Skin temperature and reproductive condition in wild female chimpanzees

Guillaume Dezecache [Corresp., 1, 2] , **Claudia Wilke** [2, 3, 4] , **Nathalie Richi** [1, 2] , **Christof Neumann** [1] , **Klaus Zuberbühler** [1, 2, 3]

1 Institute of Biology, Université de Neuchâtel, Neuchâtel, Switzerland

2 Budongo Conservation Field Station, Masindi, Uganda

3 School of Psychology and Neuroscience, University of St. Andrews, Fife, United Kingdom

4 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 for evaluating reproductive processes. Here, we explored differences in skin temperature of twenty female chimpanzees in Budongo Forest, Uganda, four of which were pregnant during data collection. Based on previous literature in other mammals, we predicted increased skin temperature of maximally swollen reproductive organs of non-pregnant females when approaching peak fertility. For pregnant females, we made the same prediction because it has been argued that female chimpanzees have evolved mechanisms to conceal pregnancy, including swellings of the reproductive organs, conspicuous copulation calling, and solicitation of male mating behaviour, to decrease the infanticidal tendencies of resident males by confusing paternity. For non-pregnant females, we found slight temperature increases towards the end of the swelling cycles but no significant change between the fertile and non-fertile phases. Despite their different reproductive state, pregnant females had very similar skin temperature patterns compared to non-pregnant females, suggesting little potential for males to use skin temperature to recognise pregnancies, especially during maximal swelling, when ovulation is most likely to occur in non-pregnant females. We discuss this pattern in light of the concealment hypothesis, i.e., that female chimpanzees have evolved physiological means to conceal their reproductive state during pregnancy.

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2 Guillaume Dezecache[1,2], Claudia Wilke[2,3,4], Nathalie Richi[1,2], Christof Neumann[1*] & Klaus

3 Zuberbühler[1,2,3*]

4 [1]Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland; [2]Budongo Conservation

5 Field Station, Masindi, Uganda; [3]School of Psychology and Neuroscience, University of St

6 Andrews, Fife, Scotland, United Kingdom; [4]Department of Psychology, University of York,

7 York, United Kingdom

8 *equal contribution

9 Corresponding author: Guillaume Dezecache guillaume.dezecache@gmail.com

11 **ABSTRACT**

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13 evaluating reproductive processes. Here, we explored differences in skin temperature of twenty

14 female chimpanzees in Budongo Forest, Uganda, four of which were pregnant during data

15 collection. Based on previous literature in other mammals, we predicted increased skin

16 temperature of maximally swollen reproductive organs of non-pregnant females when

17 approaching peak fertility. For pregnant females, we made the same prediction because it has

18 been argued that female chimpanzees have evolved mechanisms to conceal pregnancy, including

19 swellings of the reproductive organs, conspicuous copulation calling, and solicitation of male

20 mating behaviour, to decrease the infanticidal tendencies of resident males by confusing

21 paternity. For non-pregnant females, we found slight temperature increases towards the end of

22 the swelling cycles but no significant change between the fertile and non-fertile phases. Despite

23 their different reproductive state, pregnant females had very similar skin temperature patterns

24 compared to non-pregnant females, suggesting little potential for males to use skin temperature

25 to recognise pregnancies, especially during maximal swelling, when ovulation is most likely to

26 occur in non-pregnant females. We discuss this pattern in light of the concealment hypothesis,

27 i.e., that female chimpanzees have evolved physiological means to conceal their reproductive

28 state during pregnancy.

INTRODUCTION

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

IRT has also been used as a non-invasive technique to study reproductive processes of animals (Cilulko et al., 2013). For example, Hilsberg-Merz (2008) noticed that female Asian elephants (*Elephas maximus*) and Black rhinoceroses (*Diceros bicornis*) showed increased surface temperature in the area of their reproductive organs during oestrus, a pattern associated with increased attractiveness to males. In pigs, vulvar skin temperatures were higher during oestrus compared to dioestrus (Sykes et al., 2012), a pattern related to increased blood flow towards the vulva due to oestrogen secretion in the ovarian follicles (Stelletta et al., 2013). Heightened temperature of the area of the reproductive organs can be used as a tool to detect oestrus in cows, with vulva temperature peaks around 24 hours before ovulation, followed by a slight decrease towards ovulation (Talukder et al., 2014). Furthermore, it has been suggested that thermo-

53   reception may constitute a sensory strategy used by males in mammal species in order to detect

54   ovulation in females (Hilsberg-Merz, 2008), possibly in conjunction with other cues.

55   In sum, most current research using IRT has been performed on domestic and farm mammals,

56   usually in the context of veterinary diagnosis (Cilulko et al., 2013), with only little systematic

57   use in studying natural patterns, including sexual behaviour.

58

59   Here, we were interested in the skin temperature of wild female chimpanzees (*Pan troglodytes*)

60   throughout the swelling cycle. The swelling cycle can be defined as the cyclical change during

61   which a female's anogenital region gets progressively swollen and increases in size before

62   reaching maximal tumescence, followed by detumescence, whereby the swelling area shows a

63   rapid decrease in size and the skin becomes loose (Wallis, 1992; Deschner et al., 2004). In

64   chimpanzees and other catarrhine species living in multi-male societies, females tend to develop

65   exaggerated anogenital swellings during the periovulatory phase of their menstrual cycles (Nunn,

66   1999). There has been considerable debate on the biological function of exaggerated swellings,

67   particularly in regard to whether swelling size, or tumescence, constitutes a reliable indicator of

68   fertility. In chimpanzees, males show most interest in females during maximal tumescence

69   (Wallis, 1992; Deschner et al., 2004) when ovulation is most likely to occur (Deschner et al.,

