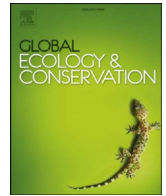




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Original Research Article

## Behavioural and demographic changes in impala populations after 15 years of improved conservation management

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## ABSTRACT

Many protected areas (PAs) have been created globally in response to the dramatic human-induced decline in biodiversity. However, not all PAs successfully preserve their biodiversity and continued monitoring is vital to assess the effectiveness of conservation efforts. Here, we repeated a study done in 2003 to assess whether investments in anti-poaching in two partially PAs (PPAs), Grumeti Game Reserve (GGR) and Ikona Wildlife Management Area (IWMA), have had quantifiable impacts on impala (*Aepyceros melampus*) populations, compared to the adjacent strictly protected Serengeti National Park. Since 2003, management of the PPAs has changed dramatically under the non-profit organisation Grumeti Fund. We predicted that if conservation management had improved, impala populations in 2018 would have higher local density, less female-skewed sex ratio, larger group sizes, and shorter flight initiation distances (FID). To assess these parameters of the impala populations, we conducted the same road-based surveys in 2003 and 2018. We found that compared to 2003, impala population density doubled in GGR, group sizes were larger in IWMA and nearly doubled in GGR, and that impala had shorter FID in IWMA in 2018. Our results suggest that the changes in conservation management could have led to the observed positive impacts for impala populations. Our study is encouraging for managers and reveals a conservation success story: if proper action is taken to increase the protection of wildlife within PPAs, wildlife populations may respond quickly and positively.

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## 1. Introduction

Biodiversity is declining at an unprecedented rate globally (Butchart et al., 2010). Human activities are driving the continued loss of biodiversity, with anthropogenic impacts on both unprotected and protected natural habitats increasing (Johnson et al., 2017). Ecosystems are being degraded and natural habitats fragmented or destroyed (Fahrig, 2003; Fischer and Lindenmayer, 2007), and overexploitation, agricultural activity, and urban development have been identified as the major threats to

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biodiversity today (Maxwell et al., 2016). In response to this dramatic decline in biodiversity, many protected areas (PAs) have successfully been created around the world. Currently, about 15.4% of the Earth's land surface is legally protected (Juffe-Bignoli et al., 2014). The designation of PAs represents one of the primary conservation strategies to conserve natural ecosystems and their biodiversity (Barnes et al., 2016).

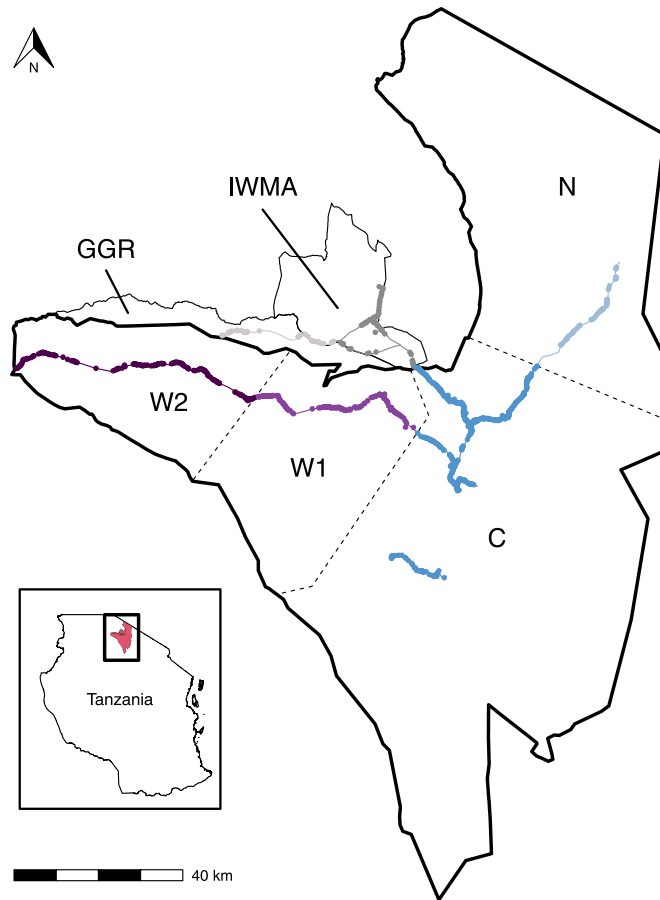
Typically, PAs are set within a matrix of multiple-use landscapes, with adjacent areas often fulfilling important ecological functions. Successful performance therefore requires elaborate and efficient management, monitoring, and anti-poaching activities beyond PA boundaries (Leverington et al., 2010; Watson et al., 2014). However, by restricting natural resource extraction or use by local communities, concerns have emerged regarding the lack of socio-economic benefits to ameliorate poverty (Brockington and Wilkie, 2015); Community-based alternatives can potentially not only provide more revenue for local communities, but also protect their wildlife effectively (Lee, 2018; Lee and Bond, 2018). Furthermore, although PAs generally have been successful at preserving their biodiversity globally (Barnes et al., 2016), some PAs have not been able to prevent wildlife population declines due to a number of factors, including PA size, location, and socio-economic conditions (Craigie et al., 2010; Barnes et al., 2016). PAs are also strongly influenced by land-use activities along their borders, and landscape degradation in areas adjacent to PAs may aggravate edge effects and alter ecosystem dynamics within the core PA (Veldhuis et al., 2019). With growing human populations and increasing pressure on biodiversity, disturbance of wildlife can also be expected to increase. Therefore, there is a need to investigate the long-term impacts humans have on ecosystems and wildlife populations. Human activities not only have the potential to impact wildlife directly through population declines, but also through more indirect effects such as changes in population demographics and behavioural characteristics, which may affect populations negatively (Frid and Dill, 2002).

