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Exploring the connections between giraffe skin disease and lion predation

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ABSTRACT

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

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

INTRODUCTION

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

The body size of ungulates also affects the nature of carnivore-ungulate interactions (Hayward & Kerley, 2008). Ungulates with smaller body size, for instance, are vulnerable to predation from a broader suite of sympatric large carnivores compared to larger-bodied ungulates in the prey assemblage (Sinclair, Mduma & Brashares, 2003; Liley & Creel, 2008; Périquet *et al.*, 2012). In African systems, carnivore predation risk of animals weighing >1,000 kg at the adult stage (e.g., giraffes - *Giraffa camelopardalis*, hippopotamus - *Hippopotamus amphibius*, rhinoceros - *Ceratotherium simum.* and *Diceros bicornis*, and elephants - *Loxodonta* spp.) is negligible (Radloff & du Toit, 2004; Owen-Smith & Mills, 2008). However, predation of juvenile animals among these species can be considerable. African lions (*Panthera leo*) account for 58-75% of mortality of giraffe calves in dry seasons when food resources are scarce (Leuthold, 1979; Pellew, 1983). Adult giraffes, on the other hand, are more difficult to capture because they fend off attacks by kicking (Carter *et al.*, 2013) or outrunning lions (Mitchell & Skinner, 2011). In addition, giraffes often forage in open habitats with intermediate-height shrubs and use fission-fusion herding to modulate predation risk (du Toit & Owen-Smith, 1989). This strategy is particularly common for female giraffes that move with calves in large herds offering protection from potential predators (Young & Isbell, 1991). The presence of lions does not appear to affect vigilance of adult giraffes (Cameron & du Toit, 2005; Périquet *et al.*, 2010). Although adult male giraffes are predominantly solitary during certain periods of their life history (Ginnett & Demment, 1997; Bond *et al.*, 2019), they are mostly able to avoid lion predation because of their large body size.

While giraffes are considered to be a preferred prey of lions (Hayward & Kerley, 2005), they generally constitute a low proportion of lion diet in systems where other prey species are concurrently available in the landscape. For instance, giraffes made up just 9.4% of lion diets in Hwange National Park, Zimbabwe, compared to buffalo (*Syncerus caffer*), which constituted 40.8% (Davidson *et al.*, 2013), despite giraffes (1.49 individuals.km^{-2}) being more abundant than buffalo (0.92 individuals.km^{-2}) in the park (Valeix *et al.*, 2007). In Kruger National Park, South Africa, giraffes comprised only 1.5% of lion kills, with zebras (*Equus quagga*), wildebeest (*Connochaetes taurinus*), eland (*Tragelaphus oryx*) and buffalo making up a larger portion of the lion diet (Pienaar, 1969). In Murchison Falls National Park, Uganda, lions were found to predate buffalo, Ugandan kob (*Kobus kob thomasi*), and hartebeest (*Alcelaphus buselaphus*), whereas the killing of giraffes was extremely rare (Brenneman *et al.*, 2009). Importantly, however, certain characteristics can alter the nature of lion-giraffe interactions. For example, lions have been found to target adult giraffes that are weakened by drought and starvation (Hirst, 1969), malnutrition (Brenneman *et al.*, 2009), young or old age (Pellew, 1983; Owen-Smith, 2008) or hunt giraffes in large prides (Wright, 1960). Emerging infectious diseases also affect predator-prey interactions (Moleón *et al.*, 2009) including those of carnivores and ungulates (Joly & Messier, 2004). However, the extent to which diseases might modify lion-giraffe interactions remains unclear.

