  
364 suited for detecting primate social colour signals. *Proc R Soc B* 284:20162458. doi:  
365 10.1098/rspb.2016.2458
- 366 Ioannou S, Chotard H, Davila-Ross M (2015) No strings attached: physiological monitoring of rhesus  
367 monkeys (*Macaca mulatta*) with thermal imaging.
- 368 Ioannou S, Gallese V, Merla A (2014) Thermal infrared imaging in psychophysiology: potentialities and  
369 limits. *Psychophysiology* 51:951–963.
- 370 Johnson PC (2014) Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. *Methods*  
371 *Ecol Evol* 5:944–946.
- 372 Kano F, Hirata S, Deschner T, et al (2016) Nasal temperature drop in response to a playback of  
373 conspecific fights in chimpanzees: A thermo-imaging study. *Physiol Behav* 155:83–94.
- 374 Kuraoka K, Nakamura K (2011) The use of nasal skin temperature measurements in studying emotion in  
375 macaque monkeys. *Physiol Behav* 102:347–355.
- 376 Michael RP, Zumpe D (1982) Influence of olfactory signals on the reproductive behaviour of social  
377 groups of rhesus monkeys (*Macaca mulatta*). *J Endocrinol* 95:189–205. doi:  
378 10.1677/joe.0.0950189
- 379 Möhle U, Heistermann M, Dittami J, et al (2005) Patterns of anogenital swelling size and their endocrine  
380 correlates during ovulatory cycles and early pregnancy in free-ranging barbary macaques  
381 (*Macaca sylvanus*) of Gibraltar. *Am J Primatol* 66:351–368. doi: 10.1002/ajp.20161
- 382 Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear  
383 mixed-effects models. *Methods Ecol Evol* 4:133–142.
- 384 Nakayama K, Goto S, Kuraoka K, Nakamura K (2005) Decrease in nasal temperature of rhesus monkeys  
385 (*Macaca mulatta*) in negative emotional state. *Physiol Behav* 84:783–790.

- 386 Nieuwenhuis R, te Grotenhuis HF, Pelzer BJ (2012) Influence. ME: tools for detecting influential data in  
387 mixed effects models.
- 388 Nishida T, Kawanaka K (1985) Within-group cannibalism by adult male chimpanzees. *Primates* 26:274–  
389 284. doi: 10.1007/BF02382402
- 390 Nunn CL (1999) The evolution of exaggerated sexual swellings in primates and the graded-signal  
391 hypothesis. *Anim Behav* 58:229–246. doi: 10.1006/anbe.1999.1159
- 392 Reynolds V (2005) The chimpanzees of the Budongo Forest: ecology, behaviour, and conservation.  
393 Oxford University Press
- 394 Riemer S, Assis L, Pike TW, Mills DS (2016) Dynamic changes in ear temperature in relation to separation  
395 distress in dogs. *Physiol Behav* 167:86–91.
- 396 Roberts SC, Havlicek J, Flegr J, et al (2004) Female facial attractiveness increases during the fertile phase  
397 of the menstrual cycle. *Proc R Soc Lond B Biol Sci* 271:S270–S272. doi: 10.1098/rsbl.2004.0174
- 398 Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods*  
399 *Ecol Evol* 1:103–113.
- 400 Scolari SC (2011) Vulvar skin temperature changes significantly during estrus in swine as determined by  
401 digital infrared thermography. *J Swine Health Prod* 19:151–155.
- 402 Steketee J (1973) Spectral emissivity of skin and pericardium. *Phys Med Biol* 18:686.
- 403 Stelletta C, Vencato J, Fiore E, Ganesella M (2013) Infrared thermography in reproduction. *Thermogr*  
404 *Curr Status Adv Livest Anim Vet Med Rome Brescia* 113–125.
- 405 Sykes DJ, Couvillion JS, Cromiak A, et al (2012) The use of digital infrared thermal imaging to detect  
406 estrus in gilts. *Theriogenology* 78:147–152.
- 407 Talukder S, Kerrisk KL, Ingenhoff L, et al (2014) Infrared technology for estrus detection and as a  
408 predictor of time of ovulation in dairy cows in a pasture-based system. *Theriogenology* 81:925–  
409 935. doi: 10.1016/j.theriogenology.2014.01.009
- 410 Team RC (2016) R: A language and environment for statistical computing. R Foundation for Statistical  
411 Computing, Vienna, Austria. 2015. URL h ttp.
- 412 Townsend SW, Deschner T, Zuberbühler K (2008) Female Chimpanzees Use Copulation Calls Flexibly to  
413 Prevent Social Competition. *PLoS ONE* 3:e2431. doi: 10.1371/journal.pone.0002431
- 414 Travain T, Colombo ES, Grandi LC, et al (2016) How good is this food? A study on dogs’ emotional  
415 responses to a potentially pleasant event using infrared thermography. *Physiol Behav* 159:80–  
416 87.
- 417 Travain T, Colombo ES, Heinzl E, et al (2015) Hot dogs: Thermography in the assessment of stress in dogs  
418 (*Canis familiaris*)—A pilot study. *J Vet Behav Clin Appl Res* 10:17–23.

