



## Original Research Article

# The impacts of human disturbances on the behaviour and population structure of impala (*Aepyceros melampus*) in the Serengeti ecosystem, Tanzania

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## ARTICLE INFO

## Article history:

Received 14 May 2018

Received in revised form 26 October 2018

Accepted 26 October 2018

## Keywords:

*Aepyceros melampus*

Human disturbance

Demography

Vigilance

Behavioural synchrony

Predation risk

Serengeti ecosystem

## ABSTRACT

Human activities can lead to various changes in wildlife populations' behaviour and dynamics. Understanding specific responses to disturbances can help conservation management better protect wildlife populations to coexist with local communities. Here, we studied the response of a model ungulate species, the impala (*Aepyceros melampus*), to different types of human activities in the Serengeti ecosystem. Impala were studied in central Serengeti National Park (CSNP), an area with relatively low human disturbance, and, with increasing levels of human disturbance, in western Serengeti National Park (WSNP), Grumeti Game Reserve (GGR), Ikona Wildlife Management Area (IWMA), and Loliondo Game Controlled Area (LGCA); pastoralism and/or hunting are the main disturbances in these areas. We hypothesised that in the exploited GGR, IWMA and LGCA areas, 1) impala would spend more time on costly behaviours, 2) sex ratios would be more female skewed, and 3) group sizes, reproduction and recruitment ratios would be lower compared to CSNP. We found that impala spent less time resting in IWMA and LGCA, as well as a significantly lower proportion of males, and lower reproduction and recruitment ratios in LGCA. Impala synchronized their behaviour, increasing their social cohesion potentially resulting in more efficient anti-predator strategies. Human activities induced a behavioural response in impala, indicating that in less regulated areas where pastoralism and hunting are allowed, these disturbances can potentially affect impala population persistence. These results highlight the importance of protected areas for wildlife populations, and the need for continuous monitoring of the impala and other ungulate populations in less regulated areas, as the underlying anthropogenic disturbances are likely impacting diverse species.

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## 1. Introduction

Human activities may lead to behavioural changes in individuals, and ultimately affect the demography and the social organization of a species (Stankowich, 2008). Disturbance caused by human activities can alter animals' perception of

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humans as potential predators; the response to disturbance can in this context be studied in the same way as the response to predation risk (Frid and Dill, 2002; Stankowich, 2008). Changes in behaviour caused by anthropogenic disturbance may force animals to allocate more time to costly behaviours, such as vigilance or increased movement activity, to decrease their predation risk. These come at the expense of restorative behaviours, such as foraging or reproduction (Houston et al., 1993). Animals adapt to this cost-benefit trade-off by varying certain aspects of their behaviour to control both the rate of energetic gain and risk of predation (Kie, 1999; Lima and Dill, 1990). A high proportion of time spent vigilant can result in reduced predation risk, but also a lower rate of energetic gain. Habitat preference can also be affected, as an animal's energetic gain and risk of predation may change depending on the distance to cover at which it feeds. This cost-benefit trade-off is an important predictor of individual fitness and may ultimately affect population dynamics (Frid and Dill, 2002).

Vigilance is considered a costly behaviour and usually refers to scanning or watching the surroundings, and is related to the probability that an animal will detect a potential threat (Illius and Fitzgibbon, 1994). Various factors may influence the proportion of time spent vigilant, including spatial and temporal patterns in predation risk (Hunter and Skinner, 1998), time-of-day and habitat structure (van der Meer et al., 2012), position within group (Beauchamp, 2007; Matson et al., 2005), presence of conspecifics (Périquet et al., 2010), and group size (Beauchamp, 2017; Lima, 1995). With increasing group size, *per capita* vigilance is predicted to be reduced while maintaining an equal overall level of vigilance in the group, resulting in a reduced trade-off between time spent vigilant and feeding.

Synchronization of behaviour can benefit individuals and groups in several ways, among other by decreasing the predation pressure on offspring, increasing the effectiveness of anti-predator strategies, and social cohesion (Duranton and Gaunet, 2016). Behavioural synchronization in the form of activity synchrony is defined as exhibiting the same behaviour at the same time (Duranton and Gaunet, 2016), either at the group level (Conradt, 1998; Ruckstuhl, 1999) or between close neighbours (May et al., 2008; Rands et al., 2014).

