

1 **Exploring the connections between giraffe skin disease and lion predation**

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18 **ABSTRACT**

19 Rates at which predators encounter, hunt, and kill prey are influenced by, among other
20 things, the intrinsic condition of prey. Diseases can considerably compromise body condition,
21 potentially weakening ability of afflicted prey to avoid predation. Understanding predator-prey
22 dynamics is particularly important when both species are threatened, as is the case with lions
23 (*Panthera leo*) and giraffes (*Giraffa camelopardalis*). Importantly, an emergent disease called
24 giraffe skin disease (GSD) may affect predatory interactions of lions and giraffes. Hypotheses
25 suggest GSD may negatively affect the likelihood of giraffes surviving lion attacks. We
26 evaluated giraffe-lion interactions in Ruaha National Park, Tanzania, where 85% of the giraffe
27 population has GSD. We monitored lion hunting behavior and estimated proportion of the giraffe
28 population with GSD and evidence of ‘lion marks’ from assumed previous lion predation
29 attempts (i.e. claw marks, bite marks, and missing tails). Although we recorded lions hunting and
30 feeding on 16 different prey species, giraffes represented the largest prey category (27%; $n = 171$
31 of 641). For age and sex cohorts combined, 26% ($n = 140$ of 548) of encountered giraffes
32 displayed evidence of previous lion predation attempts. Occurrence of lion marks was higher for
33 adults and males in the giraffe population, suggesting that these individuals were more likely to
34 survive lion attacks. We also found marginal evidence of a positive relationship between giraffes
35 with severe GSD and occurrence of lion marks. Our results identify giraffes as important prey
36 species for lions in Ruaha National Park and suggest that GSD severity plays a minor role in
37 likelihood of surviving a lion attack. This is the first study to explore connections between lion
38 predation and GSD. We explore the ecological implications of disease ecology on predator-prey
39 interactions and consider opportunities for future research on causal links between GSD and
40 giraffe vulnerability to lion predation.

41 **Key words:** *Giraffa camelopardalis*, giraffe skin disease, predation, disease ecology, spatial
42 capture-recapture, Tanzania

43 INTRODUCTION

44 Interactions between carnivores and ungulates are notably complex (Mysterud, 2013;
45 Dröge *et al.*, 2017; Montgomery *et al.*, 2019). Research into these dynamics has provided
46 insights into how prey species alter their behaviours, movements, and habitat selection in relation
47 to predation risk (Hebblewhite & Pletscher, 2002; Hebblewhite & Merrill, 2009; Vucetich *et al.*,
48 2011). Characteristics of carnivore and ungulate populations, as well as the environment in
49 which these species interact, influence the magnitude of antipredator responses (Montgomery *et*
50 *al.*, 2013; Moll *et al.*, 2017). Ungulates, for instance, modulate selection of comparatively ‘safe’
51 habitat where the probability of encountering predators is predictably lower (Thaker *et al.*, 2011;
52 Montgomery *et al.*, 2014). Ungulates also increase vigilance, although this behavior varies
53 according to group size, age and sex, body size and condition, time of day, moon phase, and
54 distance to woodland edge and waterhole (Winnie *et al.*, 2006; Crosmar *et al.*, 2012; Tambling
55 *et al.*, 2012; Mejlgaard *et al.*, 2013; Creel, Schuette & Christianson, 2014; Kuijper *et al.*, 2014;
56 Lashley *et al.*, 2014).

57 The body size of ungulates also affects the nature of carnivore-ungulate interactions
58 (Hayward & Kerley, 2008). Ungulates with smaller body size, for instance, are vulnerable to
59 predation from a broader suite of sympatric large carnivores compared to larger-bodied ungulates
60 in the prey assemblage (Sinclair, Mduma & Brashares, 2003; Liley & Creel, 2008; Périquet *et*
61 *al.*, 2012). In African systems, carnivore predation risk of animals weighing >1,000 kg at the
62 adult stage (e.g., giraffes - *Giraffa camelopardalis*, hippopotamus - *Hippopotamus amphibius*,
63 rhinoceros - *Ceratotherium simum*. and *Diceros bicornis*, and elephants - *Loxodonta* spp.) is
64 negligible (Radloff & du Toit, 2004; Owen-Smith & Mills, 2008). However, predation of
65 juvenile animals among these species can be considerable. African lions (*Panthera leo*) account

66 for 58-75% of mortality of giraffe calves in dry seasons when food resources are scarce
67 (Leuthold, 1979; Pellew, 1983). Adult giraffes, on the other hand, are more difficult to capture
68 because they fend off attacks by kicking (Carter *et al.*, 2013) or outrunning lions (Mitchell &
69 Skinner, 2011). In addition, giraffes often forage in open habitats with intermediate-height
70 shrubs and use fission-fusion herding to modulate predation risk (du Toit & Owen-Smith, 1989).
71 This strategy is particularly common for female giraffes that move with calves in large herds
72 offering protection from potential predators (Young & Isbell, 1991). The presence of lions does
73 not appear to affect vigilance of adult giraffes (Cameron & du Toit, 2005; Périquet *et al.*, 2010).
74 Although adult male giraffes are predominantly solitary during certain periods of their life
75 history (Ginnett & Demment, 1997; Bond *et al.*, 2019), they are mostly able to avoid lion
76 predation because of their large body size.

77 While giraffes are considered to be a preferred prey of lions (Hayward & Kerley, 2005),
78 they generally constitute a low proportion of lion diet in systems where other prey species are
79 concurrently available in the landscape. For instance, giraffes made up just 9.4% of lion diets in
80 Hwange National Park, Zimbabwe, compared to buffalo (*Syncerus caffer*), which constituted
81 40.8% (Davidson *et al.*, 2013), despite giraffes (1.49 individuals.km⁻²) being more abundant than
82 buffalo (0.92 individuals.km⁻²) in the park (Valeix *et al.*, 2007). In Kruger National Park, South
83 Africa, giraffes comprised only 1.5% of lion kills, with zebras (*Equus quagga*), wildebeest
84 (*Connochaetes taurinus*), eland (*Tragelaphus oryx*) and buffalo making up a larger portion of the
85 lion diet (Pienaar, 1969). In Murchison Falls National Park, Uganda, lions were found to predate
86 buffalo, Ugandan kob (*Kobus kob thomasi*), and hartebeest (*Alcelaphus buselaphus*), whereas the
87 killing of giraffes was extremely rare (Brenneman *et al.*, 2009). Importantly, however, certain
88 characteristics can alter the nature of lion-giraffe interactions. For example, lions have been

89 found to target adult giraffes that are weakened by drought and starvation (Hirst, 1969),
90 malnutrition (Brenneman *et al.*, 2009), young or old age (Pellew, 1983; Owen-Smith, 2008) or
91 hunt giraffes in large prides (Wright, 1960). Emerging infectious diseases also affect predator-
92 prey interactions (Moleón *et al.*, 2009) including those of carnivores and ungulates (Joly &
93 Messier, 2004). However, the extent to which diseases might modify lion-giraffe interactions
94 remains unclear.