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

We investigated lion-giraffe interactions in Ruaha National Park, Tanzania, which has the highest prevalence rate (86% of the giraffe population is infected) of GSD in a wild giraffe population recorded to date (Muneza *et al.*, 2017). We surveyed the giraffe population to estimate the proportion of individuals with 'lion marks' (i.e., claw marks, bite marks, and missing tails), which we assumed indicated previous lion predation attempts, recorded presence and severity of GSD, and collected data on lion hunting behavior to document lion selection of giraffes in comparison to sympatric prey species. Importantly, lion marks provide a conservative estimate of the rates of lion attack. For instance, the marks may represent more than one attack event and there are undoubtedly instances in which lions chased giraffes and did not leave a mark. It is important to note that lions are the only sympatric carnivore species likely to be responsible for these distinctive marks on giraffes (Schaller, 1972; Strauss & Packer, 2013). We examine *i*) the role of GSD in relation to likelihood of giraffes surviving a lion attack, *ii*) discuss the implications of disease ecology for predator-prey interactions more broadly, and *iii*) explore the inferences of our research for conservation.

METHODS

Study area

Ruaha National Park (20,226 km^2) is Tanzania's second largest national park and located in the south-central region of the country (Fig. 1). The park is considered a priority area for large carnivore conservation as it has important populations of cheetahs (*Acinonyx jubatus*), African wild dogs (*Lycaon pictus*), leopards (*Panthera pardus*), spotted hyaenas (*Crocuta crocuta*) and lions (Abade, Macdonald & Dickman, 2014). Habitats in the park include open savannah, wetlands (swampy and riverine habitat), and closed woodlands (Epaphras *et al.*, 2007). This ecosystem supports at least 13 species of ungulates that are vulnerable to lion predation (Table 1), including one of the largest populations of greater kudu (*Tragelaphus strepsiceros*), eland and Sable antelope (*Hippotragus niger*) in East Africa (TAWIRI, 2015). The park is home to largest giraffe population in southern Tanzania with 3,881 (±1,023) individuals recorded during aerial surveys (TAWIRI, 2015).

Photographic capture-recapture surveys

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

We also examined prevalence and anatomical location of marks (claw marks, bite marks, missing tail) assumed to be indicative of a previous lion predation attempt (Fig. 2). When prey survives an attempted carnivore attack, marks of the predation attempt can remain visible as scars (de Azevedo, 2008), which are regularly used to study predator-prey interactions (Carpenter, 1998; Fahlke, 2012). Such marks have been effectively used to examine the influence of age, sex, herd size, and height of individually-recognized Masai giraffes (*G. c. tippelskirchi*) in Serengeti National Park, Tanzania subject to lion predation (Strauss & Packer, 2013). We acknowledge, however, that our survey techniques could not distinguish between single or multiple lion predation attempts or the date of the attack(s). Thus, where these marks (hereafter referred to as lion marks) were detected, we conservatively estimated that giraffes had survived at least one previous lion predation attempt.

Spatial capture-recapture model

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

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

Both the baseline encounter rate, λ_{0ij} (when $d_{ij} = 0$), and the scale parameter of the half-normal detection function, σ_i, were allowed to vary according to individual attributes including 1) sex, with female as the reference category; 2) age class, with adult as the reference category; 3) an interaction of sex × age class; and 4) the presence/absence of severe GSD. We estimated these relationships by specifying linear models on the log scale for each parameter, $\log(\lambda_{0ij}) = \mathbf{X}_i\boldsymbol{\alpha}$ and $\log(\sigma_i) = \mathbf{X}_i\boldsymbol{\delta}$, where $\mathbf{X}_i$ is the design matrix of individual attributes and the parameters to estimate are $\boldsymbol{\alpha}$ and $\boldsymbol{\delta}$**.** In addition to the individual attributes, we included an offset term on the encounter rate to adjust for total hours (i.e., effort) spent surveying grid cell *j*, calculated as the total survey duration scaled by linear length of overlapping survey units. Latent activity centers were assumed to be uniformly distributed as a homogeneous point process such that density was expected to be constant across the region (Royle *et al.*, 2014). We eliminated calves from our SCR analysis because their movement directly depends on their mother, which does not meet the criteria of independence required for such models (Borchers & Fewster, 2016), thus our inferences are limited to adults and subadults.

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

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

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

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

Lion hunting surveys

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

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

Whereby r is the proportion of a species of the total hunts and p is the proportional availability of the species (Jacobs, 1974). Proportional availability was obtained from data on aerial surveys conducted by the Tanzania Wildlife Research Institute (2015) and our surveys on lion feeding behaviour. Jacobs' index values for a prey species D range from –1 to +1 with negative values indicating avoidance and positive values indicating selection.

