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Original article

Does illegal hunting skew Serengeti wildlife sex ratios?

Wilfred N. Marealle, Frode Fossøy, Tomas Holmern, Bård G. Stokke & Eivin Røskaft

In this article we show that the population of Serengeti Masai giraffes *Giraffa camelopardalis tippelskirchi* is extremely female biased, particularly among newborns. Our results suggest that this might be a response to heavy illegal hunting and the continuous disturbance such activities cause on giraffes, as sex ratios were more female skewed in all age groups in areas with high risk of illegal hunting. Giraffes were also more vigilant and fled at longer distances in such areas. Such female skewed sex ratios have also been found in other Serengeti species such as the ostrich *Struthio camelus*, the impala *Aepycerus melampus* and the wildebeest *Connochaetus taurinus*. In all studies, the sex ratio was more female skewed in areas in which illegal hunting is common. We found that sex ratio in giraffe calves, particularly in areas with high risk of illegal hunting, were more female skewed than in subadults or adults, indicating a female biased sex ratio at birth. If wildlife species react to a constant human disturbance by conceiving female offspring, this might cause serious conservation challenges. Conservation managers must anyway take this into account when developing future hunting regimes, not only for giraffes but also for other ungulate species under constant stress. We discuss various hypotheses aiming at explaining the female biased sex ratio in giraffes. However, further studies are needed to disentangle the causes of the skewed sex ratio observed in our study.

Key words: Africa, behaviour, conservation, giraffe, population dynamics, savannah, sex ratio

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An important challenge when conserving wildlife is to understand the causes of variation of population sex ratio, as these variations ultimately affect population dynamics. For instance, a female skewed sex ratio in the Serengeti ecosystem has been reported in several previous studies (e.g. ostrich *Struthio camelus*; Magige 2008, impala *Aepycerus melampus*; Setsaas et al. 2007 and wildebeest *Connochaetus taurinus*; Ndibalema 2009, Georgiadis 1995), particularly in areas where illegal hunting is common. Illegal hunting seems to affect males more than females in the Serengeti ecosystem (Holmern et al. 2006). However, little attention has so far been paid to this bias in sex ratio among different taxa in this ecosystem.

Ever since Fisher's (1930) classical work, adaptive explanations of sex-ratio variation in animals have been proposed through different models, the most commonly used being the Trivers-Willard (T-W model; Trivers & Willard 1973) and the Local Resource Competition (LRC; Clark 1978) models. While the first-mentioned model concentrates on the mother's social status or body condition, the latter predicts that mothers constrained by environmental factors benefit by reducing resource competition through a skewed sex ratio towards the principal dispersing sex. Such theories of sex-ratio adjustment assume that parents will adjust the sex ratio at birth (secondary sex ratio) in a manner that maximises offspring reproductive success

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(Trivers & Willard 1973). Many species exhibit skewed sex ratios at birth (Visscher et al. 2004) or a skewed subadult mortality (Slagsvold et al. 1986, Clark 1978). Although studies of invertebrates generally support predictions derived from the sex-ratio theory, evidence for adaptive sex-ratio bias in vertebrates remains controversial (Silk & Brown 2008, Hewison & Gaillard 1999, Robert et al. 2010). Some recent studies suggest, however, that sex-ratio bias at birth depend on maternal condition at conception (Sheldon & West 2004, Perret 2005, Shibata & Kawamichi 2009, Cameron et al. 1999, Cameron 2004), and therefore support the T-W hypothesis. For polygynous, sexually dimorphic mammals, where males are larger and disperse more readily than females, the latter models can be used to predict sex-ratio adjustments within different environmental contexts. Fluctuating sex ratios from male to female bias have therefore frequently been explained by such models (Bradshaw et al. 2003, Wild & West 2007).

Survival to maturity typically represents the largest component of variance in offspring reproductive success, which should make environmental factors responsible for sex-specific offspring survival strong predictors of secondary or even primary sex-ratio adjustment. Biases in offspring sex ratios are found among polygynous species with pronounced sexually dimorphism and where only females are philopatric. Sometimes the observed tendencies in the sex-ratio variations have been contradictory and their adaptive significance has been controversial. Recent studies seem to reveal that local resource competition among the philopatric sex is the most important selective force affecting birth sex ratios (Hiraiwahasegawa 1993, Hjernquist et al. 2009). Our understanding of this issue is still greatly hampered by the lack of exact knowledge about male reproductive success and the proximate mechanisms responsible for the variations in sex ratios (Hard et al. 2006, Mari et al. 2008), although several recent studies have investigated the proximate mechanisms responsible for sex-ratio variations (Grant et al. 2008, James 1996, Cameron et al. 2008, Goerlich et al. 2009, Helle et al. 2008, Cameron 2004, Love et al. 2005, Mari et al. 2008). Environmental conditions that predict lower survival of males may lead to female-biased sex ratios the following year (Monard et al. 1997).

