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1 **Sex-specific links between the social landscape and faecal**  
2 **glucocorticoid metabolites in semi-captive Asian elephants**

3

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21

22 ABSTRACT

23 Although social behaviour is common in group-living mammals, our understanding of its  
24 mechanisms in long-lived animals is largely based on studies in human and non-human primates. There  
25 are health and fitness benefits associated with strong social ties, including increased life span,  
26 reproductive success, and lower disease risk, which are attributed to the proximate effects of lowered  
27 circulating glucocorticoid hormones. However, to deepen our understanding of health-social dynamics,  
28 we must explore species beyond the primate order. Here, using Asian elephants as a model species, we  
29 combine social data generated from semi-captive timber elephants in Myanmar with measurements of  
30 faecal glucocorticoid metabolite (FGM) concentrations. These data enable a “natural experiment” because  
31 individuals live in work groups with different demographic compositions. We examine sex-specific FGM  
32 concentrations for four different aspects of an individuals’ social world: general sociality, work group  
33 size, sex ratio and the presence of immatures (< 5 years) within the work group. Males experienced lower  
34 FGM concentrations when engaged in more social behaviours and residing in female-biased work groups.  
35 Surprisingly, females only exhibited lower FGM concentrations when residing with calves. Together, our  
36 findings highlight the importance of sociality on individual physiological function among elephants,  
37 which may have broad implications for the benefits of social interactions among mammals.

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41 Keywords: *Elephas maximus*, hormones, offspring, sex ratio, sociality, stress

42

43 **1. Introduction**

44 Group living mammals engage in an array of daily social behaviours. Though such close proximity  
45 to conspecifics may heighten the spread of disease (McEwen, 2012) and lead to competition and conflict  
46 (Krause and Ruxton, 2002), social behaviours can also have positive effects, including enhanced access to  
47 resources and protection during times of need (Silk, 2007) that culminate in improved health and fitness.  
48 Research on sociality and long-term fitness have shown that individuals with strong social ties live longer  
49 (Holt-Lunstad et al., 2010; Silk et al., 2010) and enjoy higher reproductive success (Silk et al., 2003).  
50 Sociality is also tied to health benefits (Snyder-Mackler et al., 2020), and these fitness and health benefits  
51 may be proximately due to mediation of the hypothalamic-pituitary-adrenal (HPA) axis (Wittig et al.,  
52 2016). In particular, affiliative social interactions can reduce concentrations of circulating glucocorticoids  
53 (GC) that participate in the physiological stress response (Wittig et al., 2016). By contrast, prolonged high  
54 concentrations of GCs can lead to serious health problems, including cardiovascular impairments and  
55 immunosuppression (Sapolsky, 2005), as well an increased risk of depression and anxiety (Chiba et al.,  
56 2012).

57 Our understanding of the link between sociality and adrenal activity is limited, however, by two  
58 notable shortcomings. First, the majority of work on long-lived animals on this topic is limited to  
59 primates, all of which share a relatively recent last common ancestor (~<30 million years ago), although a  
60 larger body of work exists on smaller short-lived animals [reviewed in (Creel et al., 2013; Raulo and  
61 Dantzer, 2018)]. To gain a greater insight into the evolutionary causes and consequences of sociality, it is  
62 imperative to include other long-lived, highly social species. Indeed, a growing body of recent work has  
63 begun to reveal that social ties and positive interactions are not exclusive to the primate order (Cameron  
64 et al., 2009; Connor, 2007; Smith et al., 2010). Second, with research on wild populations, it is difficult to  
65 tease apart the factors affecting sociality. In particular, matrilineal kinship has been identified as the most  
66 important factor affecting the development of long-term bonds in social species (Seyfarth and Cheney,  
67 2012). It is therefore important to examine the physiological effects of sociality among non-related  
68 individuals living in native habitats exposed to similar resources and environmental contexts in which

69 their behaviours evolved. A recent review has shown that associations between different measures of  
70 sociality and the stress response vary between vertebrate species; it highlights the gap in our knowledge  
71 of how social behaviours and GCs co-vary and calls for more studies to understand variation in social  
72 behaviour (Raulo and Dantzer, 2018).

73 We explore some of these questions with Asian elephants. They offer an independent evolutionary  
74 lineage from that of primates, with a last common ancestor shared over 160 million years ago, yet present  
75 similar characteristics: long lifespan (up to 80 years), high sociality and cognitive abilities, as well as life  
76 history traits, such as extensive maternal investment and slow periods of immaturity (Moss et al., 2011;  
77 Sukumar, 1992; Vidya and Sukumar, 2005). Understanding physiological-sociality links in elephants will  
78 therefore enable cross-species generalizations. Further, elephants exhibit high social intelligence with  
79 sophisticated social behaviours, such as grief, play, and empathy (Bates, Poole, & Byrne, 2008; Plotnik,  
80 de Waal, Moore, & Reiss, 2010), as well as distinct personalities (Seltmann et al., 2019, 2018). Combined  
81 with their long lifespans, elephants therefore retain the opportunity to develop complex, enduring social  
82 bonds, as well as accrue related health benefits.