When populations are exploited at unsustainable intensities (e.g. through hunting), wildlife densities decline (Milner-Gulland et al., 2001), even in PAs (Caro, 1999b; Fischer and Linsenmair, 2001). Monitoring changes in species' population sizes and distributions can yield important insights into the threats facing a PA (Nichols and Williams, 2006). However, demographic proxies such as sex ratio and group composition are also influential drivers of population dynamics and are affected by various human disturbances (Nichols and Williams, 2006). Furthermore, monitoring population demography metrics can provide important indications about population persistence, even when population density metrics might not. For example, trophy hunting may considerably alter population dynamics and demographics of wildlife species through a disproportionate selection of adult males (Ginsberg and Milner-Gulland, 1994). Even illegal bushmeat hunting which uses passive hunting methods, such as wire snares or pitfall traps, may have a male bias (Holmern et al., 2006). Female-biased sex ratios have been found for several species, especially in more exploited areas (Setsaas et al., 2007; Magige, 2008; Ndibalema, 2009; Marealle et al., 2010). The effects of such anthropogenic activities typically affect wildlife populations inhabiting the peripheries of PAs. For example, Veldhuis et al. (2019) found that wildlife populations are "squeezed" into core areas due to human activities at PA edges. To minimise such edge effects, PAs are sometimes insulated by creating adjacent multiple-use partially protected areas (PPAs; Caro et al., 2009; Sciberras et al., 2013). PPAs balance conservation targets with varying degrees of consumptive or non-consumptive uses, such as legal hunting and nature-based tourism and can sustain similar species richness and densities as an adjacent PA (Kiffner et al., 2020b).