Diverse forms of human disturbance may not only alter ungulate behaviour, but also affect a species' demography. Social ungulates living in open habitats form larger groups than those living in closed habitats, a relationship related primarily to predator avoidance strategies (Kie, 1999). Aggregation can benefit prey animals in reducing the predation risk in many ways, such as by increasing the chances of predator detection (i.e. the many-eyes hypothesis; Pulliam, 1973), dilute predator encounter possibility and increase predator confusion (Vine, 1971), reducing *per capita* predation risk (i.e. selfish-herd hypothesis; Hamilton, 1971), and through the risk-allocation hypothesis (Lima and Bednekoff, 1999). However, aggregation should only occur when it increases individual fitness; ungulates have been observed to live in smaller groups in areas with high human disturbance, indicating that a lower group size can be preferred under such conditions (Averbeck et al., 2010; Fischer and Linsenmair, 2007; Manor and Saltz, 2003).

Wildlife hunting, especially for trophies, is often very selective for males and can skew the sex ratio in ungulate populations in favour of females due to differences in body traits and behaviour between the sexes (Coltman et al., 2003; Ginsberg and Milner-Gulland, 1994). Poaching might also have a male bias in some species (Holmern et al., 2006). The increased collective vigilance of groups of prey is likely to result in hunters favouring individuals on their own or in small groups. The preference of hunters to stalk solitary individuals may result in increased predation of males, which are more likely to be on their own or in small groups (Fitzgibbon, 1990; Jarman, 1974). Additionally, ungulate populations that experience high hunting activity tend to be more wary and likely to flee than non-hunted populations (Caro, 2005; Stankowich, 2008).

Animals typically respond to human disturbances by expressing anti-predator behaviours (Frid and Dill, 2002). Consequently, ungulate populations could suffer similar negative effects from increased human disturbance as when perceiving higher natural predation pressure. Recruitment rates in elk (*Cervus canadensis*) decreased in Yellowstone National Park due to the indirect effects (i.e. anti-predator behaviour) that emerged after the reintroduction of wolves (*Canis lupus*; Christianson and Creel, 2014; Creel et al., 2007). A decreased reproduction or recruitment ratio measured as number of calves and juveniles per adult female respectively, can be a significant driver of population dynamics. Assessing whether human disturbance is correlated with reduced reproduction ratios improves our understanding of how human disturbance affects these dynamics and allows assessing potential consequences better (Gaillard et al., 1998).

Conservation efforts are vital to mitigate anthropogenic threats to ecosystems, and biodiversity in general. This, however, depends on a thorough understanding of how human activities affect specific species. Examining the behaviour and the demography of social mammals can serve as an important tool in conservation biology (Caro, 2005). Here, we studied the behaviour and demography of impala (*Aepyceros melampus*) in the Serengeti ecosystem to investigate how they are affected by different anthropogenic disturbance. The Serengeti ecosystem, on the border of Tanzania and Kenya, has been subjected to natural and human-induced processes for centuries (Sinclair et al., 2008a). The increase in the number of people living in the areas surrounding the Serengeti National Park (SNP) poses a significant threat to animal populations through various processes such as overgrazing, habitat fragmentation and hunting (Sinclair et al., 2008b). Therefore, we hypothesised that an increasing proportion of time would be spent on costly (i.e. vigilance or moving) compared to restorative (i.e. resting or feeding) behaviours in areas with increasing levels of human disturbance, i.e. those areas surrounding the national park, and the western part of SNP, where illegal hunting is more pervasive (see *Methods*). Observed reproductive and juvenile recruitment ratios were hypothesised to be lower, and group sizes smaller, in these areas due to human disturbance. Additionally, we hypothesised that there would be a more female skewed sex ratio in areas with high hunting pressure.