83 Here, we use a unique dataset on semi-captive Asian elephants from the timber logging camps in  
84 Myanmar to examine the relationship between sociality and adrenal activity in a highly social, long-lived  
85 mammal. This population provides an exceptional opportunity to study the links between sociality and  
86 adrenal activity, as logging elephants exhibit mortality rates (Clubb et al., 2008), reproductive profiles  
87 (Lahdenperä et al., 2014), and social behaviours (Lahdenperä et al., 2016; Lynch et al., 2019) resembling  
88 those of wild elephants. The Myanma Timber Enterprise (MTE) has maintained detailed log-books for  
89 over a century on each individual throughout its lifespan which are now complimented by longitudinal  
90 measurements of faecal GC metabolite (FGM) concentrations (Crawley et al., 2021; Mumby et al., 2015;  
91 Martin W. Seltmann et al., 2020) that reflect GC accumulation over several days (Palme, 2012). Because  
92 chronic stress may affect an individual's behaviour, weight, reproduction, and immune function, measures  
93 of FGM serve as a general proxy for overall health (Wittig et al., 2016). Employed for forestry work,  
94 these elephants live in more natural environments than their most other captive counterparts (Clubb et al.,

95 2008). Logging camps consist of MTE managers and elephant handlers (i.e., mahouts) that care for  
96 several groups of 5-8 individuals each at every site. Elephants work during the day under the supervision  
97 of a mahout, but then are able to interact with other captive and sometimes wild elephants in the forests at  
98 night, thus presenting more natural conditions under which studies of sociality can be conducted.

99 In this study, we use four measures of sociality: tendency to engage in regular social interactions  
100 with conspecifics or being solitary, work group size, work group sex ratio, and presence of calves in the  
101 work group. We use this “social landscape” to explore variation in relation to individual adrenal activity  
102 as measured by FGM concentrations. Our first measure of sociality concerns individual social behaviour:  
103 engaging in regular social interactions with conspecifics or being solitary. We predict that elephants will  
104 have lower FGM concentrations when they experience regular social interactions with conspecifics and  
105 are not solitary (Wittig et al., 2016). In addition, we investigated characteristics of the social environment  
106 in which the elephants live: work group size and sex ratio, and the presence of calves in the work group.  
107 Our second prediction, therefore, is that individuals within larger work groups will have lower FGM  
108 concentrations, because the chances for more regular social interactions would be greater than for  
109 elephants in smaller working groups. Third, we hypothesize that work groups with a high female to male  
110 sex ratio will be associated with decreased individual FGM concentrations, as it may mimic groups of  
111 their wild counterparts which exhibit a similar sex skew (De Silva et al., 2013; Gupta et al., 2014).  
112 Finally, we consider presence of nursing calves; though frequently part of social groups for most group  
113 living species, they are often overlooked when assessing links between health and sociality. Interactions  
114 among immature and adult animals are expected, and non-relatives in some long-lived mammals exhibit  
115 strong interest in caring for young offspring [primates: (Silk, 1999); cetaceans: (Mann and Smuts, 1998);  
116 proboscidea: (Gadgil and Nair, 1984; Lee, 1987)]. The proximate mechanism driving this behaviour may  
117 be associated with decreased stress, and we predict that individuals in groups with calves will exhibit  
118 lower FGM concentrations. Finally, we consider males and females separately, as adrenal activity under  
119 stress exposure (Kudielka and Kirschbaum, 2005) and life-history strategies (Sukumar, 2003) are often

120 sex-specific. In addition, FGM concentrations in the study population are often generally higher in males  
121 than in females (Seltmann et al., 2020). Overall, it is crucial to expand our understanding of the link  
122 between sociality and physiology, so we can improve our interpretations of the evolution of sociality, as  
123 well as develop applied methods towards maintaining and improving welfare of captive social animals.

124

## 125 **2. Methods**

### 126 2.1 Study population

127 The timber camps of Myanmar contain the world's largest (N~3,000) remaining captive population  
128 of elephants (Hedges et al., 2018). For over a century, the Extraction Department of the MTE has kept  
129 records of each animal's permanently marked identification (ID) number and name, origin (wild-caught  
130 or captive-born), date and place of birth, mother's ID number and name, age or year of taming, birth dates  
131 and ID numbers of all offspring, date of death or last known date alive, and cause of death.