95 Giraffe Skin Disease (GSD), first recorded in Uganda in 1995, now affects giraffe
96 populations range-wide to varying degrees (Muneza *et al.*, 2016). The disease is characterized by
97 crusty, greyish-brown lesions on the limbs, neck, shoulder, and/or chest of afflicted giraffes,
98 which are classified as either mild, moderate or severe (Muneza *et al.*, 2016, 2019). While the
99 etiological agent of GSD is unknown, external symptoms of the disease have been predominantly
100 recorded in sub-adult and adult giraffes (Mpanduji, Karimuribo & Epaphras, 2011; Epaphras *et*
101 *al.*, 2012; Muneza *et al.*, 2016). To date, no study has assessed the pathophysiology of GSD,
102 though anecdotal observations suggest that severe GSD may inhibit giraffe movements
103 (Epaphras *et al.*, 2012; Muneza *et al.*, 2016), which could potentially increase vulnerability of
104 adult giraffes to lion predation. We hypothesized giraffes with GSD had a higher likelihood of
105 being selected by lions compared to healthy individuals given that affected individuals present
106 external symptoms that would make them easy prey.

107 We investigated lion-giraffe interactions in Ruaha National Park, Tanzania, which has the
108 highest prevalence rate (86% of the giraffe population is infected) of GSD in a wild giraffe
109 population recorded to date (Muneza *et al.*, 2017). We surveyed the giraffe population to
110 estimate the proportion of individuals with ‘lion marks’ (i.e., claw marks, bite marks, and
111 missing tails), which we assumed indicated previous lion predation attempts, recorded presence

112 and severity of GSD, and collected data on lion hunting behavior to document lion selection of
113 giraffes in comparison to sympatric prey species. Importantly, lion marks provide a conservative
114 estimate of the rates of lion attack. For instance, the marks may represent more than one attack
115 event and there are undoubtedly instances in which lions chased giraffes and did not leave a
116 mark. It is important to note that lions are the only sympatric carnivore species likely to be
117 responsible for these distinctive marks on giraffes (Schaller, 1972; Strauss & Packer, 2013). We
118 examine *i*) the role of GSD in relation to likelihood of giraffes surviving a lion attack, *ii*) discuss
119 the implications of disease ecology for predator-prey interactions more broadly, and *iii*) explore
120 the inferences of our research for conservation.

121 **METHODS**

122 **Study area**

123 Ruaha National Park (20,226 km²) is Tanzania's second largest national park and located
124 in the south-central region of the country (Fig. 1). The park is considered a priority area for large
125 carnivore conservation as it has important populations of cheetahs (*Acinonyx jubatus*), African
126 wild dogs (*Lycaon pictus*), leopards (*Panthera pardus*), spotted hyaenas (*Crocuta crocuta*) and
127 lions (Abade, Macdonald & Dickman, 2014). Habitats in the park include open savannah,
128 wetlands (swampy and riverine habitat), and closed woodlands (Epaphras *et al.*, 2007). This
129 ecosystem supports at least 13 species of ungulates that are vulnerable to lion predation (Table
130 1), including one of the largest populations of greater kudu (*Tragelaphus strepsiceros*), eland and
131 Sable antelope (*Hippotragus niger*) in East Africa (TAWIRI, 2015). The park is home to largest
132 giraffe population in southern Tanzania with 3,881 ($\pm 1,023$) individuals recorded during aerial
133 surveys (TAWIRI, 2015).

134 **Photographic capture-recapture surveys**

135 We conducted road-based photographic encounter surveys for giraffes from May 2015 to
136 August 2015 to quantify sex, age class (calf, subadult or adult), presence and severity of GSD,
137 and evidence of a previous lion predation attempt. We divided the accessible road network into
138 five transects, each ~100 km in length ($\bar{x} = 99.22$ km, $SD = 3.72$; Fig. 1), which we then
139 surveyed 10 times. We considered giraffes to be detectable within a 200 m buffer on either side
140 of the transect. When we encountered giraffes, we took georeferenced right-side photos of each
141 animal using a Nikon D300s DSLR camera with an auto-focus S-DX Nikkor 70-300mm f/3.5 –
142 5.6 ED VR lens to facilitate individual animal identification. Given that GSD lesions manifest
143 externally on afflicted giraffes and can be seen clearly using binoculars (Epaphras *et al.*, 2012),
144 we classified severity of the lesions in four different categories: none, mild (small skin nodules
145 of <3cm in diameter with raised hair), moderate (medium-sized patch of alopecic lesions of 10 –
146 16cm in diameter) and severe (large-sized lesions >16cm in diameter characterized by scabs and
147 cracks with raw fissure; see Muneza *et al.*, 2016). Later, we used the pattern recognition software
148 Wild-ID (Bolger *et al.*, 2012) to identify individual giraffes and obtain their unique capture
149 histories (see Muneza *et al.*, 2017).

150 We also examined prevalence and anatomical location of marks (claw marks, bite marks,
151 missing tail) assumed to be indicative of a previous lion predation attempt (Fig. 2). When prey
152 survives an attempted carnivore attack, marks of the predation attempt can remain visible as
153 scars (de Azevedo, 2008), which are regularly used to study predator-prey interactions
154 (Carpenter, 1998; Fahlke, 2012). Such marks have been effectively used to examine the
155 influence of age, sex, herd size, and height of individually-recognized Masai giraffes (*G. c.*
156 *tippelskirchi*) in Serengeti National Park, Tanzania subject to lion predation (Strauss & Packer,

157 2013). We acknowledge, however, that our survey techniques could not distinguish between
158 single or multiple lion predation attempts or the date of the attack(s). Thus, where these marks
159 (hereafter referred to as lion marks) were detected, we conservatively estimated that giraffes had
160 survived at least one previous lion predation attempt.

161 **Spatial capture-recapture model**

162 We fit a spatial capture-recapture (SCR) model to the photographic capture-recapture
163 survey data to estimate the *i*) probability of lion marks in the giraffe population and *ii*)
164 relationship between probability of lion marks and sex, age, and GSD severity while accounting
165 for individual variation in capture probability. We divided our study area into 2 x 2 km grid cells
166 and modeled the number of encounters for individual *i* in grid cell *j* as a Poisson random variable
167 with mean encounter rate λ_{ij} . Following standard SCR models (Borchers & Efford, 2008; Royle
168 *et al.*, 2014), the encounter rate decreased with increasing distance d_{ij} between the latent activity
169 center for individual *i* and the location of grid cell *j* using a half-normal function, such that:

$$170 \lambda_{ij} = \lambda_{0ij} \times \exp(-d_{ij}^2/2\sigma_i^2)$$

171 Both the baseline encounter rate, λ_{0ij} (when $d_{ij} = 0$), and the scale parameter of the half-normal
172 detection function, σ_i , were allowed to vary according to individual attributes including 1) sex,
173 with female as the reference category; 2) age class, with adult as the reference category; 3) an
174 interaction of sex \times age class; and 4) the presence/absence of severe GSD. We estimated these
175 relationships by specifying linear models on the log scale for each parameter, $\log(\lambda_{0ij}) = \mathbf{X}_i\boldsymbol{\alpha}$ and
176 $\log(\sigma_i) = \mathbf{X}_i\boldsymbol{\delta}$, where \mathbf{X}_i is the design matrix of individual attributes and the parameters to
177 estimate are $\boldsymbol{\alpha}$ and $\boldsymbol{\delta}$. In addition to the individual attributes, we included an offset term on the
178 encounter rate to adjust for total hours (i.e., effort) spent surveying grid cell *j*, calculated as the
179 total survey duration scaled by linear length of overlapping survey units. Latent activity centers

180 were assumed to be uniformly distributed as a homogeneous point process such that density was
181 expected to be constant across the region (Royle *et al.*, 2014). We eliminated calves from our
182 SCR analysis because their movement directly depends on their mother, which does not meet the
183 criteria of independence required for such models (Borchers & Fewster, 2016), thus our
184 inferences are limited to adults and subadults.