Most harvest of mammalian populations is unselective. However, when selective hunting occurs, male-dominated harvest is most common (Mcloughlin et al. 2005, Sæther et al. 2003). Male-dominated harvest may result in the deterioration of sexually selected characters; e.g. the frequency of elephants *Loxodonta* spp. without tusks increased in poached populations both in Africa and Asia (Jachmann et al. 1995, Sukumar et al. 1998), horn size decreased in bighorn sheep *Ovis canadensis* (Coltman et al. 2003) and the frequency of fiddlers in male fiddler crabs decreased (Oliveira et al. 2000). Poaching might furthermore cause females to start reproducing earlier as in African elephants *Loxodonta africana* while the effect of stress might result in skewed sex ratios (Love et al. 2005, Bonier et al. 2007, Linklater 2007, Owens & Owens 2009).

Several hypotheses have been developed to explain variation in birth sex ratios, based on the premise that variation is expected when the profitability of raising sons and daughters varies between individual parents (Røskaft & Slagsvold 1985). Different survival of the two sexes may be due to many factors such as predation, hunting or diseases (Wasser & Norton 1993). In this article, we investigate the relationships between environmental variables and calf and adult sex ratios in the Masai giraffe *Giraffa camelopardalis tippelskirchi* in the Serengeti National Park, Tanzania. We predicted that the giraffe sex ratio should follow a similar pattern as found for other species, thus being more female-skewed in areas where illegal hunting is common. We particularly wanted to test whether sex ratio among newborn calves was skewed, or alternatively, if adult male mortality is the main source of a skewed sex ratio. Finally, we discuss causes and conservation challenges and consequences of female-skewed sex ratios in areas with high illegal hunting activities.

Material and methods

Study area

The Serengeti Ecosystem covers an area of 25,000 km^2 on the border of Tanzania and Kenya (Fig. 1), and is defined by the movement of wildebeest. The eastern boundary is formed by the crater highlands and the rift valley. An arm called the western corridor stretches west to Lake Victoria. The northern boundary is formed by the Isuria escarpments and Loita plains in Kenya. The ecosystem covers several different conservation administrations (Sinclair & Arcese 1995b) and experiences bimodal rainfall pattern with long rains during

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Figure 1. Risk areas in Serengeti; the grey areas indicate high risk of illegal hunting, whereas the white areas indicate low risk of illegal hunting.

March-May and short rains in November-December, ranging from 500 mm/year in the southern dry plains to 1,200 mm/year in the wet northwestern part. The ecosystem supports about 70 larger species of mammals, including the highest concentrations of large predators in the world (Sinclair & Arcese 1995b). Serengeti contains a wide range of vegetation types. The northern sections are characterised by rolling, wooded savannahs, whereas the southeastern parts feature almost treeless plains. The western corridor is a region of wooded savannah, whereas further to the east the terrain rises steeply to massive highlands and forested areas (Kideghesho et al. 2006). The human population increase in the western parts of the ecosystem is close to 3% per year. As a result, illegal hunting is increasing and common in these areas as well as in the northern parts of the park (see Fig. 1; Campbell & Hofer 1995, Hofer et al. 2000, Holmern et al. 2006).