132 The elephants live within their native forest habitat, distributed across the country, and are used  
133 during the day for logging operations as transport and draught animals, following strict-set working  
134 hours, working days per year, and tonnage per individual. While working, the elephants' social  
135 interactions are under the control of their mahout. During the night, the elephants forage in the forest,  
136 unsupervised, and may interact and mate with both wild and tame conspecifics. Breeding rates are natural  
137 (without human intervention) and calves born in captivity are cared for by their biological mother and  
138 allomothers until weaning (Lynch et al., 2019). Working females are given rest from mid-pregnancy (11  
139 months into gestation) until the calf is 1-2 years old (Gale, 1974); mothers are then used for light duties  
140 but allowed to nurse on demand. Calves are generally weaned at the age of 4 (Crawley et al., 2019), then  
141 separated from their mother and tamed, assigned a mahout, name and registration number, and logbook  
142 that records demographic and health information. By age 17, the elephants begin full engagement in the  
143 work force until retirement at age 55 years; logbooks are maintained until death. After taming, elephants  
144 are transferred to training groups, and after retirement, elephants spend their life together with other  
145 retired elephants. We will refer to all these groups as "working groups" throughout the manuscript.

146

## 147 2.2 Focal individuals

148 We studied adult elephants born between 1956 and 2008, working within the Kawlin and Katha  
149 logging agencies in the Sagaing Division. We focused on adults over the age of 10 years because elephant  
150 males have well-defined growth phases (Sukumar et al., 1988), and this is the age when adolescents  
151 typically begin to disperse from their natal herds and transition into socially mature adulthood (Sukumar,  
152 1992). Our FGM dataset consisted of 135 samples from 95 focal individuals (range of observations per  
153 individual = 1-4, mean = 1.4), with 60 females and 35 males, ranging in age from 10-71 (mean = 26,  
154 median = 15.9), and of which 76 were captive-born and 19 were wild-caught.

155

## 156 2.3 Faecal sample collection and GC analysis

157 All faecal samples were collected on an annual basis from 2014-2018 in the hot season  
158 (March/April), when elephants do not work; FGM concentrations are thus not subject to potential  
159 workload effects. Faecal samples were collected in the morning within  $1.25 \pm 5.5$  days (mean  $\pm$  SD) of the  
160 recorded social measures to take into account the ~48-hour lag time between secretion and excretion  
161 (Wasser et al., 2000). Samples were stored in ziplock bags at  $-20^{\circ}\text{C}$  until drying in a hot air oven at  $50^{\circ}\text{C}$ .  
162 Dried samples were shipped for further analysis to the Veterinary Diagnostic Laboratory, Chiang Mai  
163 University, Thailand. Samples (0.1 g) in 5 ml of 90% ethanol were extracted twice by boiling in a water  
164 bath for 20 minutes and adding 100% ethanol to maintain volume. Samples were then centrifuged and the  
165 combined supernatants dried under air in a  $50^{\circ}\text{C}$  water bath. Samples were reconstituted by vortexing for  
166 one minute in 3 ml of ethanol, drying again, and finally resuspending in 1 ml of methanol. Extracts were  
167 diluted 1:3 in a phosphate buffer and stored at  $-20^{\circ}\text{C}$  until analysis. Concentrations of FGM were  
168 determined using a double-antibody enzyme immunoassay (EIA) validated for Asian elephants that relied  
169 on a polyclonal rabbit anti-corticosterone antibody (CJM006) (Watson et al., 2013). Second antibody-  
170 coated plates were prepared by adding 150  $\mu\text{l}$  of anti-rabbit IgG (0.01 mg/ml) to each well of a 96-well  
171 microtiter plate, and incubating at room temperature for 15-24 hours. Thereafter, the wells were emptied

172 and blotted dry, followed by adding 250 µl of blocking solution and incubating at room temperature for  
173 15-24 hours. After incubation, wells were emptied, blotted, and dried in a Sanpla Dry Keeper (Sanplatec  
174 Corp., Auto A-3, Japan) with loose desiccant in the bottom. Dried plates were heat-sealed in a foil bag  
175 with a 1g desiccant packet, and stored at 4°C until use. Samples or corticosterone standards (50 µl)  
176 followed immediately by corticosterone-horseradish peroxidase (25 µl) were added to each well except  
177 for non-specific binding wells, followed by 25 µl of anti-corticosterone antibody, and incubated at room  
178 temperature for one hour. Plates were washed four times with buffer (1:20 dilution, 20X Wash Buffer Part  
179 No. X007; Arbor Assays, MI) and 100 µl of Tetramethylbenzidine substrate solution was added, followed  
180 by incubation for 45-60 minutes at room temperature without shaking. Absorbance was measured at 405  
181 nm. The intra-assay coefficient of variation (CV) was <10.0 % as all duplicate CVs exceeding 10% were  
182 reanalysed. The inter-assay CV for low and high percent binding control samples was 11.8 %. The  
183 minimum detection limit was 0.08 ng/g of faeces.

184

#### 185 2.4 Social landscape

186 All sociality data were collected in the hot season (March/April) from 2014-2018. These data were  
187 collected during the same sampling bouts for the faecal samples. The social landscape of an individual  
188 included four measures of the elephants' social environment that considered the individual's direct social  
189 engagement, as well as the overall social composition of the work group (tendency to engage in regular  
190 social interactions with conspecifics or being solitary, work group size, work group sex ratio, presence of  
191 calves in the work group).