- 419 Wallis J (1992) Chimpanzee genital swelling and its role in the pattern of sociosexual behavior. *Am J*  
420 *Primatol* 28:101–113. doi: 10.1002/ajp.1350280203
- 421 Wallis J (1982) Sexual behavior of captive chimpanzees (*Pan troglodytes*): Pregnant versus cycling  
422 females. *Am J Primatol* 3:77–88. doi: 10.1002/ajp.1350030107
- 423 Watts DP, Mitani JC (2000) Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National  
424 Park, Uganda. *Primates* 41:357–365.
- 425 Williams JM, Lonsdorf EV, Wilson ML, et al (2008) Causes of death in the Kasekela chimpanzees of  
426 Gombe National Park, Tanzania. *Am J Primatol* 70:766–777.
- 427 Ziegler TE, Eppele G, Snowdon CT, et al (1993) Detection of the chemical signals of ovulation in the  
428 cotton-top tamarin, *Saguinus oedipus*. *Anim Behav* 45:313–322. doi: 10.1006/anbe.1993.1036
- 429

## 430 FIGURE CAPTIONS

- 431 **Figure 1** Example of IRT measurements for the ear (A) and anogenital swelling (B).
- 432 **Figure 2** Model results for differences in body surface temperature. Shown is the interaction  
433 between swelling stage and pregnancy status, using back-transformed model estimates and  
434 associated 95% confidence intervals.
- 435 **Figure 3** Model predictions for surface temperature of female chimpanzees per body part for  
436 cycling and pregnant females.
- 437 **Figure 4** Median surface temperature with 25% and 75% quartiles, of female chimpanzees per  
438 body part for cycling and pregnant females.

439

## 440 TABLES

- 441 **Table 1** Distribution of images per female (ID) and by reproductive condition (Cycling and  
442 Pregnant)

Female ID	Cycling	Pregnant
AN	9	0
HL	3	0
IN	2	0
JN	61	58
JT	39	0
KA	5	0
KL	24	55
KM	6	0
KN	19	0
KR	40	0
KU	4	72
KW	52	0
KY	38	0
ML	38	0
MN	6	0
NB	100	0
NT	100	0
OK	68	91
RH	12	0
RS	29	0
<b>Total</b>	<b>655</b>	<b>276</b>

443

444 **Table 2** Results of full model. Reference level for pregnancy was 'not pregnant' (i.e. cycling)

445 and for swelling stage '0'. *t* values for main effects comprised in interactions are omitted.

	Parameter estimate	Standard error	<i>t</i> value
Intercept	168.15	11.44	14.70
Swelling stage 1	-7.44	6.91	
Swelling stage 2	-13.94	7.77	
Swelling stage 3	-3.72	5.38	
Swelling stage 4	-12.26	6.52	
Pregnancy	-11.32	6.33	

Ambient temperature	29.65	2.17	13.69
Distance	-4.66	1.38	-3.37
Humidity	-4.89	2.21	-2.21
Swelling stage 1: pregnancy	2.36	8.98	0.26
Swelling stage 2: pregnancy	-19.81	10.82	-1.83
Swelling stage 3: pregnancy	17.62	10.32	1.71
Swelling stage 4: pregnancy	9.98	9.30	1.07