RESULTS

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

Parameter estimates from the SCR model indicated that individuals were more likely to be female (64%; $\psi_{\text{male}} = 0.36$ [0.030, 0.415]) and adult (87%; $\psi_{\text{subadult}} = 0.13$ [0.094, 0.177]) giraffes, with 85% of the study population having GSD and 60% having severe cases of the disease (Table 2). The proportion of the giraffe population with lion marks was highest (i.e. >40%) in the northeastern section of the study area (Fig. 4). We found strong evidence that lion marks were more common on male giraffes ($\beta_1 = 0.519$ [0.117, 0.923]), and the probability of subadult giraffes having lion marks was considerably lower ($\beta_2 = -0.829$ [–1.643, –0.078]; Table 2). We found marginal evidence that giraffes with severe GSD were more likely to have lion marks ($\beta_3 = 0.334$ [–0.083, 0.759]). Adult males with severe GSD had the highest occurrence of lion marks (Fig. 5).

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

DISCUSSION

We examined the potential implications of GSD on the predatory interactions of lions and giraffes. The Jacob's index values revealed that giraffes, with buffaloes a close second, were the most highly selected prey species by lions in Ruaha National Park (Table 1), consistent with predictions based on body size (Hayward & Kerley, 2005). This relationship was evident despite the fact that other concurrent prey species were more abundant than giraffes. Additionally, across a six-year monitoring period, we found that lions hunted giraffes at a higher frequency than other sympatric prey species (Fig. 6), with GSD severity as a potential modulating mechanism. Higher selection of giraffes by lions in Ruaha National Park could indicate a predatory strategy of targeting a large prey to access a higher concentration of food resources in a single kill (Loveridge *et al.*, 2009). Among the prey selected by lions in Ruaha National Park, giraffes have the largest average body mass (Table 1; Hayward & Kerley, 2005). This explanation might be supported by the fact that lions in Ruaha National Park tend to move in larger prides compared to other parks in Tanzania. Specifically, Ruaha National Park has the highest average size of a lion pride in Tanzania ($n = 5.8$), almost two lions higher than any other park (Mosser & Packer, 2009). Furthermore, the range of lion prides that we observed in Ruaha National Park was as high as 42 individuals. Thus, lions in the park could simply be targeting giraffes more often to acquire food resources for large prides or be more successful in cooperatively hunting giraffes regardless of GSD severity.

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

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

In discussing the patterns, we observed, our hope is to spur the process of identifying creative future avenues of research regarding the nuanced roles of disease in predator-prey interactions. Lions account for ~75% of giraffe calf mortality (Pellew, 1983). We do not suspect that GSD is particularly influential among lion and calf/sub-adult giraffe interactions given that symptoms of the disease are rare in these life history stages (Muneza *et al.*, 2017). Despite the general lack of GSD influence on giraffe survival, additional research may be warranted regarding potential mechanistic connections. It remains unclear, for instance, whether GSD directly influences survivability of giraffes or if vulnerability to lion predation might increase for individual giraffes with this disease. Furthermore, we observed 21 giraffes with both severe GSD and evidence of a previous lion predation attempt moving with difficulty during our surveys. From our observations, the lion marks heal but severity of GSD does not change (Muneza *et al.*, 2017). We identified one limping giraffe with a lion predation mark on the front left limb in June 2015 and later encountered that same individual in August 2015 with what appeared to be a healed lion predation wound (Fig. 7). In contrast, the GSD lesions were still visible and had the same category of severity. Given that recent studies have focused on external manifestation of GSD (Mpanduji *et al.*, 2011; Muneza *et al.*, 2016, 2019), there is a critical need to expound on the pathophysiology of GSD.