192 First, we assessed an elephant's tendency to interact with conspecifics on a regular basis or to stay  
193 solitary (tendency to engage in regular social interactions with conspecifics or being solitary). Questions  
194 were directed to the mahouts of each elephant because they work with elephants on a daily basis and  
195 develop an intimate knowledge of their animal. The answers provided by the mahouts therefore present an  
196 integrative view of the elephant's social interactions over the time-period mahouts have spent working  
197 with their focal elephant. Mahouts were asked if in their freetime their elephant is solitary (does not

198 interact with other elephants) or social (interacts with other elephants). Individuals identified associating  
199 with another were categorised as “social” (N = 29 and 79 answers for males and females, respectively)  
200 and individuals not identified as maintaining any social interactions were categorised as “solitary” (N =  
201 14 and 10 answers for males and females, respectively).

202 Second, we examined the size of the work group, only considering the number of adults present  
203 (range = 5-11, mean = 6.56). Third, we determined the adult sex ratio of the work group by calculating  
204 the proportion of females in a group (range = 0.2-1, mean = 0.59). Fourth, we examined whether  
205 immature elephants (i.e. under 5 years old) were present in the work group. This was categorised as either  
206 presence (N = 14 and 22 observations from males and females, respectively) or absence (N = 27 and 52  
207 observations from males and females, respectively) of calves in the working group. The information on  
208 work group composition was collected from recordings by local veterinarians.

209

## 210 2.5 Statistical analysis

211 All analyses were conducted with R version 3.6.2 (R Core Team, 2019) (see Supplementary  
212 Information). We examined the relationship between social interactions and individual FGM  
213 concentrations using linear mixed-effects models, implemented in the *lme4* package (Bates, Mächler,  
214 Bolker, & Walker, 2015). Models were fit with the *bobyqa* numerical optimisation algorithm. We used  
215 the natural-log transformed FGM concentration (ng/g) as the response variable to satisfy the normality  
216 assumptions of a linear model, which was more parsimonious and made model coefficients more  
217 interpretable. Separate models were explored for males and females, which often experience sex-specific  
218 differences in adrenal activity under stress exposure (Kudielka and Kirschbaum, 2005; Seltmann et al.,  
219 2020), life-history strategy (Sukumar, 2003), and behaviour (Seltmann et al., 2019; Sukumar, 2003).

220 We explored how FGM concentrations responded to the social landscape using separate models,  
221 with univariate predictors for each sociality variable. We opted to use univariate sociality predictors  
222 because the sample size was too low to estimate multivariate sociality or interaction effects whilst  
223 accounting for confounding covariates. The sociality variables included were the tendency to engage in

224 regular social interactions with conspecifics or being solitary (two-level factor), the work group size  
225 (continuous term), the work group sex ratio (continuous term), and the presence of calves (two-level  
226 factor). Thus, there were eight models exploring the links between the social landscape and FGM  
227 concentrations (four for each sex). Because there were differences in the data collection over study years,  
228 different numbers of observations were assessed for the sociality (146 observations) and working group  
229 composition variables (125 observations). For all models, we controlled for potentially confounding  
230 covariates that may influence FGM concentrations: age in years (continuous term, range =10-62) and  
231 birth origin (two-level factor, captive-born or wild-caught), which have the potential to influence elephant  
232 behaviour and physiology (Lahdenperä et al., 2018; Norkaew et al., 2019; Seltmann et al., 2020). We also  
233 included intercept-only random effects to account for repeated measures across individuals ( $n = 95$ ) and  
234 observation years ( $n = 5$ ). We assessed the significance of model terms using likelihood ratio tests (LRTs)  
235 with the  $\chi^2$  distribution, comparing test models including the univariate predictors to null models  
236 excluding the predictors of interest. Bootstrapped confidence intervals for model coefficients were  
237 calculated at the 95% level using the *confint.merMod* function in *lme4* over 500 simulations. Uncertainty  
238 in the model predictions was examined by calculating prediction intervals over 1000 simulations at the  
239 90% level using the *predictInterval* function of the *merTools* package (Knowles and Frederick, 2019),  
240 controlling for the variance of both fixed and random effects but excluding residual variance.

241

### 242 **3. Results**

#### 243 3.1 Male elephants

244 Overall, FGM concentrations varied between 19.59 and 195.8 ng/g of faeces. In our sample, males  
245 had slightly higher FGM concentrations than females, with mean concentrations of  $72.1 \pm 4.7$  ng/g (SEM)  
246 and  $64.9 \pm 2.7$  ng/g, respectively, but these were not significantly different ( $t = -1.29$ ,  $df = 81.7$ ,  $p = 0.20$ ).