## 2. Methods

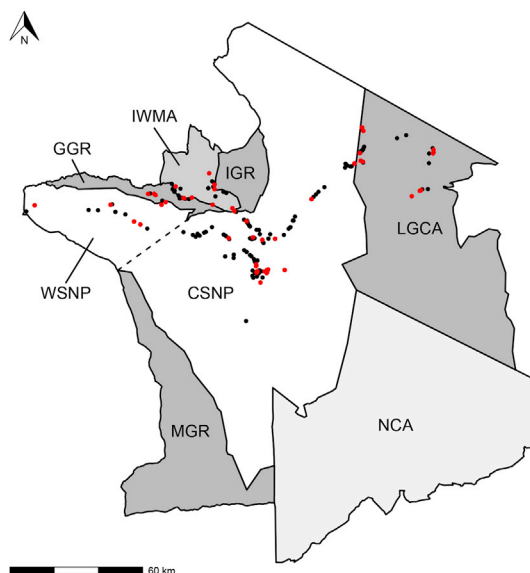
### 2.1. Study area

The study was conducted in SNP, Tanzania, and in the immediately adjoining protected areas, between May and July 2016 (Fig. 1). This coincides with the end of the long wet season and the start of the long dry season. Non-consumptive tourism and research are the main human activities in SNP. Besides some infrastructure for management (offices, ranger posts), tourism (information centres, lodges, tented camps) and research purposes; livestock grazing and resource extraction are strictly prohibited (Sinclair et al., 2008a). SNP thus served as a control area in our analyses, given the strict protection and relatively low human disturbance. However, although the SNP is strictly protected, in the western part of the SNP, called 'the western corridor', poaching is still pervasive (Holmern et al., 2006; Kaltenborn et al., 2005; Loibooki et al., 2002). We therefore distinguished between the central SNP (CSNP), and the western SNP (WSNP). In Loliondo Game Controlled Area (LGCA) and Ikona Wildlife Management Area (IWMA), human settlements, livestock grazing, and resource extraction are permitted but regulated. In the Grumeti Game Reserve (GGR) activities related to both consumptive and non-consumptive tourism are permitted and regulated, but settlements and agro-pastoralism are prohibited (Sinclair et al., 2008a). Additionally, hunting licenses are granted in the hunting season (1st July – 31st December) in both GGR and LGCA, where impala is an important game species (Thirgood et al., 2008), though especially in the last few years, hunting in GGR has been minimal. The estimated abundance of impala in the Serengeti ecosystem is around 75,000 (SE 9000) individuals (TAWIRI, 2010), and is widely distributed throughout wooded grassland and open woodlands.

In order to assess the potential effects of different human activities on the impala, the study area was divided into the above-mentioned five areas (Fig. 1). Relative to CSNP (the control area), we expected impala in the less-protected areas, along the area-specific disturbance-gradient of WSNP, GGR, IWMA and LGCA, to show an increasing response in terms of behaviour and demography.

### 2.2. Data collection

Existing roads inside and outside SNP were used to locate impala groups ( $n = 232$ ), in addition to cross-country driving where roads were unavailable. As soon as an impala group was located, the car was stopped and the GPS location and number of individuals in the group were recorded along with their respective sex and age (when possible). Individuals were considered a group if they were within 15 m of their nearest neighbour, and other family groups had to be at least 50 m away. Age was classified into three categories: adult, juvenile and calf, based on horn length and shape, and body proportions (Brooks, 1978; Simpson, 1971). Age category and sex were recorded as unknown if it was not possible to record for the given individual in the group (e.g. sex of calves).



**Fig. 1.** The Serengeti ecosystem, with central and western Serengeti National Park (CSNP and WSNP, resp.), and immediately adjoining Grumeti (GGR), Ikorongo (IGR) and Maswa (MGR) Game Reserves, Loliondo Game Controlled Area (LGCA), Ikona Wildlife Management area (IWMA), and Ngorongoro Conservation Area (NCA). Black dots indicate locations where only demography data was collected, while red dots indicate location where both behaviour and demography data was collected. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Impala have small home ranges and groups usually stay in the same area, however to control for pseudo-replication (e.g. neighbouring female and bachelor groups, resampling of groups over time) we clustered the observed groups which were co-located within 1 km of each other (rendering 27 unique clusters).

Behavioural data were collected by observing 102 focal individuals within 44 groups. Observations were made from a Toyota Land Cruiser, which in areas of thick vegetation, had to be moved frequently during data collection due to the restricted visibility. No behavioural data were collected until the impala were accustomed to our presence (i.e. impala resumed original behaviour and did not actively watch the observers), which usually took less than 10 min, to avoid influence of observer presence (Kiffner et al., 2014). Habitat of the observed group was categorized into four different types; grassland (grass dominated with <2% tree canopy), savannah (grassland with 2–20% tree cover), woodland (>20% tree cover, defined as trees > 6 m with canopy cover 20% or higher) and bushland (dense woody vegetation <6 m in height with 2–20% bush canopy). Data were recorded between 7:00 a.m. and 7:00 p.m., covering the whole period of daylight. Individual behaviour was estimated using focal animal sampling with instantaneous sampling and a fixed-interval time-point recording rule (Altmann, 1973; Martin and Bateson, 2007). The fixed-point interval was one minute, and a total of 30 min of observation was spent on each focal individual. Individual behaviour was recorded as ten mutually exclusive behavioural types: resting (laying down or standing without ruminating), grooming (including allogrooming and scratching), ruminating (ears and eyes relaxed, chewing but not foraging), feeding (grazing and browsing), moving (moving for a minimum of four consecutive steps), vigilance (head high, ears forward and not moving, eyes wide open), watching the observer (i.e. vigilance towards observer), fleeing, and rutting (exclusively male behaviour; any territorial behaviour). In the analyses, we recognised five distinct behaviours and analysed them separately: vigilant (i.e. vigilance, watching the observer, and fleeing), moving, feeding, resting (i.e. grooming, ruminating and resting), and rutting. Two researchers observed two adult individuals per group each, simultaneously (i.e. four individuals were observed at one time). This allowed us to assess synchrony: per group, the territorial male or a random female was selected as focal individual for each observer, and both the focal animal's behaviour and that of its neighbour to the right was noted at the abovementioned intervals. Synchrony was then calculated as the proportion of times the focal individual's behaviour was the same as its neighbour's. Observer skill and bias were considered and minimised through trials before data collection. Only family herds were considered, and only adult individuals were observed; to examine differences between sexes, both the territorial male (if present or visible for observation) and a randomly chosen female were observed. Data were discarded if fewer than 20 recordings were collected per focal individual, e.g. when the animal moved out of sight ( $n = 16$ ).