Human activities within and adjacent to PPAs can have a range of direct and indirect effects on wildlife, ultimately affecting population persistence (Ceballos et al., 2017). Besides human activities that are lethal to wildlife (e.g. trophy hunting and bushmeat hunting), non-lethal stimuli can indirectly affect fitness and population dynamics, as these can be seen as analogous to predation risk from natural predators (Frid and Dill, 2002). For example, African elephants were shown to have higher stress hormone levels outside of strictly protected areas (Tingvold et al., 2013; Hunnink et al., 2017). While these effects are more subtle, they can create similar trade-offs between avoiding perceived risk and fitness-enhancing activities such as feeding, resting or reproduction (Ydenberg and Dill, 1986; Caro, 2005). For example, in gregarious ungulates, group size may be adjusted as a strategy to mitigate hunting risk. Several ungulate species have shown to be in smaller groups or alone when faced with human hunters, as opposed to natural predators (Manor and Saltz, 2003; Gude et al., 2006; Fischer and Linsenmair, 2007). Being in smaller groups or alone is likely more advantageous for avoiding human hunters, as small groups or singletons are harder to spot than larger aggregations (Fischer and Linsenmair, 2007). Similarly, ungulates exposed to hunting are more likely to flee from human approaches and have greater flight initiation distances (FID) than ungulates in non-hunting areas (de Boer et al., 2004; Stankowich, 2008; Reimers et al., 2009; Muposhi et al., 2016; Hariohay et al., 2018). Taken together, these studies show that studying behavioural responses of wildlife populations can represent a useful tool for assessing the impacts of human exploitation (Caro, 2005).

Long-term monitoring of direct and indirect anthropogenic impacts are essential for assessing the efficacy of management practices in PAs and PPAs (Noss, 1990; Lindenmayer and Likens, 2009, 2010). However, long-term monitoring programs are rare due to a lack of funding and are in many instances biased towards PAs (Lindenmayer and Likens, 2009; McDonald-Madden et al., 2010). Although the importance of multiple-use areas adjacent to PAs has been acknowledged (Veldhuis et al., 2019), continued monitoring of these PPAs is vital to evaluate their contribution to conservation in terms of how and in which way they benefit wildlife populations.

Here, we present a replication of a monitoring study performed in the Serengeti ecosystem, Tanzania, fifteen years after the baseline study conducted in 2003. Since 2003, the Grumeti Fund has dramatically increased its efforts in conservation management of Grumeti Game Reserve (GGR), an adjacent PPA to Serengeti National Park (SNP; Singita, 2017; Grumeti Fund, 2018). We assess whether changes in management over the past 15 years in two PPAs (including GGR; 2003 vs. 2018) have resulted in measurable improvements in demographic and behavioural responses of impala (*Aepyceros melampus*) to human disturbances.



**Fig. 1. Map of the study area with locations of impala sightings.** Locations of impala groups (points) along transects (thin lines) in the various study areas (colours): the Serengeti National Park (bold outline) and its four subsections (dashed lines; Central area, C; Western corridor, W1 and W2; Northern area, N), and two partially protected areas (PPAs; thin outlines; Grumeti Game Reserve, GGR and Ikona Wildlife Management Area, IWMA. *Inset*: map of Tanzania with location of study area (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In 2003, [Setsaas et al. \(2007\)](#) found that, compared to the well-protected SNP, human activities resulted in reduced densities, more female-skewed sex ratios, increased wariness and longer FIDs in impala inhabiting the adjoining PPAs. Given the increased investment in conservation management, we predicted that, compared to the results from 2003, impala populations inhabiting the PPAs in 2018 would have (1) a higher density; (2) a less female-skewed sex ratio; (3) larger group sizes; (4) less flighty behaviour; and (5) shorter FID towards an approaching human, while these parameters would remain largely unchanged in SNP.

## 2. Materials and methods

### 2.1. Study area

This study was conducted in the Serengeti ecosystem (ca. 25,000 km<sup>2</sup>) in northern Tanzania. Different forms of management are implemented across the ecosystem, with six PPAs serving as buffer zones around the core area, the SNP. This study was limited to SNP and two adjacent PPAs: GGR and Ikona Wildlife Management Area (IWMA; [Fig. 1](#)). In SNP, only nature-based tourism is allowed, while in the PPAs limited licensed hunting and game cropping are also allowed. Permanent settlements or other forms of natural resource utilisation are only permitted in IWMA ([Holmern, 2007](#)).

Even though both core and buffer areas are protected, illegal activities are still pervasive. The most severely affected areas from illegal bushmeat hunting inside the SNP have been in the west and north-west ([Campbell and Hofer, 1995](#); [Holmern et al., 2007](#); [Nuno et al., 2013](#)). The PPAs are also subject to illegal bushmeat hunting, which is conducted largely by snares and on foot ([Campbell and Hofer, 1995](#); [Holmern et al., 2002](#); [Denninger Snyder et al., 2019](#)). The area is also experiencing increasing human disturbances (e.g. from illegal extraction of timber and livestock grazing), resulting in part from an increasing human population; in the areas surrounding SNP, human population size increased on average by 2.4% per year from 1999 to 2012 ([Veldhuis et al., 2019](#)).