247 All model output can be found in the Supplementary Information.

248 Male FGM concentrations were primarily linked to two key features of their social landscape – their  
249 tendency to engage in regular social interactions with conspecifics and the sex ratio of their working  
250 group. In our sample, the 33% of the males that were characterised as solitary by their mahout had  
251 significantly elevated FGM concentrations when compared to social males (Table 1; Fig. 1a). On average,  
252 solitary males had FGM concentrations 55% higher than social males. Males also exhibited lower  
253 concentrations when in working groups with higher female:male sex ratios (Table 1; Fig. 1b). Male FGM  
254 concentrations were not significantly related to either the working group size or calf presence  
255 (Supplementary Information). These results are not confounded by differences between the males due to  
256 their identity, sampling year, age or origins (Table 1).

257

### 258 3.2 Female elephants

259 Female FGM concentrations were significantly related to calf presence in the working group, with  
260 FGM concentrations 22% lower when calves were present (Table 1; Fig. 1c). However, female FGM  
261 concentrations were not related to their tendency to engage in regular social interactions with conspecifics  
262 or being solitary, sex ratio, or size of the working group (Supplementary Information). In contrast to the  
263 males, only 11% of females were characterised as solitary by their mahout, with the majority displaying  
264 long-term social bonds to other elephants. These results are not confounded by differences between the  
265 females due to their identity, sampling year, age or origin (Table 1).

266

## 267 4. Discussion

268 Our results demonstrate that concentrations of FGM in male elephants are linked to social  
269 interactions, with significantly lower concentrations observed when they have social ties with  
270 conspecifics and are in female-biased working groups. Females, on the other hand, exhibited significantly  
271 lower FGM concentrations when calves were in the same work group. Interestingly, work group size was  
272 not related to FGM concentrations in males or females. These findings have implications for improving  
273 our interpretations of the evolution of sociality, as well as for informing applied methods for improving

274 social animal welfare in general and elephant keeping in captivity in particular. Sex-differences in FGM  
275 concentrations corroborate previous findings from this population (Seltmann et al., 2020), and are  
276 commonly observed in mammals (Kudielka and Kirschbaum, 2005).

277 We find evidence for a potential proximate mechanism driving male sociality: male elephants  
278 potentially benefit from social bonds with others, exhibiting significantly lower FGM concentrations  
279 when engaging in consistent social interactions with other individuals. Because of the fundamental  
280 differences between resources that limit reproductive success in females and males (food vs fertilizations,  
281 respectively) (Trivers, 1972), it is commonly assumed that social bonds among males should be rare and  
282 restricted to kin among patrilocal species (Mitani, 2009; Mitani et al., 2012; Van Hooff and van Schaik,  
283 1994). Male elephants may exhibit some form of philopatry (Vidya and Sukumar, 2005) and show social  
284 preference towards kin (Chiyo et al., 2011; Hamilton, 1964), though data are limited. Male elephant  
285 sociality may also be understood through shared motivations and reproductive goals among both kin and  
286 non-kin. They engage in contest polygyny (Moss and Poole, 1983) and undergo asynchronous periods of  
287 sexual activity (Keerthipriya et al., 2020; Rasmussen, 2005). Reflecting these different reproductive states  
288 and depending on their age, males will alternate between residing in all-male groups when sexually  
289 inactive or mixed-sex groups when active (Keerthipriya et al., 2020; Poole and Moss, 1981), and exhibit  
290 stronger social associations to those in a similar sexual state (Goldenberg et al., 2014). Though our study  
291 population is not truly wild, the elephants studied here spend much of their time free in their natural  
292 habitat, allowing them to express many of their natural behaviours. Our setting therefore provides  
293 conditions in which male elephants experience different social conditions (presence of males, females,  
294 calves) according to the work group they are part of, which allowed us to address these questions.  
295 Overall, it is clear that sociality among males can serve important adaptive functions, including, and  
296 perhaps driven by significant modulations in adrenal activity.

297 Surprisingly, a relationship between social bonds and FGM concentrations was not observed in  
298 females. Wild elephant females spend their lives with other female relatives in matrilineal social groups  
299 (de Silva et al., 2011; de Silva and Wittemyer, 2012) and sociality is associated with improved body