Study species

The giraffe is a sexually dimorphic species, in which males are larger than females. It is a browser specialising on leaves, and the presence of Acacia trees affect their distribution (Owen-Smith 1988). Owen-Smith (1988) regarded them as megaherbivores although females do not attain the megaherbivore threshold. Giraffes are described as non-territorial, seasonal movers, moving (3-6 km/day) in loose open herds, where individuals are frequently interchanged, without a specific leader or coordination of herd movements (Pratt & Anderson 1982, Le Pendu et al. 2000, Leuthold & Leuthold 1978). Giraffes reproduce at any time of the year, after a pregnancy period of about 15 months (Pellew 1984, Bercovitch et al. 2004, Dagg & Foster 1976). The sex ratio at birth does not deviate from 1:1, and mothers seem to invest equally in sons and daughters, at least in captive animals (Bercovitch et al. 2004). Calf mortality is relatively high (Bercovitch et al. 2004). Adult males are fairly solitary, dividing their time between feeding and monitoring estrous females, whereas the females are frequently found in mixed herds composed of one or a few female cows with similar aged calves and a few juveniles (Ginnett & Demment 1997, Owen-Smith 1988, Pratt & Anderson 1982). The giraffe sex ratio and feeding ecology varies with habitat; males are more common in forests, taller and thicker vegetation, whereas females are more common in open habitats (Ginnett & Demment 1999, Young & Isbell 1991). The sex ratios in adult populations are normally close to 1:1 (Leuthold & Leuthold 1978, Pratt & Anderson 1985), although a few studies with low sample sizes indicate female-biased sex ratios (Pellew 1976, Foster & Dagg 1972). Mortality among young males appears to be somewhat higher than among females (Owen-Smith 2008, Leuthold & Leuthold 1978). The number of giraffes in the Serengeti ecosystem is approximately 9,000 (Sinclair et al. 2000).

Field methods

We monitored giraffes during a two-week period every month from August 2008 to July 2009. We drove fixed transects (Setsaas et al. 2007) where all giraffes were recorded. Each transect was surveyed twice during each observation period, and we drove a total of 11,172 km. We took photos of the animals, which could be recognised by their unique flank patterns. For each observed group, we recorded the number of individuals, their sex (horns and genitals) and the size of each individual. To confirm the sex, we approached the giraffes carefully and determined gender (male or female genitals) using binoculars. There were always two observers in the car, and each determined the sex independently. We were able to sex 2,947 out of 2,959 (99.6%) giraffes. Size was recorded to the nearest 10% of an adult giraffe (i.e. 10 different size-groups). However, during our analyses we pooled giraffes into three age-groups: 1)

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calves 10-50% (N = 519), 2) subadults 51-90% (N = 278) and 3) adults 91-100% (N = 2,150). Serengeti was divided into two illegal hunting risk areas (Setsaas et al. 2007): 1) High risk including the western corridor up to the junction towards Serena lodge and north of Seronera from the junction towards Fort Ikoma gate and 2) Low risk including Seronera, Sopa, Plains and the Ngorongoro Conservation Area (see Fig. 1). We recorded two different habitats: 1) acacia woodland, i.e. dense woodland consisting of Acacia trees, and 2) open landscapes, i.e. everything from open woodland and bush-land to open grassland. Finally we recorded the behaviour of the animals when first sighted as: 1) feeding, 2) vigilant (standing looking, sometimes turning the head or escaping) and 3) other behaviour (different kinds of mating behaviour, walking, resting, drinking and nursing).

To avoid sampling the same individual more than once, we never covered an area more than once a week. Because our field station was located in the middle of the low illegal hunting risk area we passed through the central area with low risk of illegal hunting more frequently than the high risk areas. This means that we surveyed the central area more often, and hence would expect a pseudoreplication of seeing the same female-biased group repeatedly to be most pronounced here. However, the sex ratio was the least female-biased (see results), suggesting that pseudoreplication should not be a major problem in our data set.

We collected and recorded separate data on flight initiation distance between 6:30 am and 6:30 pm during August-December 2003 based on the methods outlined in Blumstein et al. (2005). We conducted test-person approaches on a single or a group of giraffes. Individuals that were < 50 m apart were considered one group because it was difficult to conduct experiments on individuals that were separated with > 50 m. However, a group of individuals can be distributed further apart than 50 m (Van Der Jeugd & Prins 2000, Cameron & du Toit 2005). Immediately after seeing a giraffe or group of giraffes, we stopped the car and switched off the engine. We recorded the distance (i.e. starting distance STD) and angle to the animals using a rangefinder (10×40), as well as scoring the individuals as alert or not alert prior to the start of the approach. After recording these observations, the test person carefully opened the car door and started to walk at a steady pace of approximately 0.5 m/second in a direct line towards the animals. When the giraffe(s) fled the test person immediately stopped, and the observer inside the car measured the distance to the test person by the rangefinder. The distance at which the focal giraffe moved away (i.e flight initiation distance, FID) was therefore the difference between the STD and the distance to the test person. We conducted a total of 80 experiments.