70   2004). Gradual swelling tumescence is caused by increased oestrogen concentrations, while its

71   sudden decrease is caused by increased progesterone secretion (Graham et al., 1972; Emery &

72   Whitten, 2003; Emery Thompson, 2005). However, swelling size is only a probabilistic indicator

73   of fertility in chimpanzees, because maximal swelling can last up to 21 days with a mean of

74   about 13 days and thus maximal tumescence may exceed the phase of peak fertility (Emery

75   Thompson, 2005). This has been interpreted as an evolved female strategy to prolong the period

76   of sexual attractiveness and, by increasing the number of copulations with different males, to

77   confuse paternity (Nunn, 1999; Alberts & Fitzpatrick, 2012). Such a strategy is adaptive in

78   species where males commit infanticide, as is commonly observed across chimpanzee

79   communities (Williams et al., 2008; Goodall, 1986; Nishida & Kawanaka, 1985; Watts &

80   Mitani, 2000; Wilson et al., 2014).

81

82   As a first step, we were interested in whether the period of maximum tumescence, if compared to

83   earlier phases, can be identified by a unique temperature profile. In a second step, we were

84   interested in the temperature profiles of pregnant females, who have been suggested to conceal

85   their gestation in an attempt to remain attractive to males (Wallis, 1982). Pregnant chimpanzee

86   females continue to be sexually active and display sexual swellings despite being no longer able

87   to conceive. It has been suggested that the maximal anogenital swelling during pregnancy may

88   account for one fourth of the total time female chimpanzees display maximal tumescence during

89   their reproductive lifetime (Wallis & Goodall, 1993). Pregnant females are, in some instances,

90   even more sexually active than non-pregnant females (Wallis, 1982). One functional explanation

91   of this behavioural pattern is that pregnant females attempt to confuse paternity in the males of

92   their group, which may lower the infanticidal tendencies of males once an infant is born (Wallis

93   & Goodall, 1993).

94

95   Based on these findings, we hypothesised that variation in skin temperature may provide cues

96   about the three main reproductive stages of a female, that is to say, pregnancy, oestrus, non-

97   oestrus. However, based on the literature reviewed, female chimpanzees appear to have evolved

98   ways to conceal their true reproductive stage, particularly pregnancy, but also the exact time of

99   ovulation (Townsend, Deschner & Zuberbühler, 2011). If males perceive changes in skin

100   temperature, then selection should favour individuals with skin temperature profiles that do not

101   reveal their reproductive condition.

102   To address these hypotheses, we investigated skin temperature of female chimpanzees in the

103   Sonso community of Budongo Forest, Uganda. We inspected the thermal patterns of pregnant

104   and non-pregnant females to test the following predictions. First, for non-pregnant females, we

105   expected higher temperatures (particularly of the genital area) during the fertile phase (when

106   females show peak swelling sizes and when sexual proceptivity is highest [Wallis, 1992])

107   compared to non-fertile phases (when swellings are not maximally inflated and sexual

108   proceptivity is comparably lower [(Wallis, 1992]). This was expected because, in farm animals,

109   the skin temperature of the vulva can be influenced by oestrogen secretion through increased

110   blood flow (Stelletta et al., 2013).

111

112   Second, if pregnant females follow an evolved strategy to conceal their pregnancy when showing

113   sexual tumescence, we predicted similarity in skin temperature at maximum tumescence between

114   pregnant and non-pregnant females (when male mating efforts are typically concentrated, see

115   Wallis [1992]), compared to earlier swelling stages, when copulation is comparatively rarer and

116   ovulation unlikely.

117

118   **METHODS**

119   ***Ethical statement*** Permission to conduct the study was granted by the Ugandan Wildlife

120   Authority (UWA) (UWA/TDO/33/02) and the Uganda National Council for Science and

121 Technology (UNCST) (NS-475). Ethical approval was given by the University of St Andrews'

122 ethics committee.

123 *Study site* The study was carried out in the Budongo Forest Reserve, a moist semi-deciduous

124 tropical forest in western Uganda, covering 428 km^2 at an altitude of 1,100 m, between 1° 35ʹ

125 and 1° 55ʹ N and 31° 08ʹ and 31° 42ʹ E (Eggeling, 1947). Data were collected from the

126 Sonso community between November 2011 and May 2012, and between August 2013 and June

127 2014. Habituation of this community to humans began in 1990, with the majority of individuals

128 (approximate N = 70) well habituated to human observers at the time of the study (Reynolds,

129 2005).

130

131 *Materials* Surface skin temperature measurements were taken with a Testo (881-2) thermal

132 imager, which operates between 8 and 14 μm with a thermal sensitivity of <80 mK at 30°C.

133 Emissivity was set at 0.98, a value typically used for human skin (Steketee, 1973). A telephoto

134 lens was used for all images (9° x 7° / 0.5 m). The device emits no light or sound and is thus

135 ideal for working with wild animals.

136

137 *Pregnancy status* We initially used HCG pregnancy tests (which respond to the presence of >25

138 mI U/ml human chorionic gonadotropin in the urine, a hormone produced by the placenta about

139 one week after fertilisation). We later decided to estimate pregnancy status depending on the

140 presence or absence of offspring up to 229 days after the recording was taken (assuming a mean

141 gestation period of 229 days in chimpanzees [Reynolds, 2005]). This was done because it was

142 only possible to perform one or two pregnancy tests for each individual, over a short time frame,

143   so it is possible that some females may have been pregnant temporarily before or after testing.

144   Additionally, a more recent pilot study suggested that HCG pregnancy tests are unreliable in

145   wild chimpanzees, with pregnant females testing negative around their fifth month of gestation

146   (Caroline Asiimwe, personal communication).