300 condition and fitness (Meehan et al., 2016; Pinter-Wollman et al., 2009; Silk et al., 2010, 2003). Though  
301 social bonds are not unimportant for male elephants (Allen et al., 2020) and they can form all-male  
302 groups (Srinivasaiah et al., 2019), they usually live a more solitary lifestyle or in loosely-associated  
303 bachelor groups (Keerthipriya et al., 2021; Sukumar, 2003). Therefore, we expected stronger effects in  
304 females. However, strong male social bonds might be more important in the semi-captive setting than in  
305 purely wild elephants [but see e.g. (Allen et al., 2020)]. Solitary females might still be able to interact  
306 with other individuals without forming strong social bonds (de Silva et al., 2011), which is more common  
307 in Asian than African elephants (de Silva and Wittemyer, 2012) and so the lack of those bonds may not be  
308 a stressor that would result in heightened FGM concentrations. In addition, other factors like the presence  
309 of calves younger than 5 years or the fact that keepers potentially interact more with female elephants  
310 than with males (Brown et al., 2019; Crawley et al., 2019) might be more important for female GC  
311 physiology and thereby counteract the potential negative effects of solitariness in females. Mahouts have  
312 traditionally preferred handling male elephants because of their strength and the prestige (Hart and  
313 Sundar, 2000). In our study population mahouts also have a preference for bulls, but describe these as  
314 being more difficult to handle compared to females (Crawley et al., 2019). Despite these traditional  
315 tendencies, the changes in the Myanmar's handling system and the general preference for docile females  
316 across Asia (Suter et al., 2013) might imply that mahouts of female elephants spend more time interacting  
317 with their elephants, because they are easier to handle. It is also possible that female stress responsivity is  
318 lower than that of males. In humans, for example, young males show higher adrenal responses compared  
319 to young females after exposure to psychological stress (Stroud et al., 2002). Such extreme sex-biased  
320 stress responses may explain the lack of a relationship found in female elephants. Elephants in the study  
321 population also had different behavioural patterns, with males expressing less social behaviours than  
322 females (Seltmann et al., 2019), which could lead to the pronounced differences in FGM concentrations  
323 between males and females. These consistent individual differences in behavioural patterns, also called  
324 personality (Réale et al., 2007; Seltmann et al., 2018), are often tightly linked to sociality (Wolf et al.,

325 2011) and health (Mehta and Gosling, 2008), and we recommend that those should be studied in  
326 conjunction when possible.

327 We predicted a female-biased sex-ratio skew in the working group would be associated with lower  
328 FGM concentrations, and therefore overall adrenal activity, as this demographic composition would be  
329 similar to that found in wild groups (De Silva et al., 2013; Gupta et al., 2014). This was, however, only  
330 true for male elephants. Males are in competition for resources, especially mating partners, and this may  
331 be increased in groups with more males present. If higher FGM concentrations result from higher  
332 competition, it would be interesting to investigate concentrations of androgens in addition to GCs,  
333 because they are involved in the regulation of social behaviours and intra-sexual competition (Wingfield  
334 et al., 2001). In groups of Cape mountain zebras (*Equus zebra zebra*), male-skewed sex-ratios were linked  
335 to higher androgen concentrations in both sexes and lower FGM concentrations in females, showing the  
336 general link between sex ratios and different hormones related to stress, competition, social behaviours,  
337 and fitness (Lea et al., 2018). In addition, if there is only one male elephant in a group, there is no  
338 competition for dominance, nor need for sparring and dominance assessment between males; groups  
339 might be more stable, translating to less stress, especially for males. However, with more males present,  
340 there will be competition for dominance between males or more sparring events (Chiyo et al., 2011), and  
341 though established dominance hierarchies can lead to social stability (Holekamp and Strauss, 2016),  
342 constant status assessment could become stressful e.g. as seen for male chimpanzees (*Pan troglodytes*)  
343 (Preis et al., 2019). Under these circumstances, social bonds in male-biased elephant groups may weaken,  
344 which could lead to less social support linked to reduced stress (Wittig et al., 2016).

345 We found no significant relationships between FGM concentrations and group size for either sex. In  
346 African elephants, no clear evidence for ecologically- or socially-determined optimal group size was  
347 found at different levels of their multitier social organisation (Wittemyer et al., 2005). In our sample, the  
348 number of adults within work groups ranged from 5 to 11 individuals. In the wild, Asian elephants can  
349 form larger groups at higher levels of their social organisation, including several family units comprising  
350 mothers, grandmothers, calves and aunts when groups meet at water holes (de Silva et al., 2011;

351 Sukumar, 2003). However, core group sizes in the wild are somewhat similar to the work group sizes  
352 studied here. Changes in adrenal activity may therefore only become apparent in larger groups when  
353 several core units temporarily fuse together. In addition, the artificial nature of the work groups studied  
354 here, with demographic differences to wild groups, might mask any potential effects of group size on  
355 adrenal activity.

356 We found that the presence of nursing calves was associated with lower FGM concentrations in  
357 female elephants. For long-lived mammals, non-relatives have been found to demonstrate “natal  
358 attraction”, or an intense interest in immature conspecifics (Mann and Smuts, 1998; Silk, 1999). While  
359 the ultimate function of natal attraction is widely debated (Mann and Smuts, 1998; Silk et al., 2003), a  
360 significant reduction in adrenal activity may serve as the proximate mechanism. Calves in our working  
361 population are allowed to stay with their mother until taming (Crawley et al., 2020), so it is not  
362 uncommon to find them in the logging camps. Though relatedness within working groups may not  
363 generally be high, the presence of nearby relatives can increase reproductive success in young elephant  
364 mothers (Lahdenperä et al., 2016; Lynch et al., 2019). In this study population, calves often receive care  
365 by non-related allomothers, a behaviour observed in wild African (Lee, 1987) and Asian elephants  
366 (Gadgil and Nair, 1984). These strong social bonds and lack of male contribution to calf care could  
367 explain why we only find lower FGM concentrations in females when calves are present in a group.