185 As part of the SCR model, individual attributes were explicitly modeled to both estimate
186 their proportions within the giraffe population and to explore relationships with the presence of
187 lion marks. Each of the three individual attributes (sex, age class, severe GSD) were specified as
188 binary random variables with an associated probability for the non-reference category: $\Pr(\text{male}_i)$
189 $= \psi_{\text{male}}$; $\Pr(\text{subadult}_i) = \psi_{\text{subadult}}$; and $\Pr(\text{sevGSD}_i) = \psi_{\text{sevGSD}}$. While most encountered individuals
190 had an observed value for each attribute, some attribute observations were incomplete making
191 them partially latent variables. Unobserved individuals have no observations by definition. These
192 challenges were accommodated by fitting the model using a Bayesian approach with data
193 augmentation (Royle, Dorazio & Link, 2007) which is a common implementation for SCR
194 (Royle *et al.*, 2014). In this way, attribute probabilities were assigned prior distributions which
195 combined with observed proportions among encountered individuals and any adjustments due to
196 encounter rates to inform posterior distributions. This resulted in an observed value or estimated
197 latent value of each attribute for each individual i in the model. Finally, we estimated the
198 occurrence of lion marks with a logit-linear model:

$$199 \quad \text{logit}(\psi_{\text{marks}}) = \beta_0 + \beta_1 \text{male}_i + \beta_2 \text{subadult}_i + \beta_3 \text{sevGSD}_i$$

200 Here, the intercept β_0 represents the logit-scale probability of an adult female without severe
201 GSD having evidence of a lion attack, while the other regression coefficients represent the
202 relative change in this probability due to individual attributes.

203 We fit the model using Markov chain Monte Carlo (MCMC) methods in JAGS
204 (Plummer, 2003) with the jagsUI (Kellner, 2014) package in R (R Core Team, 2020). We used
205 vague prior distributions for all model parameters including Uniform(0, 1) for all probabilities;
206 Uniform(−10, 10) for log-scale intercepts; and Normal(0, 10) for all other regression coefficients
207 (Table 2). We fit 3 chains of 9,000 iterations after a 1,000-iteration adaptation period, leaving
208 27,000 values forming the posterior distribution for each parameter. Model convergence was
209 approximated by examining trace plots and ensuring an R-hat value <1.1 for all model
210 parameters. We report posterior mean values with standard deviations and 95% credible intervals
211 for model parameters. We considered regression coefficients with 95% intervals that did not
212 overlap zero as evidence for an effect. Model code was written in BUGS language and is
213 provided in supporting information (Appendix 1).

214 **Lion hunting surveys**

215 To examine patterns of prey selection by lions, we conducted opportunistic surveys to
216 record locations where lions were observed to hunt prey (i.e., chase or kill) between January
217 2009 and December 2015 in Ruaha National Park. We recorded the number of individual lions
218 detected and prey species hunted. We then used Jacobs' index to quantify relative selection of
219 different prey species in Ruaha National Park based on:

$$220 \quad D = \frac{r - p}{r + p - 2rp}$$

221 Whereby r is the proportion of a species of the total hunts and p is the proportional availability of
222 the species (Jacobs, 1974). Proportional availability was obtained from data on aerial surveys
223 conducted by the Tanzania Wildlife Research Institute (2015) and our surveys on lion feeding

224 behaviour. Jacobs' index values for a prey species D range from -1 to $+1$ with negative values
225 indicating avoidance and positive values indicating selection.

226 RESULTS

227 We recorded 336 sightings (consisting of \geq one giraffe) and collected 2,129 images of
228 giraffes from our photographic capture-recapture surveys. We detected 622 individual giraffes
229 including 333 adult females, 160 adult males, 38 subadult females, 32 subadult males, and 59
230 calves. The average giraffe herd size was 5.28 (± 0.16) individuals (range 1–36). We observed 21
231 instances of giraffes limping due to injuries likely sustained from a lion predation attempt as we
232 recorded lion marks on these individuals (Fig. 2, main panel). We were able to confirm the
233 presence or absence of lion marks among 548 giraffes in our population. Among those, 26% ($n =$
234 140) had lion marks, with female giraffes accounting for 59% ($n = 82$) of the individuals we
235 encountered with signs of attempted predation. Female giraffes also exhibited a higher variation
236 in anatomical location of lion marks (Fig. 3). We observed three calves (2.1%) with either a
237 missing tail ($n = 2$) or claw marks on the rump and limbs ($n = 1$). We recorded both severe GSD
238 and lion marks in 89 giraffes, of which 53 were female (59.5%) and 36 were male (40.5%).

239 Parameter estimates from the SCR model indicated that individuals were more likely to
240 be female (64%; $\psi_{\text{male}} = 0.36$ [0.030, 0.415]) and adult (87%; $\psi_{\text{subadult}} = 0.13$ [0.094, 0.177])
241 giraffes, with 85% of the study population having GSD and 60% having severe cases of the
242 disease (Table 2). The proportion of the giraffe population with lion marks was highest (i.e.
243 $>40\%$) in the northeastern section of the study area (Fig. 4). We found strong evidence that lion
244 marks were more common on male giraffes ($\beta_1 = 0.519$ [0.117, 0.923]), and the probability of
245 subadult giraffes having lion marks was considerably lower ($\beta_2 = -0.829$ [-1.643, -0.078]; Table
246 2). We found marginal evidence that giraffes with severe GSD were more likely to have lion

247 marks ($\beta_3 = 0.334 [-0.083, 0.759]$). Adult males with severe GSD had the highest occurrence of
248 lion marks (Fig. 5).

249 The average size of lion prides was 5.8 individuals (range 1 – 42), and we documented
250 641 unique sightings of \geq one lion hunting 16 different prey species (Fig. 6). Based on these
251 observations, giraffes were the most selected species by lion ($n = 171$) followed by buffalo ($n =$
252 119), elephant ($n = 75$), and zebra ($n = 52$). Giraffes accounted for 27% ($n = 171$ of 641) of the
253 prey species in these lion hunts. Jacobs' index revealed that giraffes ($D = 0.24$) and buffalo ($D =$
254 0.23) were positively selected by lions, whereas eland ($D = -0.21$) and greater kudu ($D = -0.14$)
255 were avoided.