147   As we relied upon the presence/absence of offspring after the average gestation period of

148   chimpanzees, it is possible that some females we designated as 'not pregnant' may have been in

149   the early stages of pregnancy when thermal images were recorded, without carrying the

150   pregnancy to term. Stillbirths and miscarriages are difficult to distinguish in the wild (Courtenay

151   & Santow, 1989) (but see Tutin [1975]). Studies in captivity indicate that miscarriages may

152   happen in around 8% of the pregnancies (Courtenay, 1987) and fetal wastage (miscarriage and

153   stillbirths) may occur following 14% of all conceptions (Littleton, 2005).

154   ***Thermography data collection*** Data collection took place between 07:00 and 16:30 local time.

155   On a given morning, a female was selected as the focal animal and followed throughout the day

156   with IRT photographs taken whenever the individual was in clear view, and photographs taken

157   of surrounding individuals ad libitum. Although we considered all females during data

158   collection, we later excluded 64 images of females with dependent infants (<4 years). Although

159   some of them may have been cycling, we excluded them because of difficulties in determining

160   their reproductive status.

161

162   All sampled individuals (20 females, 4 of which were pregnant during parts of data collection)

163   were sufficiently tolerant to observer presence within 10m. Each body part (face, ears, nose,

164   hands and feet, and swelling/genitals) was sampled only once every half hour with females

165   contributing differently to the dataset (see Table 1). For an image to be taken, the focal had to be

166   within a distance of 15m (range: less than 1m–15m) and less than 5m above ground. They had to

167   be in unobstructed view, with a body part clearly visible to the observer and in dry conditions

168   (water alters the temperature and emissivity of skin) and not exposed to direct sunlight. Readings

169   were taken from body parts that were exposed and free of hair. For each image, we estimated the

170   distance to the focal individual (in metres). Ambient temperature and humidity data were

171   collected using an electronic recorder, as these may affect infra-red readings. Swelling

172   tumescence was determined by experienced field assistants from stage 0 (absence of tumescence)

173   to stage 4 (maximum tumescence) as judged by the degree of wrinkling (Furuichi, 1987)

174   (adapted for chimpanzees: Townsend et al. [2008]). Note that the field assistants were blind to

175   the aims and hypotheses of the study.

176   ***Image analysis*** Thermal images were analysed using the Testo IRSoft analysis software. A

177   polygon image selection tool was used on each image to select specific body parts of interest for

178   subsequent thermal analysis. For each selected region of interest, we obtained the mean

179   temperature (see Figure 1 for example). Two coders (GD and CW) performed the image

180   analysis. To test for inter-observer reliability, we examined measurements of N=408 thermal

181   images taken by two coders. There was a mean difference of 0.15 +/- 0.43°C (mean difference

182   between the two sets of measurements +/- SD) between the two sets of measurements, with high

183   internal consistency (Cronbach's alpha, α = 0.99), suggesting that our method of calculating the

184   average temperature of an area of interest was consistent.

185   ***Statistical analysis*** We used a linear mixed model with Gaussian error structure and maximum

186   likelihood estimation to assess how swelling stage and pregnancy affected skin temperature of

187   female chimpanzees. In our initial model, we fitted the two-way interaction between swelling

188   stage and reproductive state. This also allowed us to specifically address the possibility that

189   variation in temperature between swelling stages may show different patterns in pregnant and

190   non-pregnant females. In addition, we controlled for ambient temperature, humidity and distance

191   between camera and subject. Because some images allowed simultaneous measurement of

192   several body parts, we fitted image ID nested in subject ID as random intercept. In this way, we

193   also accounted for multiple measurements of the same female. We fitted body part as random

194   intercept and in addition, allowed the effects of swelling stage and pregnancy state on skin

195   temperature to vary between body parts by incorporating random slopes for these variables (Barr

196   et al., 2013). Ideally, we would have incorporated similar random slopes for female ID, thereby

197   allowing between subject variation in the effects of swelling and pregnancy on temperature.

198   Unfortunately, we had to forego this step because the resulting model structure was too complex

199   for our data set. Before model fitting, we inspected distributions of variables and transformed

200   them to achieve symmetric distributions (see Supplementary Information). In addition, we scaled

201   all numeric variables to mean=0 and standard deviation=1 (Schielzeth, 2010). We checked for

202   homogeneity and normality of model residuals visually and calculated variance inflation factors

203   (Fox & Weisberg, 2010). Neither check indicated serious deviations from modelling

204   assumptions. We then calculated Cook's distance as a measure for the influence of each single

205   individual in our data set on our model results. Here we found a number of individuals with

206   substantial influence on our results. Specifically, Cook's distance for all four females in our data

207   set that were pregnant during the study exceeded the critical threshold (c.f. Nieuwenhuis, te

208   Grotenhuis & Pelzer [2012]). Furthermore, we tested full models against our null models (see

209   below) in a leave-one-out fashion to assess the potential influence of single females: we fitted the

210   full and null model with a data set from which one female was excluded per turn. Here,

211   exclusion of one female (OK – see Table 1) led to the full model not being significant (p > 0.05),

212 although the signs of the parameter estimates remained unchanged. Despite this consistency in

213 the direction of our results, the interaction between swelling stage and pregnancy must be

214 interpreted with some caution, as their statistical significance hinges on one individual. However,

215 the signs of our major result concerning the differences between pregnant and non-pregnant

216 females remained consistent, regardless of which female we excluded.