368 In summary, male and female elephants exhibit significant differences in FGM concentrations in  
369 response to their social landscape. This study highlights the importance of considering the social causes  
370 and consequences of physiological and behavioural changes in males within a matrilocal species.  
371 Furthermore, our results support the long-standing view that social buffering helps reduce the aversive  
372 effects of stress in bonding partners (Wittig et al., 2016). Considering that social factors are linked to  
373 stress, and that increased GCs can be related to a decrease in female (Lea et al., 2018) and male (Nargund,  
374 2015) fertility, the social landscape should be considered when making decisions about welfare and  
375 management of populations (Brown et al., 2019). Specifically, given the instability of the population of  
376 Myanmar’s timber elephants (Jackson et al., 2019), one should consider our results also in the light of

377 management applications. For example, solitary males should receive extra care and handling, or efforts  
378 could be made to ensure that these solitary individuals have access to social partners to improve their  
379 welfare. More research however is necessary to investigate the underlying reasons for why these  
380 individuals tend to be solitary, as it could also be an active choice by the animal to avoid social  
381 interactions. Furthermore, the relationship between the presence of calves and female elephant FGM  
382 concentrations should be noted and perhaps calves should be allowed to stay as long as possible with their  
383 natal group. Another approach to reduce stress, at least in male elephants, would be to make sure that all  
384 working groups have a female-skewed sex ratio. This could be achieved because sex-ratio of the adult  
385 population is markedly biased towards females due to excess mortality of males (Lahdenperä et al. 2018).  
386 However, before revised policy recommendations can be made, the potential links between higher FGM  
387 concentrations and other health modifications, such as reduced immunity, higher infection levels or  
388 altered body condition should be investigated. Several factors that have been shown to affect social  
389 behaviour as well as neuroendocrine activity were not included in our study. Though none of the male  
390 elephants in our study were in musth, olfactory cues from males in musth from neighbouring camps could  
391 have potentially affected social behaviour and neuroendocrine activity of focal elephants. Musth can have  
392 profound effects on elephant social behaviour and neuroendocrinology (Jainudeen et al., 1972;  
393 Keerthipriya et al., 2020) and hence affect the relationship between the social landscape and FGM  
394 concentrations. However, we were not aware of any cases of musth in neighbouring camps and hence we  
395 do not think that olfactory cues from neighbouring camps would have biased our results. In addition,  
396 estrous female elephants show several changes in behaviour and neuroendocrinology (Hildebrandt et al.,  
397 2011), which can also impact the the relationship between the social landscape and FGM concentrations.  
398 Unfortunately, data on musth and female cycling was not available for this study. Furthermore, it should  
399 be noted that we cannot account for any nocturnal social interactions. While data on nocturnal activity of  
400 elephants is limited, and largely focuses on fully captive systems, there is evidence that elephants in these  
401 circumstances may be stationary for large periods of the night (Lukacs et al., 2016; Wilson et al., 2006),  
402 and that activity depends on age and access to outside areas (Evison et al., 2020), suggesting that most

403 social activity takes place during diurnal hours. How this applies in wild and semi-captive conditions  
404 remains unknown. While our study aimed at characterising the general level of sociality of individual  
405 elephants in the long-term, taking into account within-individual variation due to several factors, we  
406 suggest that using social measures on a more finer scale or using social network characteristics could  
407 provide us with more details to improve our understanding of our results. Finally, mahout personality and  
408 the quality of mahout-elephant relationships (Liehrmann et al., 2021) can affect the complex interplay  
409 between social behaviours and correlating physiological measures, and therefore more research which  
410 includes those factors is necessary to fully understand elephant health. Our study therefore opens many  
411 new research avenues and helps to fill a knowledge gap on the link between sociality and GC physiology  
412 of large mammals living in their natural habitat, and sheds light on the multifaceted costs and benefits of  
413 sociality.

414

#### 415 **CRedit authorship contribution statement**

416 **Martin W. Seltsmann:** Conceptualization, Funding acquisition, Investigation, Methodology, Project  
417 administration, Writing - original draft; Writing - review & editing. **John Jackson:** Data curation, Formal  
418 analysis, Investigation, Visualization, Writing - review & editing. **Emily Lynch:** Formal analysis, Writing  
419 - original draft. **Janine L. Brown:** Methodology, Validation, Writing - review & editing. **Win Htut:**  
420 Investigation, Resources, Writing - review & editing. **Mirkka Lahdenperä:** Conceptualization, Funding  
421 acquisition, Validation, Writing - review & editing. **Virpi Lummaa:** Conceptualization, Funding  
422 acquisition, Investigation, Resources, Supervision, Writing - review & editing

423

#### 424 **Declaration of competing interests**

425 The authors declare that they have no known competing financial interests or personal relationships  
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427

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441

#### 442 **Data accessibility**

443 Data and code are available as electronic supplementary material.

444

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679 *Figure legends*

680 **Fig. 1.** The social landscape and faecal glucocorticoid metabolite concentration in Asian elephants. The  
681 influence of focal individual sociality (a) for 34 male elephants (43 observations) and sex-ratio (b) for 32  
682 male elephants (41 observations), and the effect of the presence of immature elephants (c) for 46 female  
683 elephants (74 observations). For all panels, the blue points are raw data points. For panels a and c, the  
684 black horizontal lines are the raw means, and the black points are model predicted values with prediction  
685 intervals at the 90% confidence limit. For panel b, the black line is the predicted line with the 90%  
686 prediction interval shaded in grey.