### 2.3. Data analyses

First, effects of areas with different land use regimes on group demography were assessed. Demographic variables included group size, reproductive ratio, juvenile recruitment ratio, and sex ratio. Reproductive ratio was calculated as the number of calves per adult female (calf:adult female ratio), while juvenile recruitment ratio was calculated as the number of juveniles per adult female (juvenile:adult female ratio). To test for overall differences in sex ratio, calf:adult female ratio, and juvenile:adult female ratio between areas, a Pearson's Chi-squared test of independence and a Chi-squared post-hoc test with pairwise comparisons were applied. Thereafter, generalized linear mixed models (GLMM) were used to relate the demographic variables at group level to assess differences between areas with different land use regimes. GLMM modelling was performed in R version 3.4.2 using the *glmer* function of the *lme4* package (Bates et al., 2014). Sex ratio could however not be assessed on group level due to sexually differentiated group compositions (i.e. family versus bachelor herds). Prior to analyses, the fit of each intercept model using a Poisson (R package *lme4*, function *glmer*) or negative binomial distribution (R package *MASS*, function *glmer.nb* (Venables and Ripley, 2003)) was compared. Further analyses were based on the better fitting distribution. Reproductive ratio and juvenile recruitment ratio used, respectively, number of calves and juveniles as response variable and included an offset on log-transformed number of adult females. We corrected for potential spatial and temporal variation by including Julian day and cluster as random effects. We used Akaike's Information Criterion corrected for small sample sizes (AICc) to select the best fitting model to the data (Burnham and Anderson, 2002). Of the competing models ( $\Delta\text{AICc} \leq 2$ ), the most parsimonious model was preferred and discussed here. All models used in the analyses were first compared to their respective intercept model and only accepted when the  $\Delta\text{AICc}$  value of the latter was larger than 2; model residuals were visually checked to be normally distributed. Mixed effect models were compared to their respective intercept models by analysis of variance (ANOVA; Table S1).

To test if impala synchronized their behaviour with their neighbour, we tested whether the observed proportion of synchrony was significantly different than the proportion of synchrony that would be expected by chance, given the observed frequency of behaviours in our data. We created a variable with random distribution of behaviour types, but in line with the observed frequencies of those behaviours, to obtain a synchrony measure for this test data. After aggregating the data per individual, yielding a mean ratio of synchrony, we then applied a Welch Two Sample *t*-test to compare average ratio of synchrony between observed and test data. This was done for moving, feeding, resting, and vigilance behaviour and for overall synchrony.

We applied generalized linear mixed models (GLMM) to relate the proportion of time performing different behaviours (resting, feeding, moving, vigilant, rutting) to explanatory variables. Number of scans spent on specific behaviours versus other behaviours was fitted with a two-column variable with binomial distribution. To correct for any temporal differences, we included Julian day as a random effect. Similarly, cluster and group ID were included as random effects to account for