217

218 To test the significance of our full model, we built an informed null model, which contained the

219 random effects structure as described above and the three control fixed effects (ambient

220 temperature, humidity, distance). We then tested our full model against this null model using a

221 likelihood ratio test (LRT, Dobson & Barnett, 2008). Similarly, we tested the interaction by

222 comparing the model including the interaction (i.e. the full model) against a model without the

223 interaction (swelling stage and reproductive state as main effects only). We calculated marginal

224 and conditional R^2 following (Nakagawa & Schielzeth, 2013) and (Johnson, 2014), using the

225 MuMIn package (Bartoń, 2016). We fitted all models in R 3.3.0 (R Core Team, 2016), using the

226 lme4 package (v. 1.1-12, Bates et al. [2015]).

227

228 From the existing literature (Hilsberg-Merz, 2008; Scolari et al., 2011; Sykes et al., 2012;

229 Talukder et al., 2014), we predicted an increase in temperature throughout the swelling cycle in

230 non-pregnant chimpanzees, with a peak temperature at full tumescence, in particular at the area

231 of the reproductive organs, when females are fertile. Second, and following the hypothesis that

232 female chimpanzees have evolved physiological and behavioural strategies to conceal

233 pregnancy, we predicted pregnant females to show similar patterns of skin temperature changes

234 at peak tumescence when the probability of conception is at its highest for non-pregnant females.

235

236 To address the two predictions, we assessed skin temperature associated with swelling and

237 reproductive state, at various body parts, controlling for ambient temperature, humidity and

238 recording distance.

239

240 **RESULTS**

241 Our full model (containing swelling stage and reproductive state and their interaction plus the

242 control terms: distance, humidity and ambient temperature) was significantly different from the

243 null model (containing the control terms only) (LRT: $\chi^2_9 = 19.48$, p = 0.0214, $R^2_m = 0.33$, $R^2_c =$

244 0.90, Table 2). Concerning our variables of interest – reproductive state and swelling stage – we

245 found that the model containing the interaction between the two was significantly different from

246 a model from which the interaction term was removed (LRT: $\chi^2_4 = 9.72$, p = 0.0455). Thus, our

247 results indicate that skin temperature showed greater variability in pregnant females (N=4) than

248 non-pregnant females (N=20). Generally, pregnant females had lower skin temperatures than

249 non-pregnant females when deflated and during smaller swelling stages (stages 0 – 2, Figure 2),

250 of less than 1°C overall. This pattern changed later in the cycle, with pregnant females having

251 higher skin temperature compared to non-pregnant females (stage 3, Figure 2), again with a

252 magnitude of less than 1°C. During maximum tumescence (swelling stage 4), temperatures of

253 non-pregnant and pregnant females appeared most similar compared to all other swelling stages.

254 This was true for all body parts measured (Figures 3 and 4).

255

256 Finally, and contrary to our predictions, we did not find a clear increase in temperature

257 throughout the swelling cycle (Figure 2), at the area of the reproductive organs and elsewhere

258   (Figure 3). There was a modest increase in skin temperature between stages 1-2 and stages 3-4,

259   in both pregnant and non-pregnant females, in particular around (but not restricted to) the vulvar

260   area (Figure 3). Yet, we did not find a clear difference between the skin temperature at maximal

261   swelling (where female proceptivity is higher [Wallis, 1992]) and reduced swelling stages.

262   Finally, skin temperature seems comparable or even slightly higher during detumescence than at

263   maximum tumescence.

264

265   **DISCUSSION**

266   Our aim was to assess whether skin temperature may reveal the reproductive state of female

267   chimpanzees, using IRT, a well-developed technique in veterinary medicine, with yet little

268   application so far in the field of behavioural ecology. We compared wild female chimpanzees

269   throughout their swelling cycle and predicted that (i) non-pregnant females should show higher

270   skin temperature when oestral than when anoestral, as well as an increase in skin temperature

271   (with maximal temperature at the end of the swelling cycle, particularly at the area of the

272   reproductive organs), following previous observations in other species (Hilsberg-Merz, 2008;

273   Scolari et al., 2011; Sykes et al., 2012; Talukder et al., 2014). We also predicted that (ii) pregnant

274   females should approximately overlap with the temperature patterns exhibited by non-pregnant

275   females, despite their radically different hormonal state at maximum swelling (stage 4) when

276   males are sexually interested in them. This second prediction is based on the hypothesis that

277   pregnant females have evolved gestation concealing strategies, as they incur an adaptive

278   advantage in concealing pregnancy, to enhance the benefits of paternity confusion by

279   promiscuous mating as long as possible.

280

281 Our results were consistent with the first prediction, by showing slightly higher temperatures of

282 the anogenital regions when transitioning from stages 1-2 to 3-4 (Figure 2), consistent with what

283 has been found in other mammal species (Hilsberg-Merz, 2008; Scolari et al., 2011; Sykes et al.,

284 2012; Stelletta et al., 2013; Talukder et al., 2014). However, this pattern was true for most body

285 parts considered, not solely for the anogenital region (Figure 3). Although it is hard to directly

286 compare our results to previous studies using IRT because of different definitions and methods,

287 the differences we found in our results are of similar magnitudes (about 1°C) compared to other

288 studies (Scolari et al., 2011; Sykes et al., 2012). In both human and non-human female primates,

289 skin colour and tone can change during the fertile period (Roberts et al., 2004; Dubuc et al.,

290 2009), and such variation may be perceived by males (Higham et al., 2011). Variation in skin

291 colour, presumably caused by blood flow and associated temperature changes, may affect the

292 entire body, including the face, and not be restricted to the periovulatory area.