256

257 **DISCUSSION**

258 We examined the potential implications of GSD on the predatory interactions of lions and
259 giraffes. The Jacob's index values revealed that giraffes, with buffaloes a close second, were the
260 most highly selected prey species by lions in Ruaha National Park (Table 1), consistent with
261 predictions based on body size (Hayward & Kerley, 2005). This relationship was evident despite
262 the fact that other concurrent prey species were more abundant than giraffes. Additionally, across
263 a six-year monitoring period, we found that lions hunted giraffes at a higher frequency than other
264 sympatric prey species (Fig. 6), with GSD severity as a potential modulating mechanism. Higher
265 selection of giraffes by lions in Ruaha National Park could indicate a predatory strategy of
266 targeting a large prey to access a higher concentration of food resources in a single kill
267 (Loveridge *et al.*, 2009). Among the prey selected by lions in Ruaha National Park, giraffes have
268 the largest average body mass (Table 1; Hayward & Kerley, 2005). This explanation might be

269 supported by the fact that lions in Ruaha National Park tend to move in larger prides compared to
270 other parks in Tanzania. Specifically, Ruaha National Park has the highest average size of a lion
271 pride in Tanzania ($n = 5.8$), almost two lions higher than any other park (Mosser & Packer,
272 2009). Furthermore, the range of lion prides that we observed in Ruaha National Park was as
273 high as 42 individuals. Thus, lions in the park could simply be targeting giraffes more often to
274 acquire food resources for large prides or be more successful in cooperatively hunting giraffes
275 regardless of GSD severity.

276 We detected spatial variation in the proportion of the giraffe population with evidence of
277 previous lion predation attempts. Specifically, we found that the northeastern section of the study
278 area (Serengeti Ndogo transect; Fig. 1) had the highest proportion of giraffes with lion marks
279 (Fig. 4), though the area also had the highest density of giraffes in the park. This area is adjacent
280 to open savannah and woodland habitat directly next to the Great Ruaha River, which provides
281 the only year-round natural source of water for wildlife in the park used by giraffes and other
282 prey (Mtahiko *et al.*, 2006). We suspect that lions may be using hunting grounds near water to
283 increase hunting success (*sensu* Funston, Mills, & Biggs, 2001; Spong, 2002). However, lion
284 hunting behavior and giraffe availability do not alone explain why giraffes are highly selected
285 prey for lions in Ruaha National Park. We detected a weak positive relationship between giraffes
286 with severe GSD and the occurrence of lion marks. It is unknown whether this relationship exists
287 in other giraffe populations where GSD has been recorded given that there is variation in
288 manifestation of the disease across the range of giraffes (Muneza *et al.*, 2016). As such,
289 additional research is required to assess the impact of GSD on lion-giraffe interactions across the
290 range of these species.

291 Lions have also been found to select for vulnerable characteristics in prey populations
292 including malnourishment, disease, and life history stage (Hirst, 1969; Brenneman *et al.*, 2009;
293 Moleón *et al.*, 2009). Some have speculated that the presence of severe GSD lesions on the limbs
294 of Masai giraffes might limit their movements and subsequent ability to evade lion predation
295 (Karimuribo *et al.*, 2011; Epaphras *et al.*, 2012). We detected marginal evidence of a positive
296 relationship between giraffes with severe GSD lesions and occurrence of lion marks (Table 2,
297 Figure 6), suggesting that GSD severity did not affect the likelihood of surviving a lion attack.
298 However, we did not identify any direct links between GSD and likelihood of surviving a lion
299 attack. The patterns that we detected are correlative rather than mechanistic. Additional research
300 will be needed to assess whether GSD physically weakens giraffes, thereby making them easier
301 prey of lions. We found that while male giraffes constituted ~36% of the population in the study
302 area, they were more likely to have lion marks (odds ratio = $\exp(\beta_1) = 1.68$ [1.12–2.52]; Table
303 2). Male giraffes are more likely to survive a lion attack (Pellew, 1983; Carter *et al.*, 2013)
304 whereas females and subadults with smaller body sizes (van Sittert, Skinner & Mitchell, 2010)
305 are less likely to survive a lion attack. Thus, as GSD appears to be a progressive disease, we
306 suspect that adult male giraffes may be better able to survive long enough for GSD lesions to
307 advance in severity (Muneza *et al.*, 2016). Additional surveys in different seasons that include
308 mortality data can help determine the direct links between the progression of GSD severity and
309 probability of surviving lion attacks.

310 In discussing the patterns, we observed, our hope is to spur the process of identifying
311 creative future avenues of research regarding the nuanced roles of disease in predator-prey
312 interactions. Lions account for ~75% of giraffe calf mortality (Pellew, 1983). We do not suspect
313 that GSD is particularly influential among lion and calf/sub-adult giraffe interactions given that

314 symptoms of the disease are rare in these life history stages (Muneza *et al.*, 2017). Despite the
315 general lack of GSD influence on giraffe survival, additional research may be warranted
316 regarding potential mechanistic connections. It remains unclear, for instance, whether GSD
317 directly influences survivability of giraffes or if vulnerability to lion predation might increase for
318 individual giraffes with this disease. Furthermore, we observed 21 giraffes with both severe GSD
319 and evidence of a previous lion predation attempt moving with difficulty during our surveys.
320 From our observations, the lion marks heal but severity of GSD does not change (Muneza *et al.*,
321 2017). We identified one limping giraffe with a lion predation mark on the front left limb in June
322 2015 and later encountered that same individual in August 2015 with what appeared to be a
323 healed lion predation wound (Fig. 7). In contrast, the GSD lesions were still visible and had the
324 same category of severity. Given that recent studies have focused on external manifestation of
325 GSD (Mpanduji *et al.*, 2011; Muneza *et al.*, 2016, 2019), there is a critical need to expound on
326 the pathophysiology of GSD.

327 Our study shows that GSD may not have a direct impact on lion-giraffe interactions.
328 Additional investigation into GSD-induced behaviours of and physiological changes in giraffes
329 may elucidate any potential variations in these interactions. Diseases influence predator-prey
330 interactions and can lead to collapse of entire populations either directly or indirectly (Joly &
331 Messier, 2004; Jones *et al.*, 2007; Moleón, Almaraz & Sánchez-Zapata, 2008; Puechmaille *et al.*,
332 2011). This is particularly important given that we know little about the indirect effects of
333 diseases on populations such as changes in demographic structures (Lachish, McCallum & Jones,
334 2009) or variation in vulnerability to predation. Understanding these dynamics can improve and
335 inform wildlife management decisions and policy. In conclusion, we recommend additional

336 research that seeks to find the mechanistic connections that may underpin correlations between
337 GSD and lion predation in different ecosystems.

338

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530

531 **TABLES**

532 **Table 1.** Common ungulates found in Ruaha National Park and associated population estimate, Jacobs' index, average body mass, and
 533 lion (*Panthera leo*) dietary preference. Population estimates are based on data gathered by the Tanzania Wildlife Research Institute
 534 (2015), whereas lion dietary preference was adapted from Hayward & Kerley (2005). We calculated Jacobs' index for species where
 535 both lion hunting and population estimates were available.