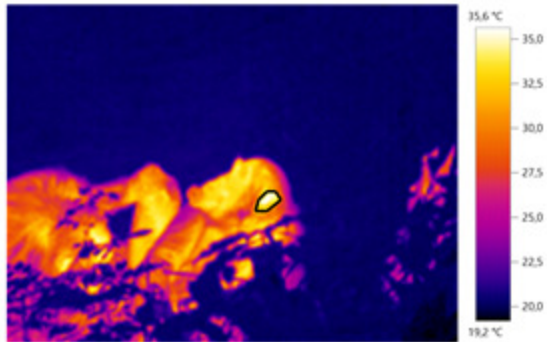
# **Figure 1**(on next page)

Figure 1

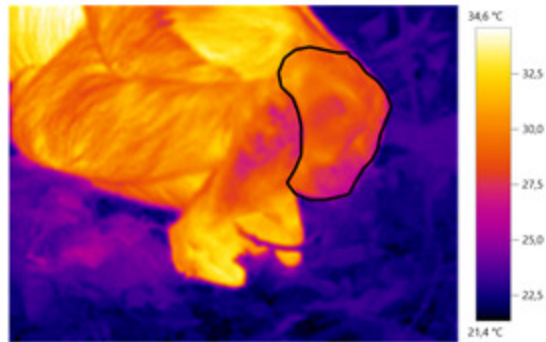
Example of IRT measurements for the ear (A) and anogenital swelling (B).