293

294 Regarding our second prediction, we found smaller changes in skin temperature in non-pregnant

295 compared to pregnant females. Crucially, for stage 4, we observed more similar skin

296 temperatures between pregnant and non-pregnant females, compared to the other swelling stages

297 (Figure 2), a pattern true for all body parts considered (Figure 3). Our data is therefore consistent

298 with the prediction that, during gestation, chimpanzee females approximate behavioural and

299 physiological cues that characterise non-pregnant females, which functions to conceal their

300 reproductive state. This could be part of an evolved strategy to deceive males by remaining

301 sexually attractive to them and ultimately to confuse paternity and lower infanticide risk after

302 parturition. Alternatively, the overlap in anogenital temperature could be the by-product of

303 physiological mechanisms involved in anogenital swelling. In the context of the concealment

304 hypothesis, it is worth mentioning that pregnant females show less clear transitions between

305 swelling stages compared to non-pregnant females. Instead, swelling sizes appear to change

306 more erratically, and hence a probably simpler means for males would be to attend to gradation

307 of swelling changes. Previous work has already shown that females show irregular swelling

308 patterns during the early stages of pregnancy (Wallis & Goodall, 1993).

309

310 Sexual swellings during pregnancy have also been reported in other non-human primates, such as

311 sooty mangabeys (*Cercocebus atys*) (Gordon et al., 1991) and Barbary macaques (*Macaca*

312 *sylvanus*) (Möhle et al., 2005), but in these species the swelling patterns between pregnant and

313 non-pregnant females seem to differ. Whether males are responsive to non-monotonic changes in

314 swelling and, if so, whether this affects their mating behaviour and future infanticidal tendencies,

315 would be worth exploring.

316

317 The important question of whether temperature changes are perceivable by males remains

318 unresolved. In humans, thermal discrimination has been investigated in the domain of

319 psychophysics, using tasks where participants are presented with pairs of materials and

320 instructed to choose the cooler of two objects. Thermal discrimination varies with the nature and

321 size of contact sites as well as the baseline temperature of the skin around the contact site (Ho &

322 Jones, 2006). Also, the rate and magnitude of temperature changes play a considerable role in the

323 discrimination of thermal increments (Jones & Berris, 2002; Ho & Jones, 2006). The thenar

324 eminence at the base of the thumb is one of the most sensitive body parts with reported thermal

325 discrimination of less than 0.1°C (Ho & Jones, 2006). If chimpanzees possess temperature

326   discrimination capacities similar to humans, then males should be able to perceive the

327   temperature changes reported in this study.

328

329   It is also worth mentioning that primate males almost certainly use additional signs to make

330   fertility assessments of females during their sexual swelling cycles, particularly olfactory signals

331   (Michael & Zumpe, 1982). In humans (*Homo sapiens*), female body odour during highly fertile

332   days is preferred by males (Gildersleeve et al., 2012). In other primate species, olfactory cues

333   may also play a role (Ziegler et al., 1993; Converse et al., 1995; Clarke, Barrett & Henzi, 2009),

334   but, to our knowledge, relevant systematic research in chimpanzees has not been conducted (Fox,

335   1982). Regarding visual signals, skin colour and tone can change during the fertile period in

336   human and non-human primate females (Roberts et al., 2004; Dubuc et al., 2009), and such

337   variation may be perceived by males (Higham et al., 2011). In humans, facial redness has been

338   linked to the vasodilatation caused by oestradiol (Jones et al., 2015), a pattern in blood flow

339   around the facial area that may be associated with increase in skin temperature. Finally, female

340   sexual behaviour itself can reveal the most fertile period of the swelling cycle (Engelhardt et al.,

341   2005). Future studies should also investigate whether non-pregnant vs. pregnant female

342   chimpanzees show reliable differences in those areas.

343

344   We acknowledge several limitations to our research. First, we did not find a clear increase in skin

345   temperature when comparing anogenital areas of females in fertile and non-fertile stages.

346   Second, only four pregnant females contributed to our dataset, so it would be important to

347   replicate these findings with a larger sample of pregnant females. Third, we did not collect any

348   hormonal data and were therefore unable to determine the point of likely ovulation. A validation

349 study is necessary and would moreover be feasible in captive settings. Finally, we had no

350 behavioural data to show that males are directly responsive to changes in skin temperature, and

351 can be deceived by pregnant females who may have similar skin temperature profiles as fertile

352 individuals. Such behavioural data could have also helped to control for other potential factors

353 that may have affected skin temperature, such as the amount of physical activity when resisting

354 solicitations from males (Stumpf & Boesch, 2005). Nevertheless, we consider it plausible that

355 males can be affected by pregnant females' skin temperature, mainly because shifts in blood

356 flow, and their corresponding changes in skin temperature, may affect skin colouration in the

357 face.

358

359 In sum, our data appear consistent with the prediction that, during gestation, chimpanzee females

360 approximate skin temperature as well as behavioural and visual cues that characterise non-

361 pregnant females. Yet, it is still possible that skin temperature does not constitute a deceptive

362 signal in chimpanzees. Rather, skin temperature may simply be a by-product of the physiological

363 mechanisms driving anogenital tumescence. Furthermore, we offer inconclusive evidence of a

364 thermal pattern associated with fertility. Skin temperature seems to increase throughout the

365 swelling cycle, but with no clear differences in skin temperature compared to when females are

366 anoestral. Our research offers a tentative exploration of changes in skin temperature associated

367 with fertility and pregnancy in wild female chimpanzees, which future research can build on,

368 using IRT to tackle important questions in the field of behavioural ecology.

369

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378

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553

554   **FIGURE CAPTIONS**

555   **Figure 1** Example of an IRT measurement. The polygon is drawn around the left ear of the

556   individual, which can be seen lying on the ground.

557   **Figure 2** Model results for differences in skin surface temperature. Shown is the interaction

558   between swelling stage and pregnancy status, with model estimates and associated 95%

559   confidence intervals back-transformed to the original scale (for modelling, surface temperature

560   was squared, see Supplementary Information).