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

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TABLES

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

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

antelope					abundance
Sable antelope	*Hippotragus niger*	3,896	-	235	Taken in accordance to relative abundance
Warthog	*Phacochoerus africanus*	3,940	-0.12	83	Taken in accordance to relative abundance
Zebra	*Equus quagga*	4,937	0.02	271	Preferred

Table 2. Parameter estimates from the spatial capture–recapture (SCR) model of Masai giraffes (*Giraffa camelopardalis tippelskirchi*) in Ruaha National Park, Tanzania, in 2015. The individual attribute probabilities are on the probability scale, while other parameters (e.g., α, δ, β) are on the logit scale. These parameters include probabilities for individual attributes such as population membership (ψ), sex (ψ_{male}), age class (ψ_{subad}), signs of GSD (ψ_{GSD}) and number of legs with severe lesions (φ_k); loglinear regression coefficients for the encounter rate (α) and the scale parameters of the half-normal detection functions (δ and β); and derived parameters of 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]
$\psi_{Marks\,[1]}$	# of legs with severe GSD	0.28	[0.19, 0.38]
$\psi_{Marks\,[2]}$	# of legs with severe GSD	0.31	[0.23, 0.39]
$\psi_{Marks\,[3]}$	# 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 × 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 × 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]

FIGURE LEGENDS

Figure 1. The study area in Ruaha National Park, Tanzania surveyed for Masai giraffe (*Giraffa camelopardalis tippelskirchi*) distribution and lion (*Panthera leo*) activity (May to August 2015). The different lion sightings depict instances where lions were either hunting or feeding on giraffe.

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

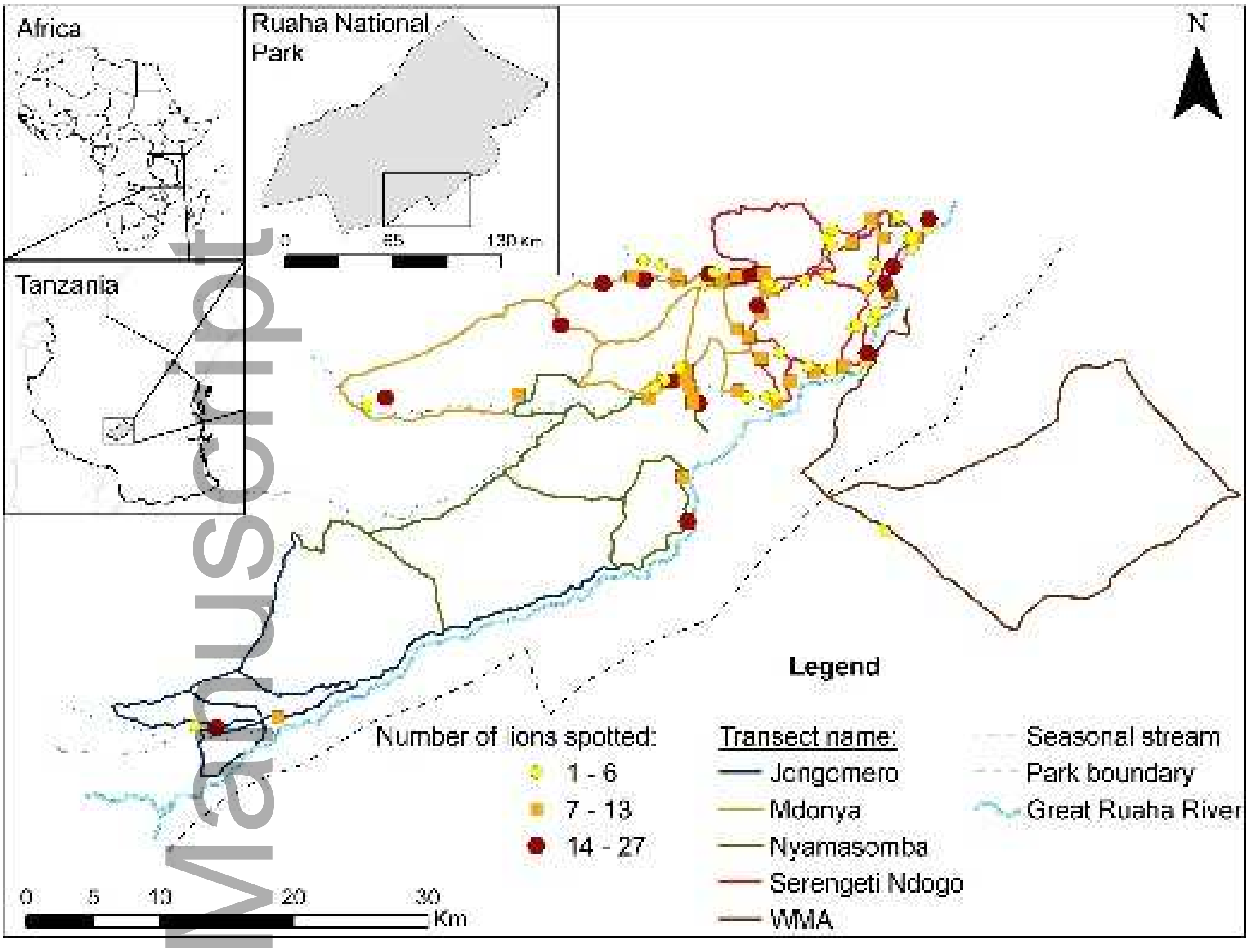
Figure 3. Proportion of Masai giraffe (*Giraffa camelopardalis tippelskirchi*) population with evidence of previous lion (*Panthera leo*) predation attempts and GSD lesions. The graph is based on giraffes, by age and sex, that were encountered and individually identified during the road-based photographic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