Statistical analyses

We tested sex ratios and frequencies of different behaviours using χ^2-tests and different variables that might influence sex ratio or behaviour variation using Generalised Linear Models (GLMs).

We used Analysis of Covariance (ANCOVA) to model the variables that affect FID. Predators do not approach prey at fixed distances, hence STD certainly influences FID as has been shown by Blumstein et al. (2005). Other predictor variables included in the global model were: alertness, i.e. whether or not the focal individual or group was alert prior to the approach whereas individuals that were feeding or resting were considered to be in a non-alert situation while vigilant and moving individuals were considered to be in alert state, area (low or high risk area), vegetation (open or woodland), group size and the interaction area*STD.

We evaluated the strength of evidence for each model based on Akaike Information Criterion corrected for small samples (AIC_c) following Burnham & Anderson (2002) and selected the most parsimonious model with the highest Akaike weight (ω_i). The Akaike weight indicates the probability that the model is the best among the whole set of candidate models and was used to compare the relative performance of models rather than only absolute AIC_c. In the analysis FID and STD were square-root transformed to attain normality.

Results

Sex ratio

Giraffe sex ratio was female skewed in all three major age groups ranging from 67.2% (N = 519) females in the calf-group ($\chi^2 = 61.7$, df = 1, $P < 0.001$), 54.3% (N = 278) in the subadult group ($\chi^2 = 2.07$, df = 1, $P = 0.150$) to 62.1% in the adult group (N = 2,150; $\chi^2 = 126.7$, df = 1, $P < 0.001$). Sex ratios differed significantly statistically between the age groups in high risk areas ($\chi^2 = 5.98$, df = 2, $P = 0.050$), but not in low risk areas ($\chi^2 = 5.41$, df = 2, $P = 0.067$; Table 1). Areas

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Table 1. Numbers of males and females in different age groups (adults, subadults and calves) and in relation to risk of illegal hunting (high or low), habitat (woodland or open) and season (dry or wet). See text for statistics.

	Age group					
	Number of adults		Number of subadults		Number of calves	
	Males	Females	Males	Females	Males	Females
Low-risk	426	510	56	48	46	74
High-risk	388	826	71	103	124	275
Woodland	378	669	55	70	85	177
Open habitat	436	667	72	81	85	172
Dry season	394	620	58	74	80	148
Wet season	420	716	69	77	90	201

with high risk of illegal hunting were significantly more female skewed (67.4% females) than areas with low or no risk of illegal hunting (54.5% females; $\chi^2 = 49.8$, df = 1, $P < 0.001$). All three age groups were statistically significantly female skewed in high risk areas (calves: $\chi^2 = 57.1$, df = 1, $P < 0.001$, subadults: $\chi^2 = 5.89$, df = 1, $P = 0.015$, adults: $\chi^2 = 158.0$, df = 1, $P < 0.001$; see Table 1), while two age groups were significantly female skewed in low risk areas (calves: $\chi^2 = 6.53$, df = 1, $P = 0.011$, subadults: $\chi^2 = 0.615$, df = 1, $P = 0.433$, adults: $\chi^2 = 7.54$, df = 1, $P = 0.006$; see Table 1). All age groups were more female skewed in high risk areas than in low risk areas but only statistically significantly so for subadults and adults (calves: $\chi^2 = 2.21$, df = 1, $P = 0.138$, subadults: $\chi^2 = 4.46$, df = 1, $P = 0.035$, adults: $\chi^2 = 41.3$, df = 1, $P < 0.001$). Sex-ratios differed statistically significantly between age groups in open areas ($\chi^2 = 8.06$, df = 2, $P = 0.018$) but not in woodland areas ($\chi^2 = 4.90$, df = 2, $P = 0.086$; see Table 1). Finally, sex ratios differed statistically significantly between age groups during the dry season ($\chi^2 = 11.2$, df = 2, $P = 0.004$) but not in the wet season ($\chi^2 = 5.27$, df = 2, $P = 0.248$; see Table 1).