between- and within-group differences. To assess which covariates affected behaviour, potential differential factors and strategies were modelled separately and thereafter combined. While impala require to take account of differential factors such as sex, time-of-day (categorized as morning 6am–11am, noon 11am–4pm, and evening 4pm–7pm) or land use area (non-adjustable); they may be able to adjust their strategy optimizing their preferred behaviour (adjustable). Potential strategies (and related covariates) include: encounter dilution and confusion effects (group size; Vine, 1971), the pass-along effect of vigilance (synchrony; Beauchamp, 2007), risk reduction through social cohesion (synchrony; Conradt and Roper, 2000), the selfish-herd hypothesis (position within the group; Hamilton, 1971), and the risk-allocation hypothesis (habitat; Lima and Bednekoff, 1999). We compared single-parameter models including one of each of the covariates mentioned above as fixed effect to the intercept model. Based on the best single-parameter models, additive models were constructed, and compared to the single-parameter models to identify the covariates in the best model (Table S2). All covariates were retained when  $\Delta AICc$  remained  $<2$ . Prior to analyses collinearity among the covariates was tested using the *pcor* function of the R package *ppcor* (Kim, 2015). Only sex and synchrony were significantly correlated with each other ( $r_s = -0.367$ ,  $t = -3.504$ ,  $p = 0.001$ ).

### 3. Results

Overall, there was a significant difference in sex ratio between areas with different land use (Table 1). The sex ratio was significantly more female skewed in LGCA compared to CSNP and GGR ( $\chi^2$  post-hoc test: respectively  $p < 0.001$  and  $p = 0.002$ ). The sex ratio did not differ significantly among any of the other areas. Overall, a significantly lower calf:adult female ratio was found in LGCA compared to the other areas (Table 1). At group level, reproductive ratio (Table S1) was significantly lower in LGCA relative to CSNP ( $p = 0.003$ ) and WSNP ( $p = 0.037$ ). Overall, juvenile:adult female ratio was also significantly lower in LGCA compared to the other areas (Table 1). At group level, juvenile recruitment ratio was, however, not significantly affected by area (Table S1). Group size, family herd size and bachelor herd size were not significantly different among the five areas (Tables 1 and 2).

Impala synchronized their behaviour significantly more than would be expected by chance (Table 2). All behaviours apart from feeding were significantly synchronized, especially vigilance and moving (Table 2).

Impala behaviour was significantly affected by the proportion of synchrony with neighbouring females, in addition to either sex or land use area; all the best models included synchrony (Table S2). Resting was affected by land use area, sex and synchrony (respectively  $F = 4.046$ ,  $F = 0.122$  and  $F = 11.928$ ; Table S2). Impala rested significantly less in LGCA (odds ratio (OR) [ $\pm$  95% C.I.]: 0.308 [0.144–0.658]) and IWMA (OR: 0.208 [0.077–0.564]) compared to CSNP (OR: 1.588 [0.642–3.930]); respectively:  $z = -3.041$ ,  $p = 0.018$  and  $z = -3.087$ ,  $p = 0.016$ ). There tended to be less resting in IWMA compared to GRR (OR: 0.837 [0.341–2.054];  $z = -2.415$ ,  $p = 0.105$ ); resting in WSNP did not differ significantly from the other areas (OR: 0.910 [0.221–3.738]). Males and females rested for equal amounts of time (OR: 1.040 [0.811–1.333],  $z = -0.307$ ,  $p = 0.759$ ). Resting decreased with increasing synchrony (OR: 0.155 [0.041–0.586],  $z = -2.750$ ,  $p = 0.006$ ).

Feeding differed by sex and increased with synchrony (Table S2). Males tended to spend a slightly higher proportion of their time feeding (OR: 1.023 [0.814–1.286],  $F = 0.039$ ). More time was spent feeding when synchronized (OR: 23.966 [6.886–83.407],  $F = 32.631$ ). The low effect of sex in the additive model indicates that this was mainly due to differences in synchrony between sexes. Moving tended to be negatively associated with synchronization (OR: 0.347 [0.084–1.437],

**Table 1**

Sex ratio (male:female), mean group size per herd type ( $\pm$ SE), calf:adult female (C:AF) ratio, and juvenile:adult female (J:AF) ratio of impala groups in the different study areas ( $n$  = number of individuals for all measurement except for group size where  $n$  = observations).  $\chi^2$  is given for the overall test.