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

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

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

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



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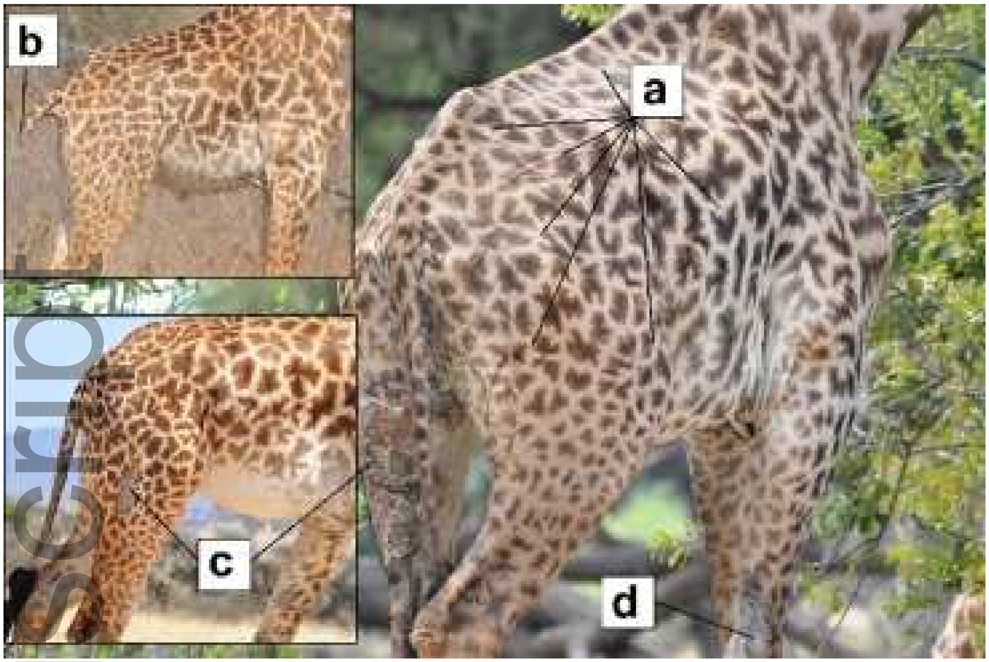