561   **Figure 3** Model predictions for skin surface temperature of female chimpanzees per body part

562   for non-pregnant and pregnant females. The temperature axis shows values back-transformed to

563   the original scale (for modelling, surface temperature was squared, see Supplementary

564   Information).

565   **Figure 4** Median skin surface temperature with 25% and 75% quartiles, of female chimpanzees

566   per body part for non-pregnant and pregnant females. In contrast to Figures 2 and 3, we show

567   untransformed raw data here (see Supplementary Information).

568

569

570   **TABLES**

571   **Table 1** Distribution of images per female (ID) and by reproductive condition (Non-pregnant

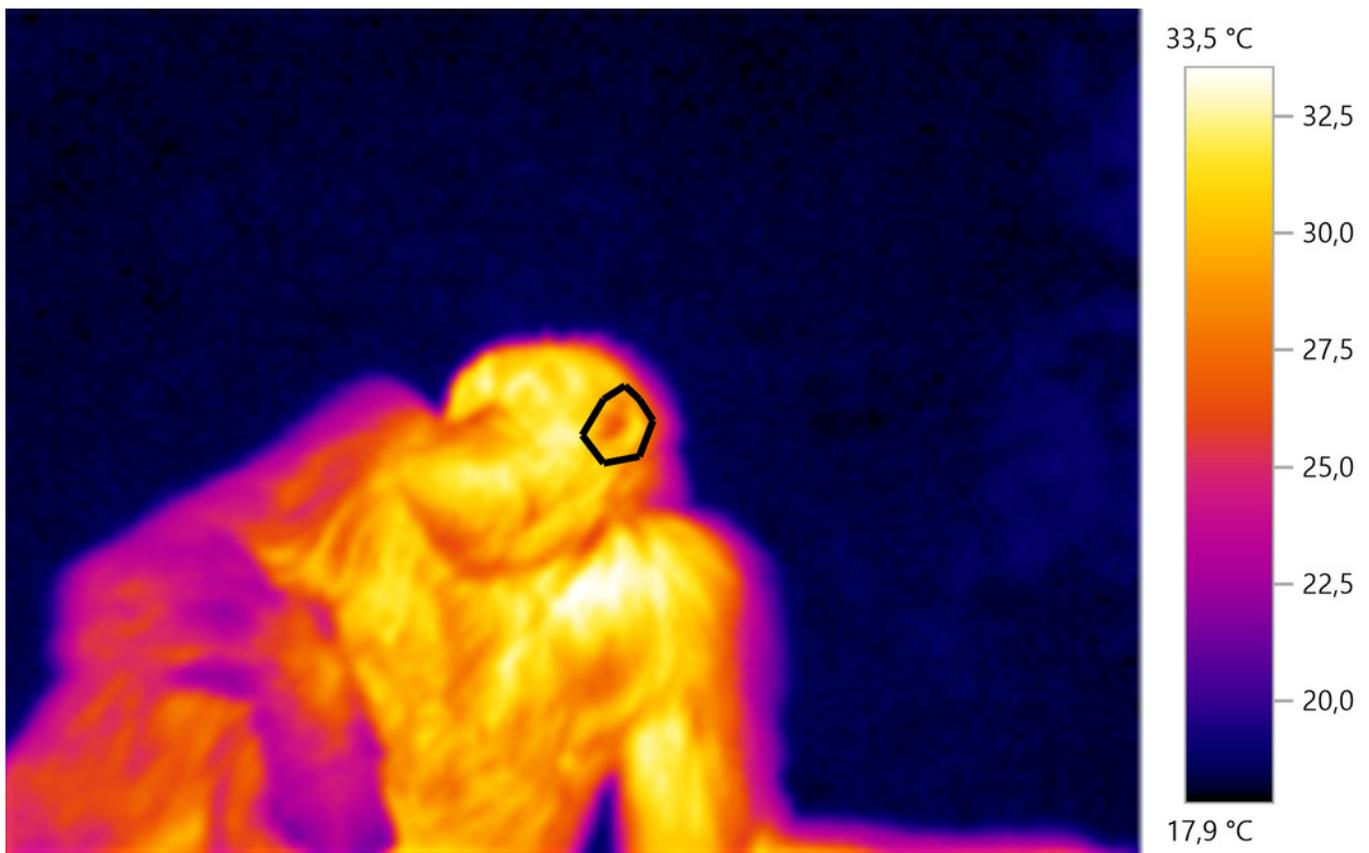
572   and Pregnant).