A GML with sex as dependent variable with risk of illegal hunting (low or high), season (dry or wet), habitat (wooded or open) and age-group (calf, subadult or adult) as independent variables (intercept) was statistically significant ($\chi^2 = 14.6$, df = 5, $P = 0.012$). Risk of illegal hunting (Wald $\chi^2 = 10.7$, df = 1, $P = 0.001$) was the only variable that independently explained the female skewed sex ratio, whereas age-group (Wald: $\chi^2 = 2.28$, df = 2, $P = 0.320$), season (Wald: $\chi^2 = 0.47$, df = 1, $P = 0.829$) and habitat (Wald: $\chi^2 = 0.457$, df = 1, $P = 0.499$) did not.

Behaviour

Giraffes were more vigilant in areas with a high risk of illegal hunting (18.3% in high risk and 10.1% in low risk areas) and were feeding more frequently in low risk areas (66.9% in high risk vs 77.7% in low risk areas). All other kinds of behaviour were more similar in the two areas (12.2 vs 14.8%, respectively; $\chi^2 = 46.4$, df = 2, $P < 0.001$). Males were more vigilant (11.0 and 22.0%, in low and high risk areas, respectively) than females (9.2 and 16.4%, in low and high risk areas, respectively), whereas females were feeding more frequently (80.5 and 70.0% in low and high risk areas, respectively) than males (74.8 and 60.7% in low and high risk areas, respectively). Males were also engaged more frequently (15.8%) in other activities than were females (12.4%). The difference in frequencies of the three behaviour categories between males and females was statistically significant in high risk areas ($\chi^2 = 15.4$, df = 2, $P < 0.001$) but almost only statistically significant in low risk areas ($\chi^2 = 5.8$, df = 2, $P = 0.055$).

A GLM with behaviour (feeding or vigilant (other behaviour excluded)) as the dependent variable with risk of illegal hunting (low or high), season (dry or wet), habitat (wooded or open), gender (male or female) and age-group (calf, subadult or adult) as independent variables (intercept) was statistically significant ($\chi^2 = 81.5$, df = 8, $P < 0.001$). Both habitat (Wald: $\chi^2 = 41.8$, df = 1, $P < 0.001$; more vigilant in open habitats), risk of illegal hunting (Wald: $\chi^2 = 26.2$, df = 1, $P < 0.001$; more vigilant in high risk areas), season (Wald: $\chi^2 = 7.78$, df = 1, $P = 0.005$; more vigilant in wet season) and gender (Wald: $\chi^2 = 6.86$, df = 1, $P = 0.009$; males more vigilant) independently significantly explained the variation in behaviour, whereas age group (Wald: $\chi^2 = 2.89$, df = 2, $P = 0.235$) and the inter-

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Table 2. The five most parsimonious models with flight initiation distance (FID) as dependent variable of 20 models considered.

Model	K	adj. R^2	AICc	ΔAIC_c	ω_i
Starting distance + alert + area + group size	6	0.759	225.5	0.000	0.251
Starting distance + alert + area + group size + vegetation	7	0.764	226.6	1.083	0.146
Starting distance + alert + area + group size + starting distance*area	7	0.764	226.6	1.094	0.145
Starting distance + alert + area	5	0.747	227.3	1.818	0.101
Starting distance + alert + area + group size + vegetation + starting distance*area	8	0.768	227.7	2.217	0.083

action between age and gender (Wald: $\chi^2 = 0.147$, df = 2, P = 0.929) did not.

Of the total 20 candidate models (all containing STD as a variable), we considered four models that had a $\Delta AIC_c < 2$ in the analysis on FID (Table 2). Since the first three models contained more variables, we judged the most parsimonious model to be model number four, which contained only three variables: STD, alert and illegal hunting risk area (Table 3). FID increased with STD, and animals showing alert behaviour had larger FID than those that where not alert prior to the approach. Likewise, animals in high risk areas showed longer FIDs.

Discussion

In accordance with previous studies (e.g. Pellew 1984, Ginnett & Demment 1997, 1999, Owen-Smith 2008) the feeding behaviour varied between habitats and seasons. Furthermore, giraffes were more nervous (i.e. expressed by vigilance or flight distance) in areas with high risk of illegal hunting, males being more vigilant than females. Cameron & du Toit (2005) used a different method than we did to record vigilance behaviour, and found a quite high rate of vigilance of giraffes in the Kruger National Park in South Africa. However, we found that giraffes in high risk areas fled at longer distances and showed higher levels of vigilance than individuals in low risk areas. It therefore seems reasonable to conclude that giraffes were more nervous in high risk areas, males being more nervous than females.

Table 3. Estimates for the most parsimonious model (i.e. model 4) and of model 1 of flight initiation distance (FID).