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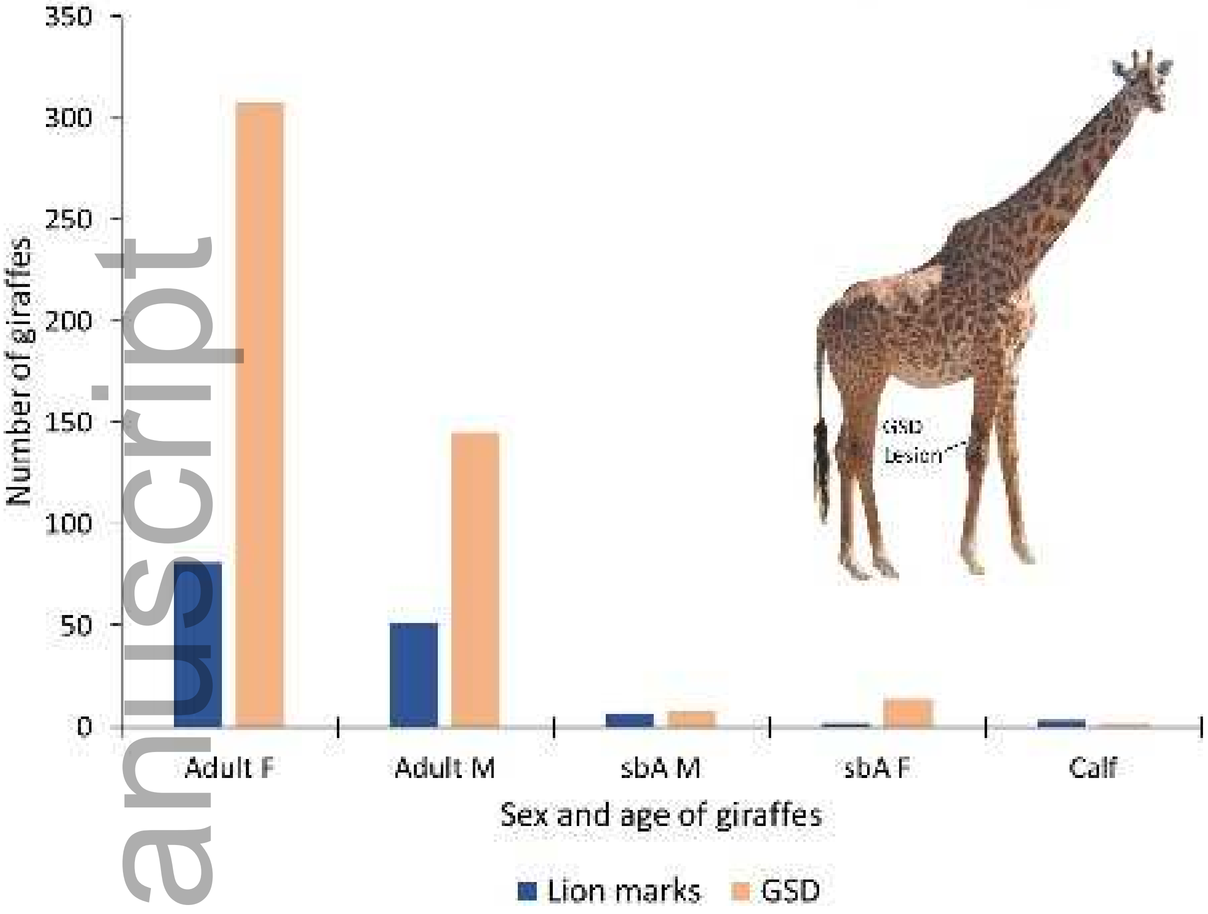

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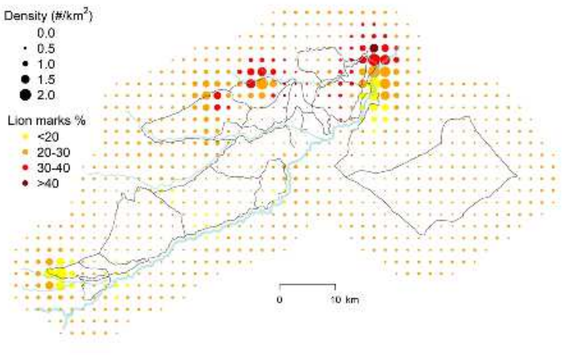