Prior to 2003, only six rangers undertook anti-poaching in the Ikorongo and Grumeti Game Reserves from their headquarters in Fort Ikoma (i.e., 1 ranger/167 km<sup>2</sup>; URT, 2002). In 2003, the non-profit organisation Grumeti Fund took over the management of these game reserves adjacent to the north western side of SNP and has since been increasing its investment in wildlife conservation, community development, and anti-poaching considerably (Singita, 2017). Self-reported funding totalled US\$4.8 million in 2018, of which approximately 10% went to community outreach, 5% to research and monitoring, 14% to conservation management, and 29% to anti-poaching and law enforcement (Grumeti Fund, 2018). In 2018, Grumeti Fund employed 132 rangers in their anti-poaching program (i.e., 1 ranger/7.5 km<sup>2</sup>) and invested in modern equipment, including night vision technology, covert cameras, and drone-based air support (Grumeti Fund, 2018). These investments and efforts have had measurable results, where standing biomass of resident wildlife in the Grumeti concessions increased from roughly 12 kg/ha in 2003–52 kg/ha in 2018, a 4.3-fold increase. Population trends of several ungulates increased dramatically between 2003 and 2014, for example, buffalo (*Syncerus caffer*; 10-fold), eland (*Taurotragus oryx*; 8-fold), elephant (*Loxodonta africana*; 4-fold), and impala (2-fold; Goodman, 2014). Although predator populations are notoriously difficult to estimate, extrapolation from sighting data suggests that the lion (*Panthera leo*) population increased 10-fold as well (Grumeti Fund, 2018).

## 2.2. Impala

Impala are a medium-sized, sexually dimorphic antelope species widely distributed throughout eastern and southern Africa (Estes, 2012). The impala population in Serengeti has been estimated to be ca. 43,800 ± 6200 individuals in SNP (TAWIRI, 2010), and ca. 14,300 (95% CI: 10,700–19,000) individuals in the Grumeti Game Reserves complex, which includes the GGR and IWMA (Goodman, 2014). Impala are usually found in woodland and bushland habitat, but also in the interface between woodland/bushland and savannah or grassland (Estes, 2012). Impala are non-migratory, but they will move seasonally between habitats within a limited home range, in relation to the abundance and availability of resources in the dry and wet season (Jarman and Jarman, 1974). Impala are both grazers and browsers, grazing on a range of grasses and browsing in a range of vegetation types within their home area. The diet changes seasonally, as does their preference for vegetation types (Jarman, 1974). Impala are a gregarious and polygynous species, that are usually observed in distinct social groups; female herds, bachelor herds, and singleton males (Estes, 2012). Impala populations in the Serengeti ecosystem have been shown to adjust their behaviour (Setsaas et al., 2018) and physiology (Lunde et al., 2016; Hunnink et al., 2020) in response to higher human activities in the adjacent PPAs, compared to the SNP.

## 2.3. Data collection demography

We repeated the 2003 study (Setsaas et al., 2007) in 2018, and employed the same methodology so as to facilitate a temporal comparison. The study area was divided into six parts (Fig. 1). The SNP itself was divided into four areas; Central area (C), Northern area (N), Western corridor 1 (W1) and Western corridor 2 (W2), in order to separate areas within the park with different levels of human activity. We also collected data in two adjacent PPAs; GGR and IWMA. The total study period included August to December in 2003, which covers the end of the long dry season, and June to July in 2018, which encompasses the start of the long dry season. Since both studies are conducted in the long dry season, we do not expect seasonal differences to affect our results.