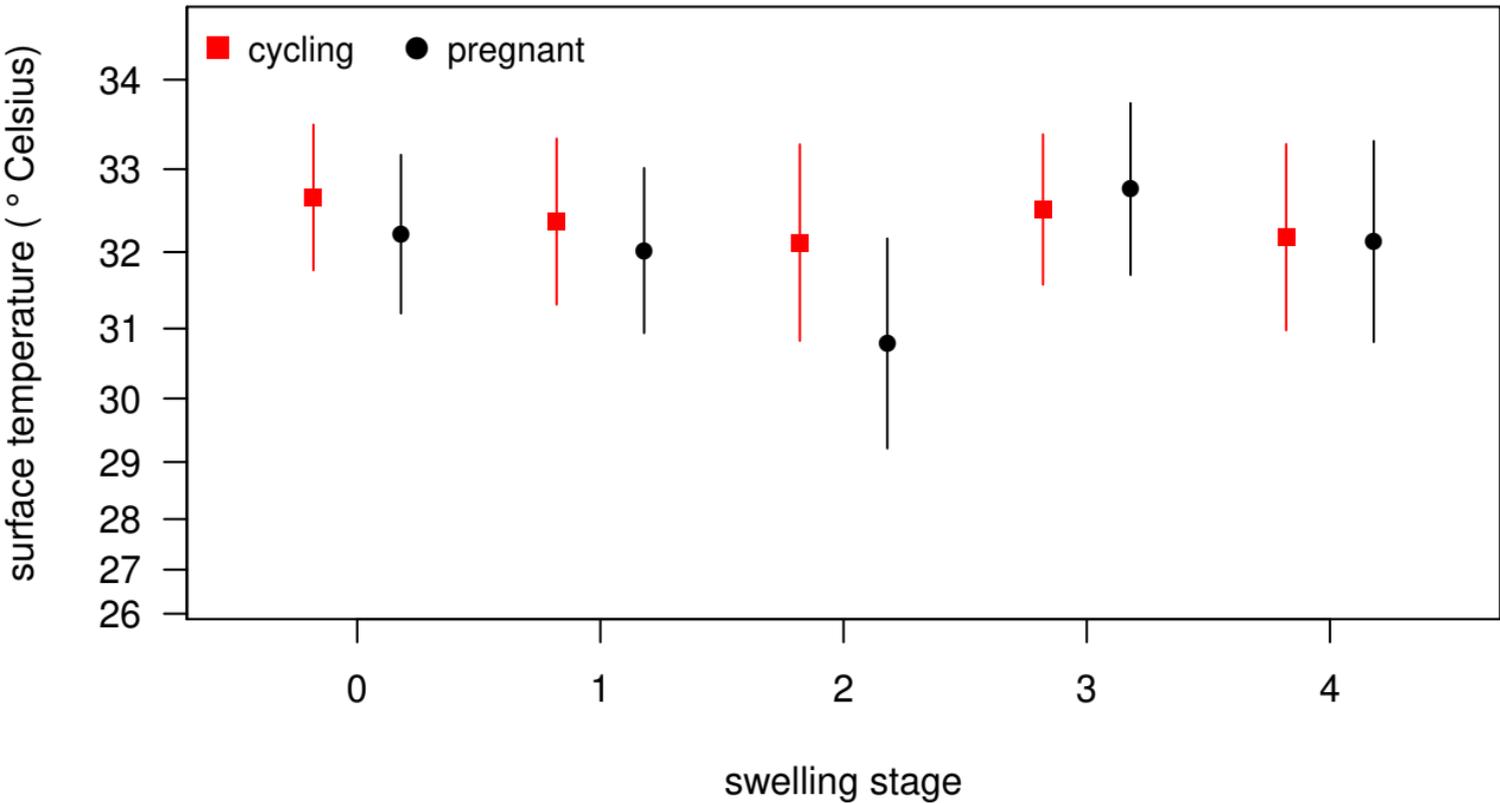
573   **Table 2** Results of full model. Reference level for pregnancy was `Non-pregnant' and for

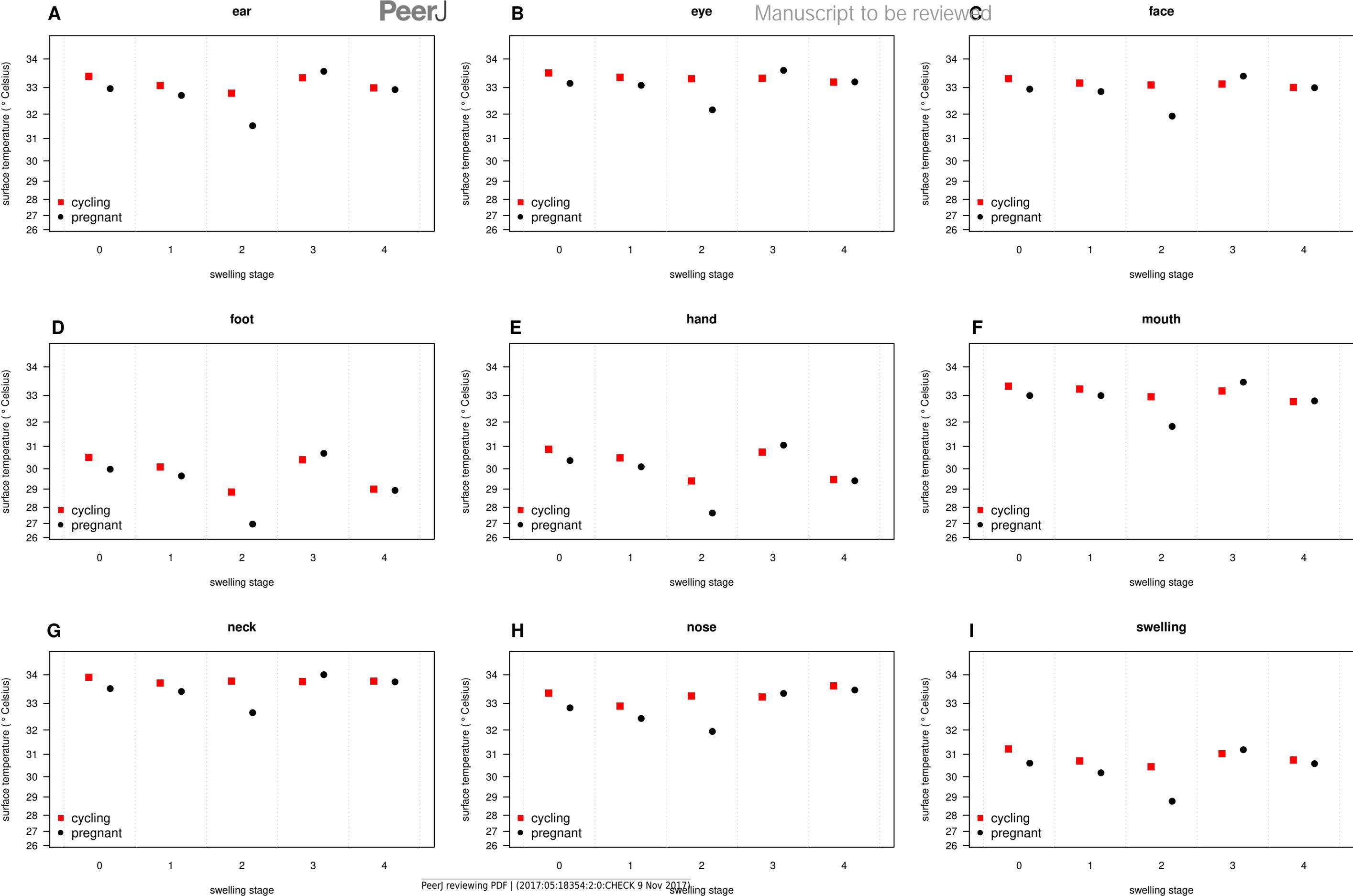
574   swelling stage `0'. t values for main effects comprised in interactions are omitted.