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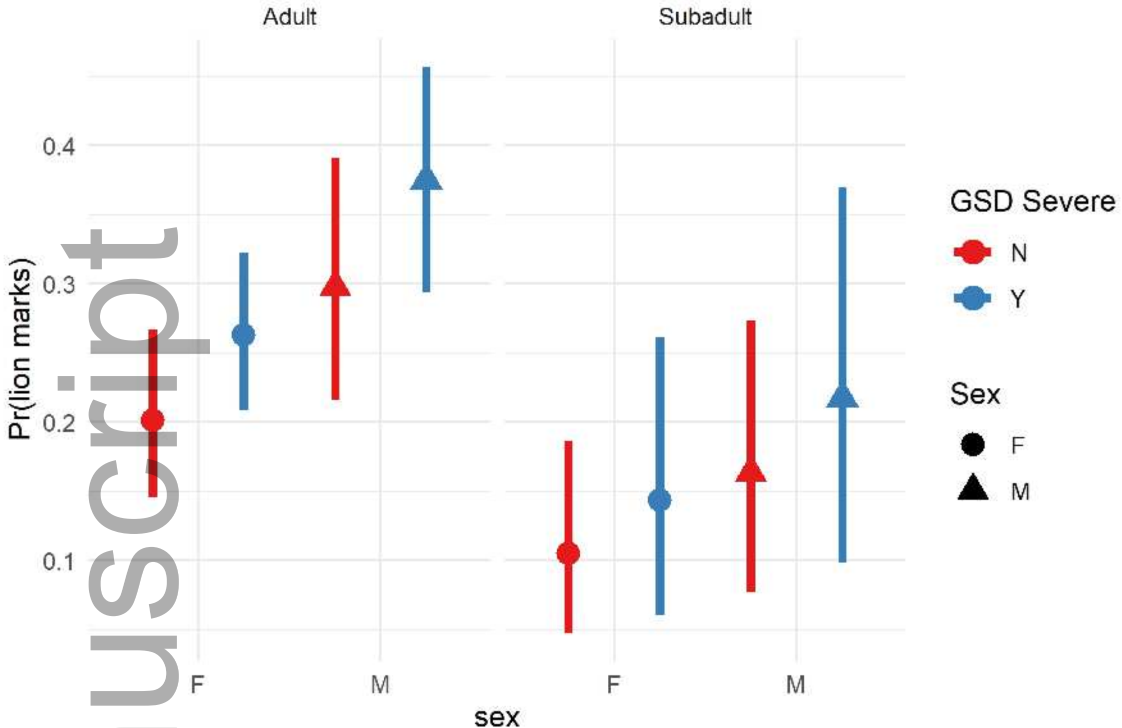