Common name	Scientific name	Population estimate <i>n</i>	Jacob's index <i>D</i>	Average adult body mass (kg)	Lion dietary preference
Buffalo	<i>Syncerus caffer</i>	29,211	0.23	481	Preferred
Duiker	<i>Sylvicapra grimmia</i>	12,187	-	25	Avoided
Eland	<i>Tragelaphus oryx</i>	2,135	-0.21	400	Taken in accordance to relative abundance
Elephant	<i>Loxodonta africanus</i>	15,836	0.13	1600	Avoided
Greater kudu	<i>Tragelaphus strepsiceros</i>	2,266	-0.14	270	Taken in accordance to relative abundance
Hartebeest	<i>Alcelaphus buselaphus</i>	3,323	-	150	Taken in accordance to relative abundance
Impala	<i>Aepyceros melampus</i>	16,087	0.02	56	Avoided
Masai giraffe	<i>Giraffa camelopardalis tippelskirchi</i>	3,881	0.24	900	Preferred
Reedbuck	<i>Redunca arundinum</i>	2,623	-	61	Avoided
Roan antelope	<i>Hippotragus equinus</i>	2,338	-	280	Taken in accordance to relative abundance
Sable antelope	<i>Hippotragus niger</i>	3,896	-	235	Taken in accordance to relative abundance
Warthog	<i>Phacochoerus africanus</i>	3,940	-0.12	83	Taken in accordance to relative abundance
Zebra	<i>Equus quagga</i>	4,937	0.02	271	Preferred

536

537 **Table 2.** Parameter estimates from the spatial capture–recapture (SCR) model of Masai giraffes
538 (*Giraffa camelopardalis tippelskirchi*) in Ruaha National Park, Tanzania, in 2015. The individual
539 attribute probabilities are on the probability scale, while other parameters (e.g., α , δ , β) are on the
540 logit scale. These parameters include probabilities for individual attributes such as population
541 membership (ψ), sex (ψ_{male}), age class (ψ_{subad}), signs of GSD (ψ_{GSD}) and number of legs with
542 severe lesions (φ_k); loglinear regression coefficients for the encounter rate (α) and the scale
543 parameters of the half-normal detection functions (δ and β); and derived parameters of
544 population size (N).

Parameter	Effect	Median	95% CRI
ψ		0.75	[0.67, 0.84]
ψ_{sex}		0.35	[0.30, 0.41]
ψ_{GSD}		0.86	[0.83, 0.89]
$\psi_{\text{Marks [1]}}$	# of legs with severe GSD	0.28	[0.19, 0.38]
$\psi_{\text{Marks [2]}}$	# of legs with severe GSD	0.31	[0.23, 0.39]
$\psi_{\text{Marks [3]}}$	# of legs with severe GSD	0.30	[0.22, 0.41]
ψ_{age}		0.13	[0.09, 0.18]
$\varphi_{k=1}$		0.67	[0.61, 0.72]
$\varphi_{k=2+}$		0.45	[0.39, 0.51]
α_0		-1.57	[-0.87, -1.27]
α_1	male	-0.47	[-0.90, -0.09]
α_2	subadult	0.35	[-0.32, 0.95]
α_3	sex \times age	-0.50	[-1.39, 0.43]
α_4	# of legs with severe GSD	-0.12	[-0.38, 0.12]
α_5	predation marks	-0.49	[-1.11, 0.13]
α_6	legs * marks	0.28	[-0.19, 0.77]
δ_0		0.91	[0.78, 1.06]
δ_1	male	0.14	[-0.05, 0.33]
δ_2	subadult	-0.32	[-0.59, -0.02]
δ_3	sex \times age	0.56	[0.14, 0.96]
δ_4	# of legs with severe GSD	-0.02	[-0.14, 0.09]
δ_5	predation marks	-0.04	[-0.30, 0.25]
δ_6	legs * marks	0.02	[-0.19, 0.23]
N		1819	[1614, 2040]
D		0.55	[0.49, 0.62]

545
546

547 **FIGURE LEGENDS**

548 **Figure 1.** The study area in Ruaha National Park, Tanzania surveyed for Masai giraffe (*Giraffa*
549 *camelopardalis tippelskirchi*) distribution and lion (*Panthera leo*) activity (May to August 2015).

550 The different lion sightings depict instances where lions were either hunting or feeding on
551 giraffe.

552 **Figure 2.** Examples of previous lion (*Panthera leo*) predation attempts (a = claw marks; b =
553 missing/partially amputated tail; c = bite marks) and manifestation of giraffe skin disease (GSD)
554 on the limbs of Masai giraffe (*Giraffa camelopardalis tippelskirchi*) (d) that we recorded in
555 Ruaha National Park, Tanzania (May to August 2015).

556 **Figure 3.** Proportion of Masai giraffe (*Giraffa camelopardalis tippelskirchi*) population with
557 evidence of previous lion (*Panthera leo*) predation attempts and GSD lesions. The graph is based
558 on giraffes, by age and sex, that were encountered and individually identified during the road-
559 based photographic capture-recapture (SCR) surveys in Ruaha National Park and showed signs
560 of attempted predation by lions (n=143) and at least one GSD lesion (n=477). (F = female; M =
561 male; sbA = sub-adult).

562 **Figure 4.** The predictive map of Masai giraffe (*Giraffa camelopardalis tippelskirchi*) density and
563 proportion of the giraffe population with lion marks in Ruaha National Park, Tanzania developed
564 using spatial capture-recapture (SCR) models. The grid cell resolution was 2km x 2km and the
565 map shows areas of higher giraffe survivability from lion attacks.

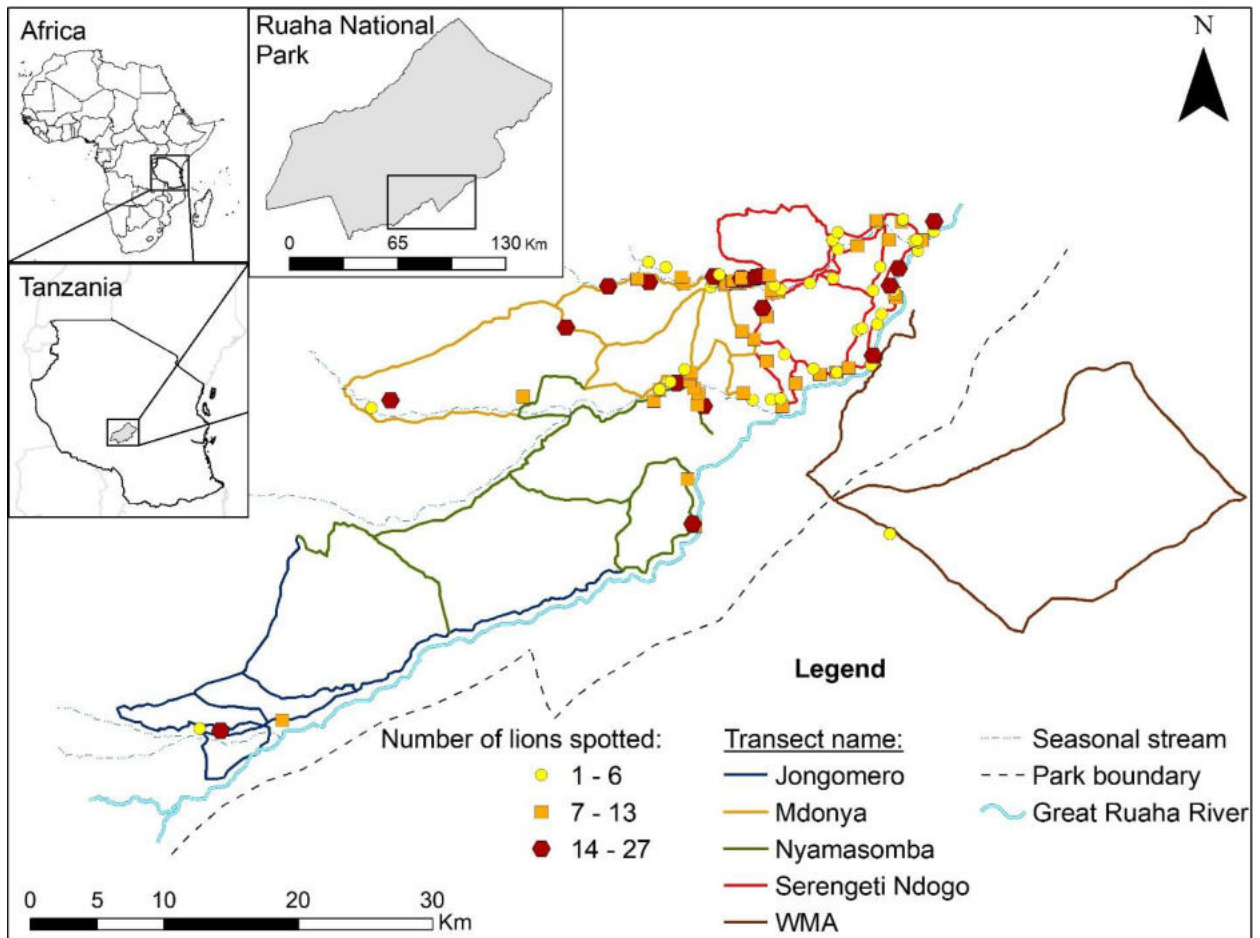
566 **Figure 5.** Probability estimates of Masai giraffe (*Giraffa camelopardalis tippelskirchi*) with
567 external manifestations of severe and non-severe GSD having lion marks in Ruaha National
568 Park, Tanzania.