Area	Sex ratio	n	Group size	n	Family herd size	n	Bachelor herd size	n	C:AF ratio	n	J: AF ratio	n
$\chi^2$	30.928*		2.294 <sup>ns</sup>		4.733 <sup>ns</sup>		0.645 <sup>ns</sup>		33.088*		20.533*	
CSNP	1: 2.24 <sup>a</sup>	2470	22.77 ( $\pm$ 2.32)	115	39.20 ( $\pm$ 3.61)	55	7.70 ( $\pm$ 0.98)	60	0.10 <sup>a</sup>	148:1539	0.34 <sup>a</sup>	527:1539
LGCA	1: 3.63 <sup>b</sup>	820	18.13 ( $\pm$ 2.77)	46	25.86 ( $\pm$ 3.79)	28	6.11 ( $\pm$ 1.58)	18	0.02 <sup>b</sup>	14:582	0.22 <sup>b</sup>	130:582
GGR	1: 2.39 <sup>b</sup>	830	27.16 ( $\pm$ 5.03)	32	40.42 ( $\pm$ 6.91)	19	7.77 ( $\pm$ 1.87)	13	0.07 <sup>a,b</sup>	39:533	0.29 <sup>a</sup>	154:533
WSNP	1: 3.12 <sup>a</sup>	350	21.00 ( $\pm$ 5.29)	18	33.50 ( $\pm$ 7.39)	10	5.38 ( $\pm$ 1.58)	8	0.12 <sup>b</sup>	28:233	0.33 <sup>a</sup>	76:233
IWMA	1: 2.90 <sup>a</sup>	390	19.33 ( $\pm$ 3.32)	21	29.00 ( $\pm$ 3.75)	12	6.44 ( $\pm$ 1.49)	9	0.06 <sup>a,b</sup>	16:264	0.23 <sup>a</sup>	60:264

Alphabetical superscript denotes significant differences between groups; \* $p < 0.001$ , <sup>ns</sup>  $p > 0.05$ .

**Table 2**

Observed and randomly generated synchrony ratios (SR), and frequencies of the different impala behaviours.

	Observed		Test data		t-statistic	df	p-value
	SR	Freq.	SR	Freq.			
Feeding	0.53	0.46	0.48	0.47	1.439	184.24	0.152
Vigilant	0.33	0.05	0.07	0.05	4.120	77.10	<0.001
Resting	0.38	0.33	0.29	0.31	2.614	168.39	0.010
Moving	0.40	0.16	0.16	0.17	6.062	158.90	<0.001
Total	0.51		0.34		9.249	181.20	<0.001



$F = 7.028$ ) and males moved more than females (OR: 1.331 [1.002–1.769],  $F = 3.855$ ). The proportion of time spent vigilant varied by sex and proportion of synchrony (the latter only slightly:  $\Delta AICc = 1.1$ ; respectively  $F = 18.946$  and  $F = 3.271$ ; Table S2). Males were less vigilant relative to females (OR: 0.267 [0.148–0.483]), however vigilance decreased with increasing synchrony (OR: 0.014 [0.001–0.157]). Rutting in males was slightly affected by group size ( $\Delta AICc = 1.6$ ): rutting behaviour increased with group size (OR: 1.031 [0.998–1.065],  $F = 3.192$ ). Given the importance of synchrony, the potential differentiating effect of sex, time-of-day and land use area on the proportion of time spent synchronized were further assessed. While sex affected synchrony, time-of-day and land use area did not ( $\Delta AICc$  from the intercept model ( $AICc = 471.8$ ): 14.2,  $-3.5$  and  $-8.0$ , respectively). Males were less synchronized compared to females (OR: 0.693 [0.581–0.827],  $F = 16.648$ ).

## 4. Discussion

In the face of rapid human-induced changes, it is necessary to understand how the diverse threats and pressures impact wildlife populations' behaviour and demography. Our results show that human activities in less regulated areas significantly reduce the time impala spent resting, exacerbate a female skewed sex-ratio, and reduce observed reproductive and recruitment ratios; group size did not differ between study areas. Impala synchronized their behaviour, increasing social cohesion. Contrasting the different management areas regarding their level of human disturbance indicated that behaviour and demography in impala was mostly affected in areas where land-use practice including livestock grazing and agriculture is allowed (IWMA and LGCA). Relative to the control area in the central part of SNP, potential indirect disturbances (e.g. bushmeat hunting or livestock incursions) seemed not to affect impalas significantly (WSNP and GGR).

### 4.1. Behavioural responses to disturbance

Negative interactions with humans are known to have significant impacts on ungulate behaviour, especially those associated with perceived predation risk such as vigilance and flight (Frid and Dill, 2002; Stankowich, 2008). Flight distances have also been reported to increase in ungulates exposed to disturbing human activities (Stankowich, 2008). By spending time and resources on these 'costly behaviours', less time and energy are spent on restorative behaviours (e.g. foraging and resting), potentially contributing to reduced individual fitness. These behaviours can thus be used as indicators to study the level of perceived human disturbances, and in extension, management effectiveness (but see Goldenberg et al., 2017). Our analyses indicate impala reduce time spent resting in areas with higher levels of human disturbance, as was observed in IWMA and especially in LGCA.