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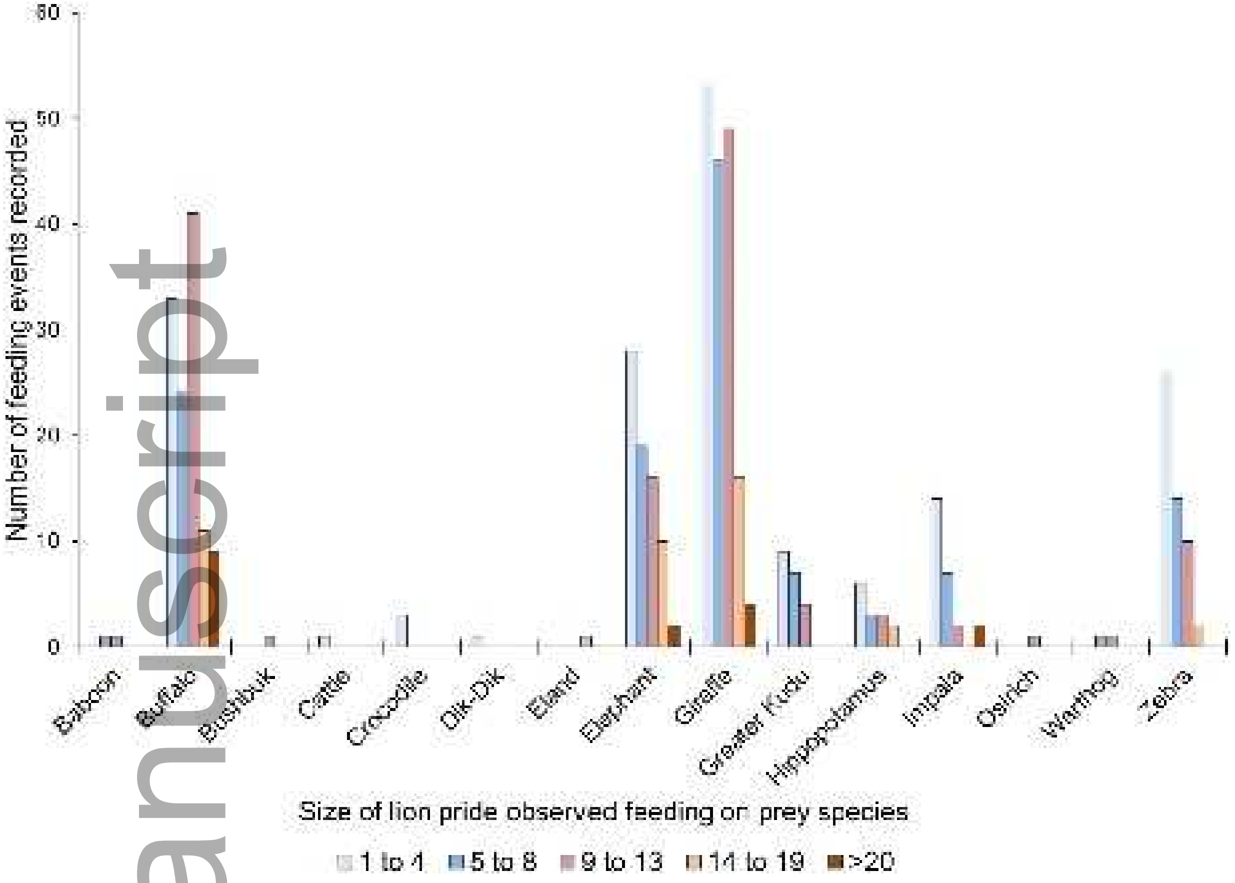

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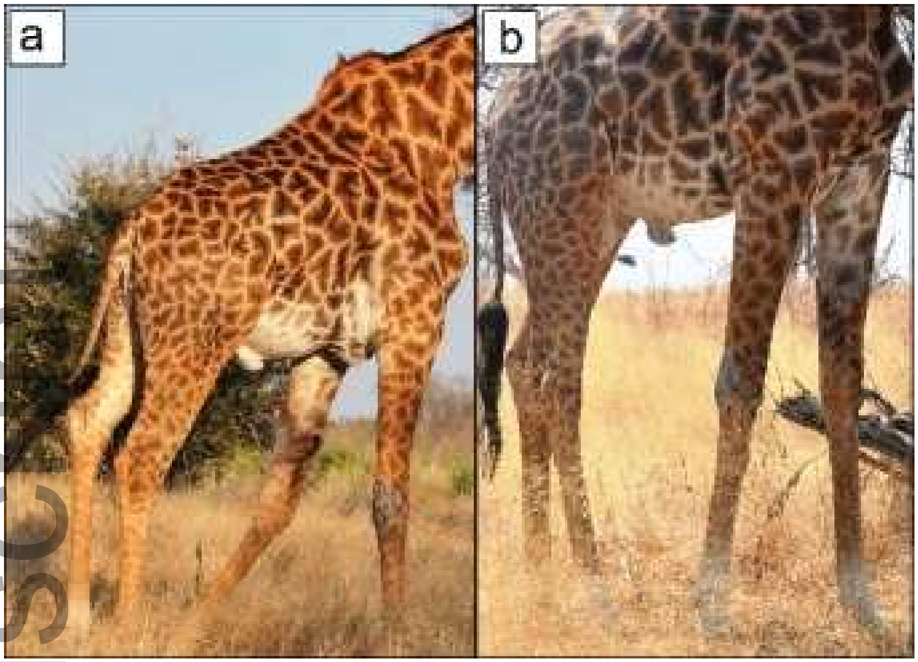

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