569 **Figure 6.** The diversity of prey species that lions (*Panthera leo*) were observed consuming in
570 Ruaha National Park, Tanzania during our survey. For this study, the cause of prey species
571 mortality was not identified.

572 **Figure 7.** Lion predation mark on the front left limb of a male Masai giraffe (*Giraffa*
573 *camelopardalis tippelskirchi*) in Ruaha National Park, Tanzania. While the wound slowly
574 recovered with time, externally at the very least (photo ‘a’ was taken a month apart from photo
575 ‘b’), the giraffe still had a noticeable limp when moving around and the lion marks on the hind
576 limbs and flank were still visible.

577

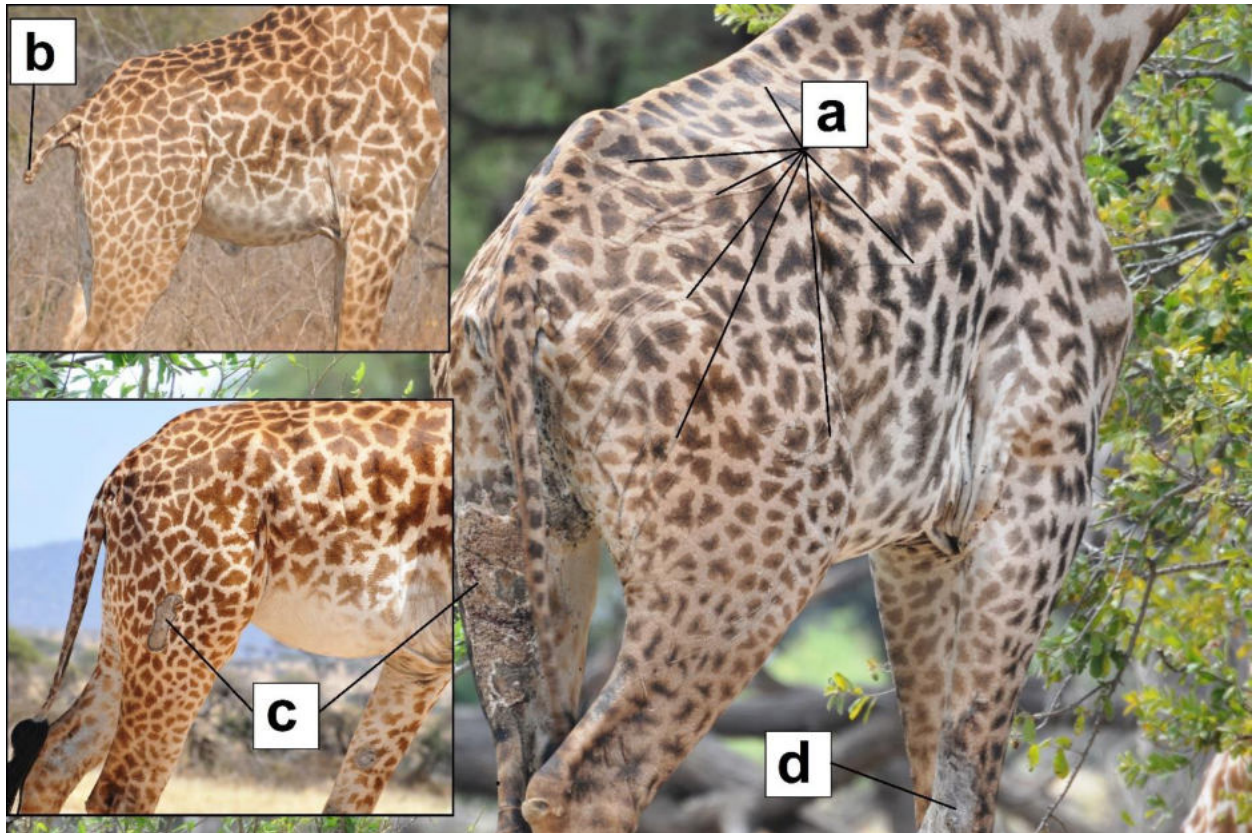
578 **Figure 1**



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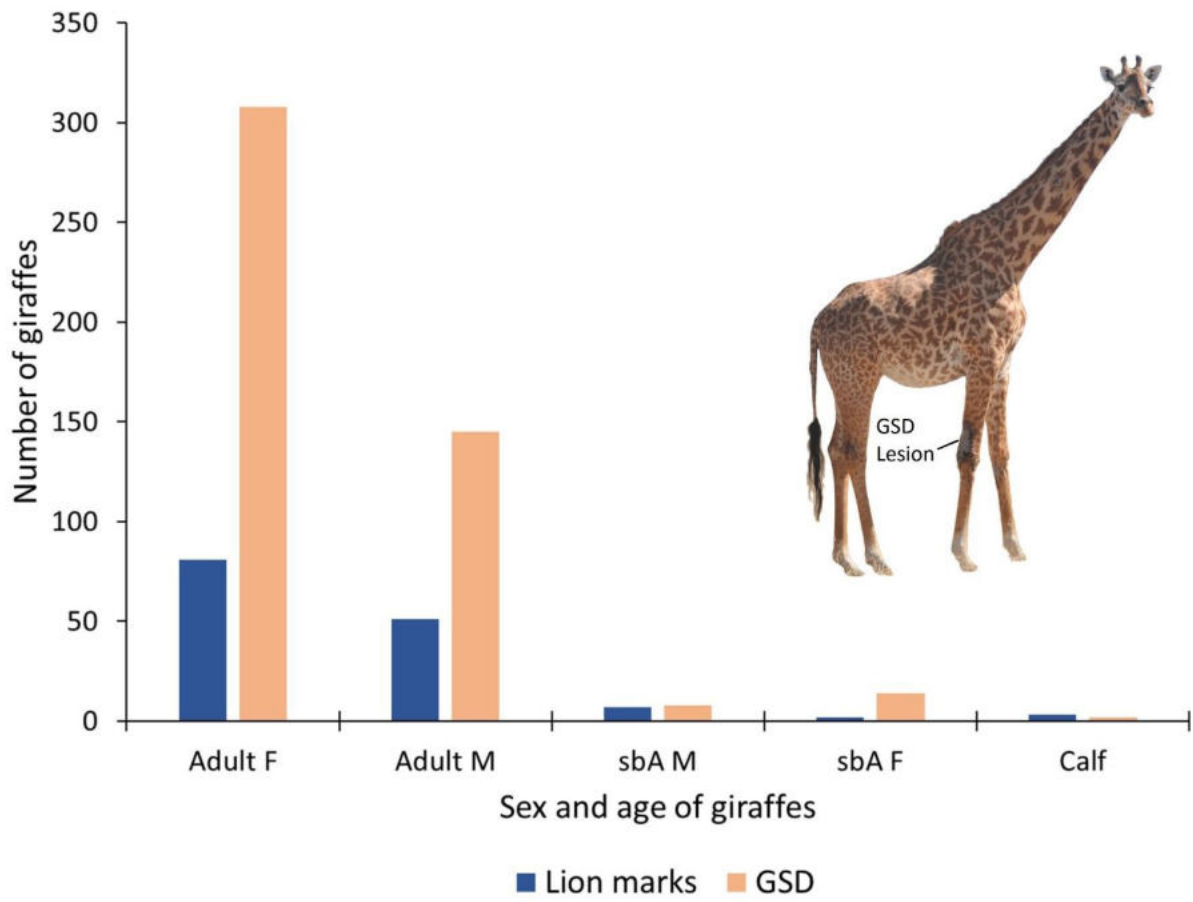
581 **Figure 2**



582

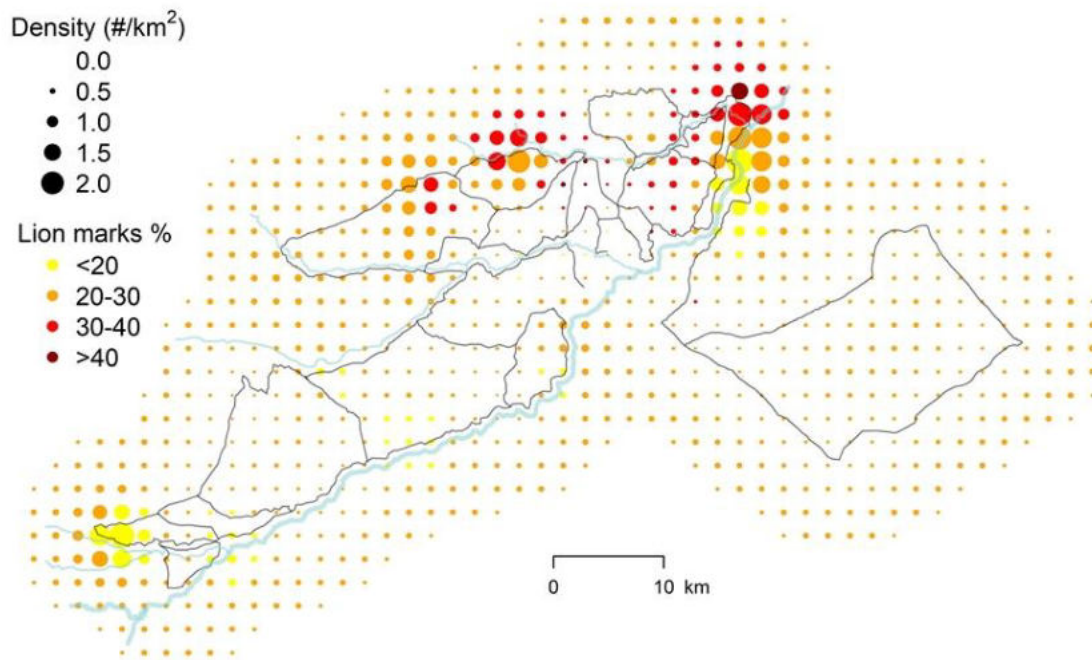
583

584 **Figure 3**



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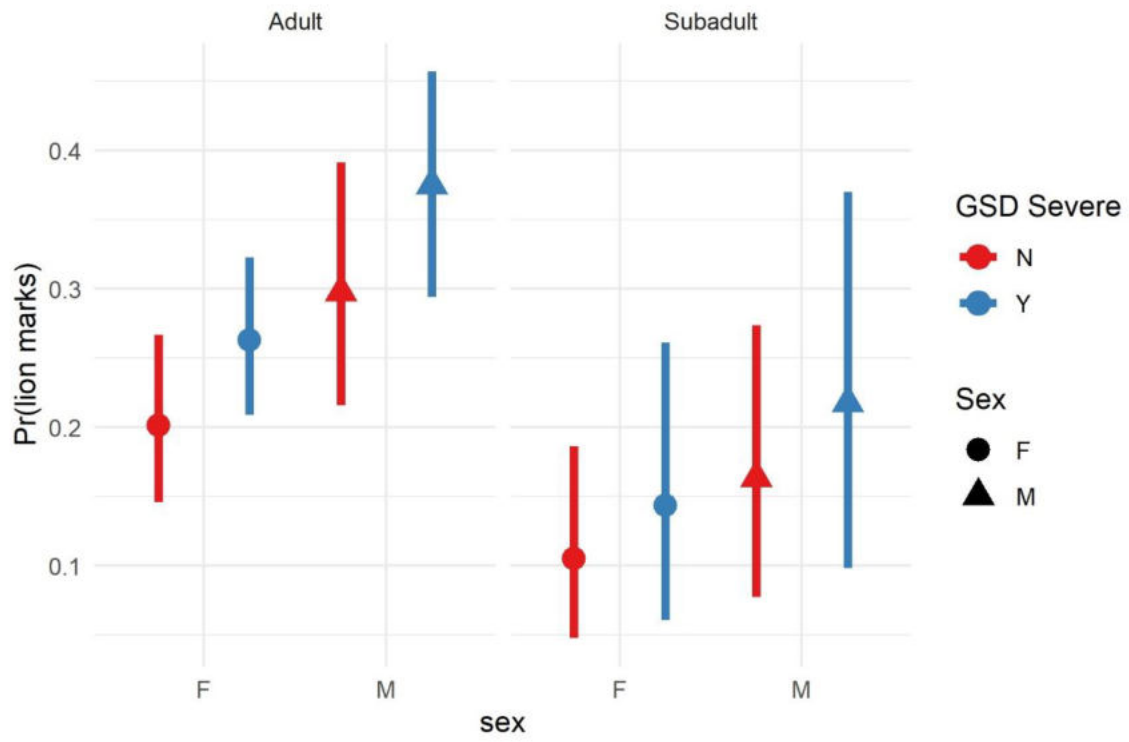
586 **Figure 4**