Although CSNP has been well protected for a prolonged period, the intensity of threats in areas such as GGR have, until fairly recently, been far greater. The implementation of effective conservation management, aimed at reducing anthropogenic threats to wildlife populations can, however, positively influence animal behaviour. The Grumeti Area, and GGR in particular, has undergone drastic changes in conservation management over the past decade, with a heightened focus on non-consumptive tourism. This has led to an increased employment of local people in tourist facilities, and poachers have been trained and employed as rangers. This, together with increased efforts in law enforcement, has reduced poaching intensity (Goodman, 2014). Prior to the implementation of these conservation measures, the impala behaviour and demographics (discussed below) reflected exposure to anthropogenic impacts (Setsaas et al., 2007). However, our results suggest that these measures have positively influenced impala behaviour in this area in terms of, amongst other, vigilance. Impala in GGR did not spend a higher proportion of time on vigilant behaviour compared to the control area, CSNP, or any of the other study areas.

Males spent a higher proportion of time on moving and feeding, and a lower proportion of time on vigilance compared to females. Since most males observed in this study were territorial (as opposed to bachelor), this result was expected. Territorial males generally invest more time and energy in reproductive behaviours such as courtship of females, competitive interactions with rival males, and maintaining their territory, at the expense of for instance vigilance (Jarman and Jarman, 1973). Increased feeding time might be necessitated by the energetic cost of extensive rutting behaviour (Oliver, 2002).

Predation risk strongly influences vigilance behaviour in impala (Hunter and Skinner, 1998; van der Meer et al., 2015). Impala are readily preyed upon by carnivores such as lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyena (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*) (Hayward and Kerley, 2008). As spending time vigilant is costly to the animal, prey species have developed various anti-predation strategies. Our analyses indicated that impala behaviour was synchronized, which can facilitate more efficient anti-predator strategies. Earlier studies have shown that behavioural synchrony may enhance spatial cohesion (King and Cowlshaw, 2009; Pays et al., 2007) and stimulate social cohesion through sexual segregation (Conradt, 1998; Conradt and Roper, 2000). Impala form sexually segregated groups of family herds with females, a dominant male and their offspring and nearby bachelor herds. Reasons for this sexual segregation may be caused by reproductive cycles but also each group having a 'common fate' regarding the need for similar behavioural activities (Murray, 1981). Although carnivores are present in all our study areas, the recent decline in other wild prey species in LGCA (unpublished data) may have increased predation pressure on impala. This could be exacerbated by the fact that impala are non-migratory (available to resident predator populations year-round), and LGCA does not attract many migratory species (relatively small seasonal influx of alternative prey species to dilute the predation pressure on impala). Additionally, impala young are particularly vulnerable to predation, and in combination these factors may partially explain the area's low recruitment ratios.

#### 4.2. Demographic perturbations

The effects of licensed hunting are not limited to behavioural changes but can also have significant effects on population dynamics (Ginsberg and Milner-Gulland, 1994; Milner et al., 2007; Palazy et al., 2012). Trophy hunting in particular often targets large, breeding males. This phenotype-based selective hunting can reduce genetic variability and skew sex ratios (Coltman et al., 2003; Harris et al., 2013). Here, the sex ratio of impala populations was found to be skewed towards females in all the study areas. This was expected, as male antelopes often have a higher mortality rate related to a higher male predation risk due to differences in morphology and behaviour (Jarman and Jarman, 1973). However, the sex ratio in LGCA was found to be significantly more female skewed compared to CSNP and GGR. This may be the result of excessive hunting in this area. The hunting block in LGCA was frequently used by hunters who primarily select for adult males (Holmern et al., 2004; Thirgood et al., 2008). Skewed sex ratios due to hunting activities have also been found in other ungulates (Fischer and Linsenmair, 2007; Marealle et al., 2010; Milner-Gulland et al., 2003). Additionally, Holmern et al. (2006) found that illegal hunting practises were male biased (but see: Averbeck et al., 2010). Male impala generally have a more risk-prone behaviour during the rutting season, which makes them more vulnerable to hunting activities. The observed female skewed sex ratio might thus be explained by both legal and illegal hunting activities.