Coefficients	Estimate	SE	T	P
Model 4:				
Intercept	3.009	0.502	5.990	< 0.001
Starting distance	0.536	0.040	13.233	< 0.001
Alert	-0.542	0.247	-2.195	0.0312
Area	0.655	0.225	2.914	0.0047
Model 1:				
Intercept	2.810	0.503	5.591	< 0.001
Starting distance	0.532	0.039	13.389	< 0.001
Alert	-0.678	0.252	-2.694	0.0087
Area	0.657	0.221	2.977	0.0039
Group size	0.195	0.097	2.0	0.0491

Furthermore, we have shown that sex ratio of Serengeti giraffes is female skewed. This skew was significantly more pronounced towards females in areas with high risk of illegal hunting than in low risk areas. All three age groups were significantly female skewed in areas with high risk of illegal hunting, whereas the subadult sex ratio was not significantly skewed in low risk areas. This observed sex-ratio bias may either be a result of sex allocation or of differential mortality among sexes.

Illegal hunting activities in the Serengeti ecosystem and in some parts of the national park occur throughout the year although they are peaking during the dry season (Holmern et al. 2007). Bushmeat is commonly found in villages surrounding Serengeti National Park (Kaltenborn et al. 2005). Although the giraffe is not the most frequent species found among poached animals (around 1-2% of poached animals, while the giraffe population is < 0.5% of the total ungulate population), it is still a target for illegal hunting (Arcese et al. 1995, Ndibalema & Songorwa 2007). Furthermore, there is some evidence that illegal hunting is targeting males more than females (Holmern et al. 2006). However, there is no reason to believe that a male-biased illegal hunting should account for the observed female-biased sex-ratio among newborn calves.

However, illegal hunting may indirectly lead to a female-skewed sex ratio in as far as giraffes in high risk areas encompass a higher level of stress by steadily having to escape groups of illegal hunters setting up snares in the bush. Giraffes are constantly more nervous in high risk areas as proved by the larger flight distances and more vigilant behaviour in such areas. This is supported by a study

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performed by Caro (2005) who showed that mammal species subject to covert human hunting pressure are more worried of observers than species that are less heavily exploited.

The proportion of female calves was very high, especially in areas with high risk of illegal hunting. Small calves were found during all months (ranging from eight in February to 27 in March). One explanation for the skewed sex ratios is that giraffes conceived and gave birth to more females in high risk areas than in low risk areas. Studies on non-human mammals indicate that mothers in good condition around conception bias their litters towards sons (Cameron 2004). Recent research on the role of glucose in reproductive functioning has shown that excess glucose favours the development of male blastocysts, providing a potential mechanism for sex-ratio variation in relation to maternal condition around conception. Furthermore, many of the conflicting results from studies on sex-ratio adjustment would be explained if glucose levels *in utero* during early cell division contributed to the determination of offspring sex ratios (Cameron 2004). Even among humans, poor mothers tend to give birth to more daughters after catastrophes, wars or during economic unstable periods (Catalano 2003, Catalano et al. 2005). The situation in the high risk areas in Serengeti is biologically not unlike such a 'catastrophic' situation in humans.

Females with high corticosteroids levels produce more daughters than females with low corticosteroids levels (Bonier et al. 2007, Love et al. 2005, Linklater 2007). Our results are therefore congruent with the hypothesis that distorted sex ratios, and especially female-biased sex ratios, are likely to arise within populations subjected to higher environmental disturbances (Paoletti & Cantarino 2002). A high stress level caused by a constant disturbance by illegal hunters walking in the bush searching for snares and trapped animals (Wato et al. 2006) might therefore be a likely explanation for the skewed female sex ratio found among the Serengeti giraffe calves. Thus, the stress caused by illegal hunting might be a likely explanation for the skewed sex ratio found among adult giraffes, particularly in areas of high risk of illegal hunting where the sex ratio was significantly more female biased in all age groups. However, we lack data on spatial variation in corticosteroid levels among giraffes in the Serengeti and can just point to this explanation as plausible for the skewed sex ratios observed in our present study. Therefore, future studies should be designed to test the 'stress hypothesis' in more detail.