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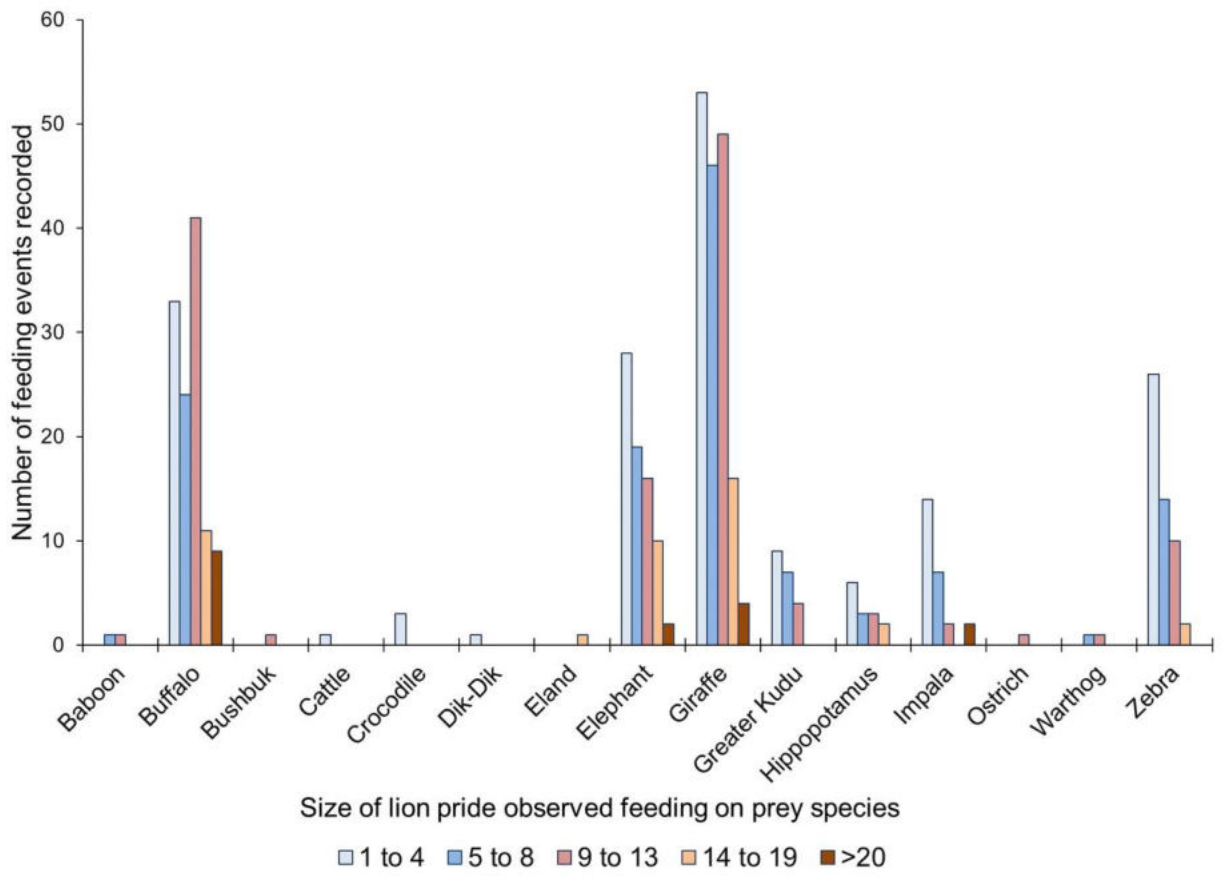
588

589 **Figure 5**



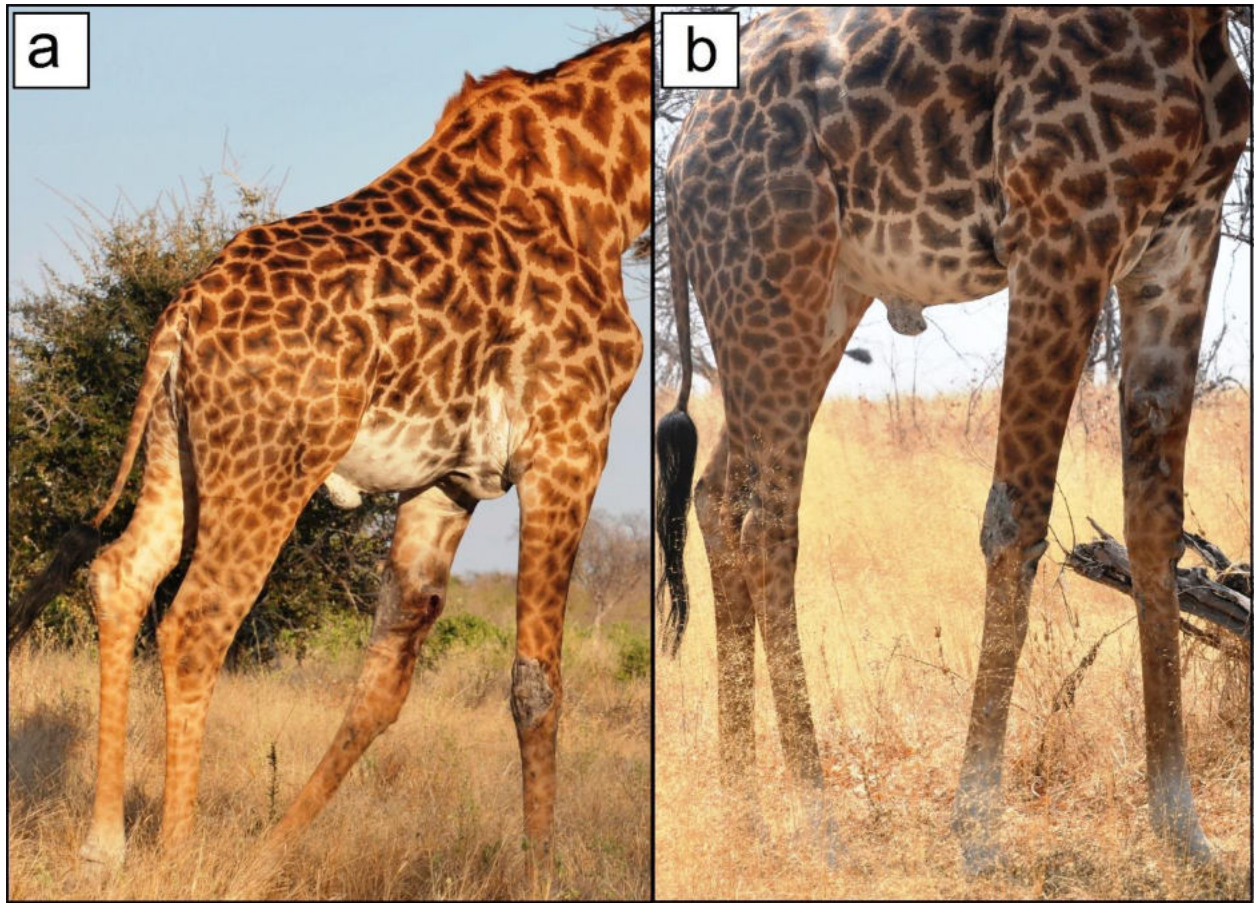
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591 **Figure 6**



592

593 **Figure 7**



594