The sex ratio in GGR was found to be similar to the control area, CSNP, which is contrary to the findings of Setsaas et al. (2007). These results suggest that illegal hunting is either limited in this area or independent of sex, so that the selective pressure on males is not affecting population demography. As mentioned above, the Grumeti Fund has in the last two decades focused on rehabilitation of the wildlife populations of Grumeti Game Reserve and surrounding areas, and Ikorongo Game Reserve (Goodman, 2014). The increased investment in resource protection is likely to have been beneficial for wildlife populations in these areas, particularly in terms of reduced poaching (Thirgood et al., 2008).

However, our results do suggest that the hunting activities in LGCA might have a significant impact on the sex ratio of the local impala population. Even in harem breeding ungulates such as the impala, a female skewed sex ratio caused by removing breeding males can have significant ripple effects in population dynamics by, among other, lowering reproductive rate, and, in extreme cases, to a population collapse (Milner-Gulland et al., 2003). Although we found significantly lower reproductive ratio and juvenile recruitment ratio in LGCA, this is unlikely to be caused by the observed female skewed sex ratio in this area. For such effects to take place, a far more skewed sex ratio is likely to be needed (Fairall, 1985; Ginsberg and Milner-Gulland, 1994; Swanson et al., 2014).

The most pronounced behavioural and demographic differences were evident in LGCA. Besides hunting, livestock herding and human settlements are the main form of human disturbance in LGCA. High levels of human disturbance may indirectly reduce survival and reproduction by causing animals to divert a large proportion of time and energy away from resource acquisition (Frid and Dill, 2002). Livestock herding or pastoralism may lead to interspecific competition for food and habitat between livestock and wildlife (e.g. Dunham et al., 2003), and behavioural adaptations to reduce interactions with humans, both of which could contribute to a decrease in reproductive effort, and consequently, a lower recruitment (Dunham et al., 2003; Prins, 1992, 2000). Furthermore, human settlements and pastoralism might contribute to habitat alteration and degradation (Ogutu et al., 2009), including edge effects and increased exposure to diseases from livestock (Bengis et al., 2002). Further evidence of indirect effects of human disturbance on wildlife is presented in other experimental studies, having various effects on, among other, reproductive success (Freeman et al., 2014) reproductive rate (Phillips and Alldredge, 2000), activity patterns (Wronski et al., 2015), predation risk (Leblond et al., 2013), space use (Manor and Saltz, 2005), and stress levels (Hunninck et al., 2017).

There was a tendency for family herd size to be smaller in LGCA compared to CSNP, but this was not statistically significant. Impala were expected to have smaller group sizes in areas with higher human disturbance, as has been observed in other studies (Averbeck et al., 2010; Manor and Saltz, 2003). However, contrasting results have also been observed in impala earlier (Setsaas et al., 2007). In a social ungulate species such as the impala, group size can play an important role in group functions (Jarman, 1974), anti-predator behaviour (Creel et al., 2014), and intraspecific competition while foraging (Fritz and Garine-Wichatitsky, 1996). However, in many species, the relationship between group size and vigilance is not straightforward, and is likely influenced by many other factors, obscuring a potential linear relationship between the two (Beauchamp, 2008; but see Beauchamp, 2017). This might explain the contrasting and non-significant results in this and other studies.

#### 5. Conclusion

The growing human population surrounding SNP has increasing impacts on the natural system through land uses such as pastoralism and hunting. Our results indicate that human-induced disturbances have a pronounced effect on the behaviour and demography of impala populations in the Serengeti ecosystem. In accordance with our hypotheses, LGCA, the area with the highest level of human disturbance, has resulted in a more female skewed sex ratio, lower observed reproductive and recruitment rate, and reduced time spent on restorative behaviour (i.e. resting). As these effects could have potentially significant implications for the persistence of impala populations in the area, monitoring of the behaviour and demography of impala is needed to better understand the implications and long-term effects of human-induced disturbance in the Serengeti ecosystem. Though the current study included only impala, it could be expected that the anthropogenic factors underlying the results also affect the behaviour and demographics of other ungulate species in the Serengeti ecosystem. Consequently,

the results from our single-species study may be indicative of more pervasive human-induced effects, and these need to be properly understood in order to identify appropriate mitigation measures.

### Role of the funding source

This research was supported by the European Union's Horizon 2020 research and innovation program under grant agreement No. 641918 (AfricanBioServices).

### Acknowledgements

We are grateful to the Tanzanian Wildlife Research Institute (TAWIRI), Tanzania National Parks (TANAPA) and the Tanzanian Commission of Science and Technology (COSTECH) for permission to conduct this study. We are grateful to the anonymous reviewers whose suggestions greatly helped in improving this manuscript.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2018.e00467>.

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