Transects were driven along existing roads between 7:00 am and 7:00 pm, covering a total of 3336 km (2003: 2050 km, 2018: 1286 km). Transects did not overlap, such that no area was covered in more than one transect (Fig. 1). The transects were driven an equal number of times alternately forwards and backwards in each year, to control for potential diurnal biases in density (Jarman and Jarman, 1973). During each transect we took records of all impala that were seen, regardless of distance from the road. We employed the routinely used distance sampling approach (Buckland et al., 2015) to determine the density of impala, which allows obtaining unbiased estimates of animal densities, assuming that (1) animals on the transect (i.e., road) are always detected, (2) all animals are detected in their initial locations, and (3) all measurements are correctly recorded (Thomas et al., 2010).

When impala were sighted, the vehicle was stopped immediately, and we recorded our GPS position and the distance to the impala (i.e., singleton or estimated middle of the group) using a rangefinder (Leica Rangemaster 900). We measured the angle of the road and angle of the straight line between the observers and the impala, relative to true north, using a compass. These measurements allowed the computation of the perpendicular distance from the object (impala) to the transect (road), which are required to apply distance sampling (Thomas et al., 2010). We fitted detection functions, which reflect both the decrease in detectability with distance and the lower proportion of animals that are potentially detectable (Buckland et al., 2015).

We also recorded the total number of individuals (group size), group type (bachelor [only males], female [adult females, subadults, and territorial male], or single male), number of individuals of each age class (adult, subadult, calf, or unknown) and sex (male, female, or unknown), the initial behaviour per group the instant the group was discovered (i.e., resting, feeding, moving, vigilant, watching the observer, or fleeing), and habitat (open or closed). Groups were defined as clusters of individuals no more than 50 m from its nearest neighbour. Juvenile males were considered subadults when they were big enough to have visible horns, and adults when the horns had the characteristic S-shape/lyre-shape. Age class of females was determined by relative body size. We recorded the initial behaviour of the majority of the animals in a group. Resting was defined as laying down or standing resting (including ruminating), feeding was defined as either grazing or browsing, and moving was defined as taking more than two steps without feeding and not actively scanning. An animal was defined as vigilant if it lifted its head and

paid attention to its surroundings. Watching the observer was defined as being vigilant towards the car/researchers. Fleeing was defined as running or leaping away. As per [Setsaas et al. \(2007\)](#), 'closed' habitat encompassed woodland and bushland, while 'open' habitat encompassed wooded/bushes grassland and grassland.

#### 2.4. Flight experiments

FID experiments were always done by the same test person in each year (T. Holmern in 2003 and L.M. Flølo in 2018). Both test persons were tall Caucasians and wore clothes in neutral colours. The difference in test person is therefore unlikely to have significantly affected the results. FID experiments were conducted by walking at a constant pace towards either groups of impala or singletons. When approaching a group of impala, one impala in a central position with respect to the group was chosen as the focal individual to direct the approach. Groups or individuals recognised in areas previously covered were avoided, to avoid sampling the same impala more than once. Before a new experiment was initiated, the new group had to be out of visual contact with other groups, to avoid interference. Experiments were not carried out if (1) a potential predator was in sight, (2) a tourist car was nearby, (3) it was raining, (4) the test animals could not see the approacher, (5) if the animals were currently moving off due to reasons other than the car, or (6) if the animals fled before the approach could start. The experiments were abandoned if the animals ran due to other reasons than the test person, such as mating/territorial behaviour, or influence from other species.

Prior to the start of the approach, the starting distance (SD) and angle to the animal(s) relative to true north were measured using a rangefinder and a compass, respectively. In addition, the impala were scored as either alert or not alert. The test person walked at a constant speed in a direct line towards the focal animal or group. When the impala fled, the test person stopped instantly. If not all the animals in a group fled simultaneously, the approach was halted when the majority of the individuals had fled. The test person then measured the distance back to the car. The FID was calculated as the difference between the SD and the distance from the test person to the car when the approach was halted.

#### 2.5. Statistical analyses

We analysed the five response proxies (i.e., population density, sex ratio, group size, initial behaviour, and FID) separately, and, considering the type of data, applied appropriate statistical tests. Statistical analyses were carried out with R (v. 4.0.3; [R Core Team, 2020](#)) using RStudio (v. 1.3.1093; [RStudio Team, 2020](#)). In all analyses we contrasted the different study areas across 2003 and 2018.