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689 *Figure 1*

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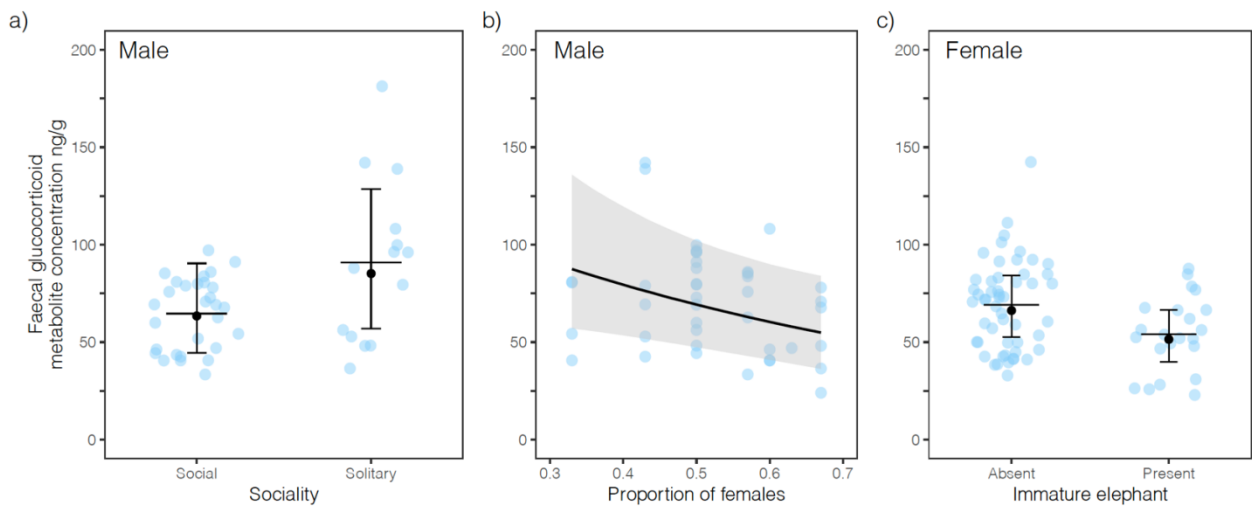
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696 **Table 1.** Model coefficients, confidence intervals and likelihood ratio test results for 3 key models  
 697 exploring the impact of the social landscape on faecal glucocorticoid metabolite (FGM) concentrations.  
 698 Estimates and confidence intervals for the fixed effects are given on the log-odds scale. Significant terms  
 699 are highlighted in bold.

Model	Sex	Effect	Term	Confidence intervals			LRT $\chi^2$	p-value
				Estimate	2.5%	97.5 %		
1	Male	Fixed	Intercept	68.3	49.4	93.6	-	-
			<b>Sociality - Solitary</b>	<b>1.55</b>	<b>1.15</b>	<b>2.05</b>	<b>8.73</b>	<b>0.003</b>
			Age	1.00	0.99	1.01	0.06	0.81
			Birth origin - Wild	0.92	0.58	1.46	0.18	0.67
		Random	Individual	0.08	0.00	0.15	-	-
			Year	0.10	0.00	0.20	-	-
			Residual	0.11	0.04	0.14	-	-
2	Male	Fixed	Intercept	112.5	54.5	222.7	-	-
			<b>Female:male sex-ratio</b>	<b>0.26</b>	<b>0.07</b>	<b>1.02</b>	<b>4.56</b>	<b>0.03</b>
			Age	1.01	1.00	1.02	3.20	0.07
			Birth origin - Wild	0.88	0.53	1.50	0.24	0.62
		Random	Individual	0.11	0.02	0.18	-	-
			Year	0.07	0.00	0.16	-	-
			Residual	0.11	0.05	0.14	-	-
3	Female	Fixed	Intercept	60.1	47.3	75.6	-	-
			<b>Immature elephant - Present</b>	<b>0.78</b>	<b>0.64</b>	<b>0.95</b>	<b>6.44</b>	<b>0.01</b>
			Age	1.01	1.00	1.01	3.57	0.06
			Birth origin - Wild	0.81	0.65	1.02	3.23	0.07
		Random	Individual	0.03	0.00	0.10	-	-
			Year	0.08	0.00	0.15	-	-
			Residual	0.13	0.09	0.15	-	-