A



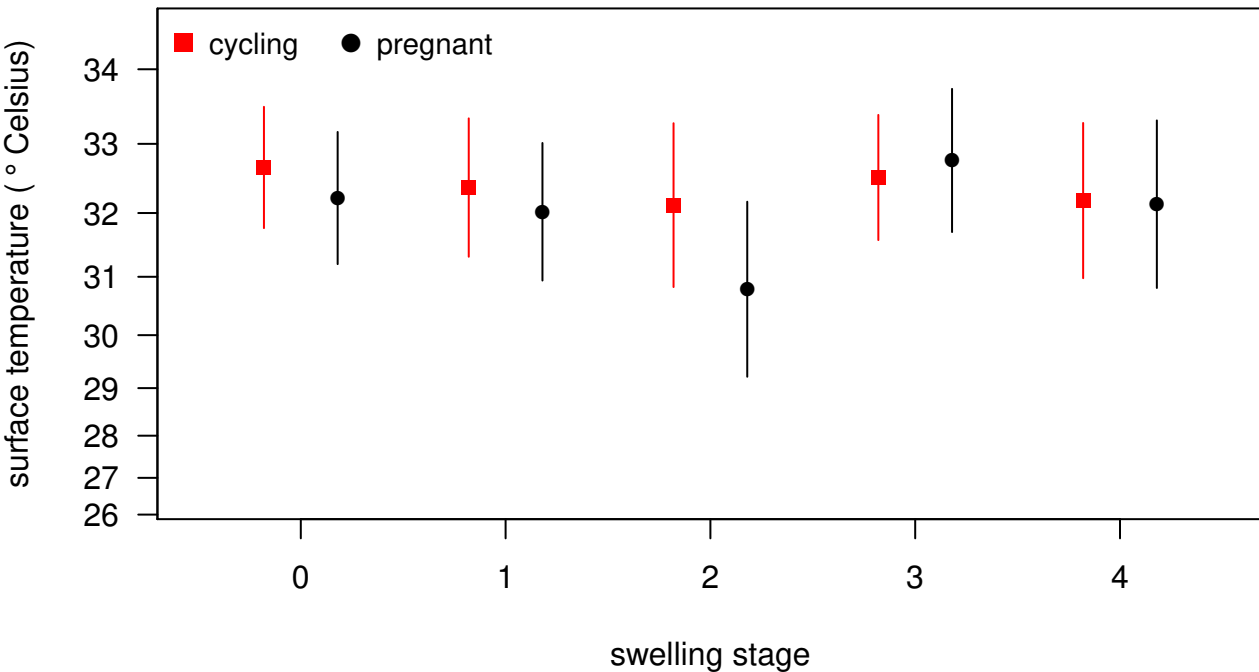
B



## Figure 2 (on next page)

### Figure 2

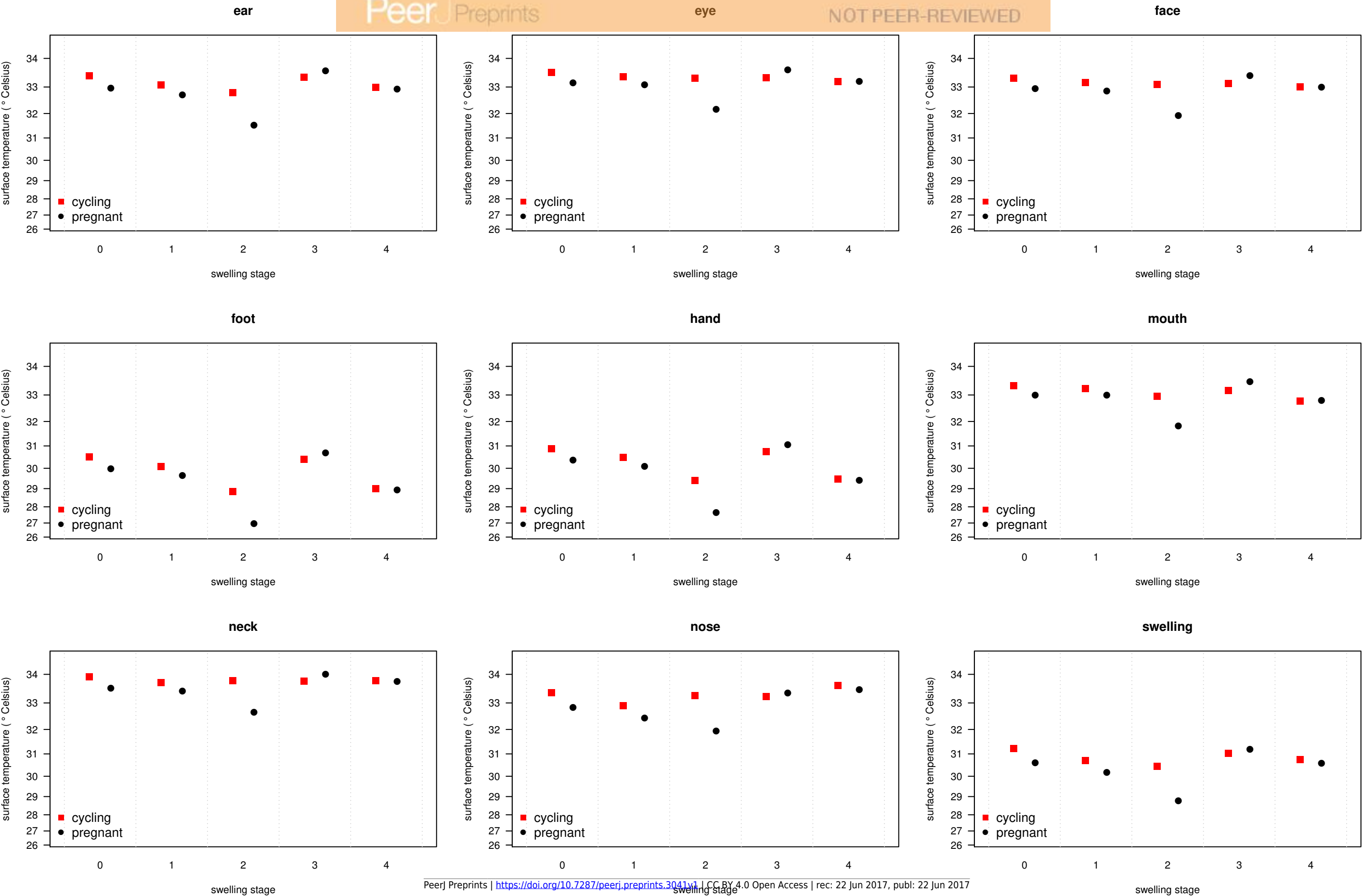
Model results for differences in body surface temperature. Shown is the interaction between swelling stage and pregnancy status, using back-transformed model estimates and associated 95% confidence intervals.



# **Figure 3**(on next page)

## Figure 3

Model predictions for surface temperature of female chimpanzees per body part for cycling and pregnant females



# Figure 4(on next page)

## Figure 4

Median surface temperature with 25% and 75% quartiles, of female chimpanzees per body part for cycling and pregnant females.

surface temperature ( ° Celsius)