Why are tourist activities not causing the same disturbance on giraffes? Tourists remain on the roads and are not allowed to leave the cars while in the park; they therefore cause no direct disturbance and did not present a threat to giraffes. Wildlife also ignores the tourist cars particularly in areas with low risk of illegal hunting (Nyahongo 2008). Flight distance experiments as well as vigilance behaviour indicate that viewing wildlife from vehicles has only a minor effect on the animals in the Serengeti National Park (Setsaas et al. 2007, Nyahongo 2008).

It has been indicated that subadult male giraffes may experience a higher mortality than subadult females (Leuthold & Leuthold 1978); however, it is not a likely explanation that newborn male calves in Serengeti experience a higher mortality than newborn female calves. We observed more males in the subadult group than in the calf group indicating a higher mortality among female calves or a higher emigration by young subadult females. Furthermore, giraffes were significantly more vigilant in high risk areas supporting our contention that giraffes are stressed. Cameron & du Toit (2005) showed a vigilance rate of around 20% in Kruger giraffe cows, which is higher than the rate found in our study (using a different method); however, giraffes were significantly more vigilant and fled at longer distances in high-risk areas, indicating that they were more stressed in these areas. Our results may support the T-W model in that females spent less time feeding in high risk areas leading to a generally worse condition in such areas. An alternative explanation is that giraffes were satiated in high risk areas, however, why then should they spend this extra time in vigilant positions? Why were they fleeing at longer distances in high risk areas? Our data may support a T-W model which predicts that females in a worse condition in sexually dimorphic species should produce more daughters. There is, on the other hand, no indication that subadult males were dispersing out of the area giving no support to the LRC.

Serengeti is a national park with a high density of predators. The giraffe is a target species - particularly for lions *Panthera leo* as found in other areas in Africa (Owen-Smith & Mills 2008, Hayward & Kerley 2005). Lions tend to kill more giraffe males than females (Owen-Smith 2008). Normally, animals are more vulnerable to predation through engagement in risk-prone foraging in dense habitats

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(Sinclair & Arcese 1995a). Thus, we would expect giraffes to be more prone to predation in dense habitats where lions more easily can approach giraffes unnoticed. However, we found no difference in sex-ratio between dense and more open habitats, although the Serengeti lions are more common in woody areas where their typical prey species are common all year around (Packer 1990, Sinclair & Arcese 1995c). It is, however, unlikely that giraffes are among the most common targeted prey in these areas. Thus, predation is unlikely, or as best weak, as an explanation for the female-skewed sex ratio among Serengeti giraffes.

Establishment of a male-biased sex ratio at birth is possible if dispersal is genetically determined and there is a genetic linkage between sex-ratio determination and dispersal. However, this is not a likely explanation for our results. That males are more difficult to observe, because they are living in dense habitats, is not a likely explanation for our findings either, because we controlled for this factor. Even if subadult males survive much better than subadult females, a female-skewed birth rate may still be an explanation for the observed skewed female ratio among adults, although it is not likely.

Conservation consequences

To our knowledge, our study is among the first studies indicating that an effect of a heavy illegal hunting pressure in a wild mammal population may be a principal cause behind a female-biased sex ratio at birth. This adds up to the list of uncertainties regarding the long-term effects of high hunting pressures. We suggest that populations experiencing illegal hunting, which unlike hunted populations, are under a constant level of stress, may respond by skewing sex ratios towards females. Consequences of such a female-biased birth ratio together with male biased deaths due to illegal hunting (or selective predation by carnivores) may be driving the sex-ratio towards an even higher female bias. A sex allocation effect may be common among sexually dimorphic mammals which are affected by human influence, and managers should take this into account in order to sustain viable populations of such species (Robertson et al. 2006).

Conclusion

We have shown that giraffe sex-ratio in the Serengeti National Park is extremely female skewed, particularly in areas where illegal hunting is common. The cause of the observed sex-ratio bias may be multitudinous. Mothers might allocate resources to the sex with the highest expected fitness, because reproductive success might on average be higher in that sex (Clutton-Brock 1991). If adult males are targeted more than females by illegal hunters, females might on average have a higher life expectancy than males. Another adaptive explanation is that females in illegally hunted areas are in a worse condition because of the constant stress caused by hunters, and they are thereby producing more daughters (i.e. a T-W effect). Whatever the cause, more in-depth studies are needed to test body condition and level of stress hormones in female giraffes. Furthermore, more studies are needed in order to test how giraffes are targeted by the illegal hunters and how this is affecting the giraffe population in the Serengeti.

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