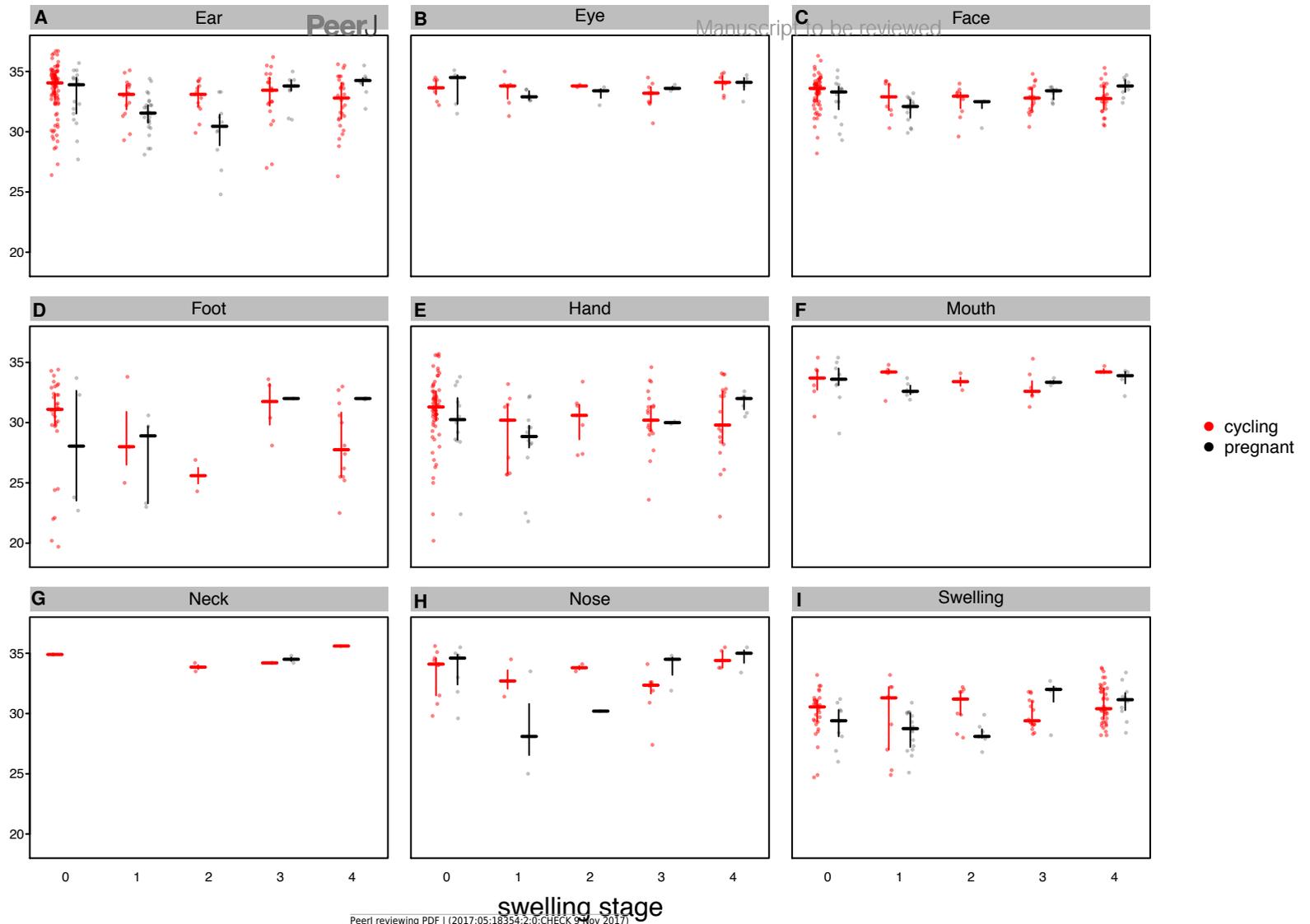
Figure 1

Example of IRT measurement.

The polygon is drawn around the left ear of the individual which can be seen laying on the ground.

Model results for differences in body surface temperature.

Shown is the interaction between swelling stage and pregnancy status, with model estimates and associated 95% confidence intervals back-transformed to the original scale (for modeling, surface temperature was squared, see supplementary information).

Model predictions for surface temperature of female chimpanzees per body part for non-pregnant and pregnant females.

The temperature axis shows values back-transformed to the original scale (for modeling, surface temperature was squared, see supplementary information).

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

In contrast to figure 2 and 3, we show untransformed raw data here (see supplementary information).

Distribution of images per female (ID) and by reproductive condition (non-pregnant and pregnant).

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

create

create

create

Results of full model.

Reference level for pregnancy was `not pregnant' and for swelling stage `0'. *t* values for main effects comprised in interactions are omitted.

create

	Parameter estimate	Standard error	t 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