##### 2.5.1. Population density

Density analyses ([Buckland et al., 2015](#)) were conducted using the R package *unmarked* (v. 0.12.3; [Fiske and Chandler, 2011](#)). The data from 2003 and 2018 were analysed separately. In both data distributions, observations beyond 300 m were excluded (i.e., right-truncation). We considered 8 continuous strata, one for each transect; each transect was repeated on average 6 times (range: 4–10). The distance data were divided into 15 bins of 20 m each. First, the data were fitted with null models to determine the best key detection function (half-normal, hazard rate or exponential); detection functions were fitted for each stratum separately. Then, the best fitting model for detection was established by comparing the null model to the model including study area as covariate (i.e., the 6 areas included in this study; [Fig. 1](#)). Similarly, the best fitting model for abundance was then established by comparing the null model with the model including study area as covariate. Model selection was based on Akaike Information Criterion adjusted for small sample sizes (AICc; [Burnham and Anderson, 2002](#)). The best model returned predictions of the number of impala groups per km<sup>2</sup> in each of the study areas (C, W1, W2, N, GGR, and IWMA; see [Fig. 1](#)). The density of impala individuals was estimated by multiplying the density of groups with the mean group size in each area, and the corresponding 95% confidence intervals (CI) for individual densities were calculated using the delta method ([Seber, 1982](#); [Buckland et al., 2015](#)). Densities were considered to be significantly different if the means of two areas did not lie within the 95% CI of each other.

##### 2.5.2. Sex ratio

Differences in observed sex ratio (OSR) between years and within areas were analysed using Pearson's Chi-squared tests. All individuals that could be sexed were included in the analyses. We used the Holm-Bonferroni p-value correction to account for multiple testing.

##### 2.5.3. Group size

To test whether mean group size was different in 2018 compared to 2003 in the different study areas, we used a negative binomial generalised linear model (GLM; *glm.nb* function, *MASS* v. 7.3–51.4) with year, area, their interaction, and group type (i.e., bachelor or female) as predictors. We excluded single males from this analysis as they skewed group size estimates. Post-hoc analyses were done with the *emmeans* function, *emmeans* v.1.4.2.

**Table 1**  
Demographic proxies.

Area	N		OSR		N		Group size	
	2003	2018	2003	2018	2003	2018	2003	2018
C	3496	2321	1: 1.55	1: 2.03	260	147	20.3 ± 1.2	23.0 ± 1.7
W1	1104	824	1: 1.63	1: 2.32	77	52	24.1 ± 2.5	22.3 ± 2.7
W2	728	1014	1: 1.79	1: 2.23	66	70	15.6 ± 1.7	21.8 ± 2.3
N	427	164	1: 2.01	1: 2.35	26	11	24.1 ± 4.1	26.0 ± 6.8
GGR	124	387	1: 3.77	1: 3.21	11	21	14.1 ± 2.4	22.7 ± 3.3
IWMA	261	662	1: 1.69	1: 2.25	27	35	15.7 ± 4.1	24.3 ± 4.6

Observed sex ratio (OSR; males:females) and mean female group size ± standard error for impala within each of the study areas in the Serengeti ecosystem, for both 2003 and 2018. Number of observations (N) is included. C=Central area, W1=Western corridor 1, W2=Western corridor 2, N=Northern area, GGR=Grumeti Game Reserve, and IWMA=Ikona Wildlife Management Area.

#### 2.5.4. Initial behaviour

We tested whether the frequency of initial behaviours when a group was encountered was different between 2003 and 2018 in the different study areas, by using a Pearson Chi-square test, and applying a post-hoc test using the Holm-Bonferroni p-value correction to account for multiple testing.

#### 2.5.5. Flight behaviour

To analyse FID, we first tested whether the presence of other species nearby (within approximately 50 m) had a significant effect on the FID of impala. We applied a negative binomial GLM with FID as response variable and presence of other species as predictor. Presence of other species was found to not affect FID (Likelihood Ratio test of negative binomial models; LR stat. = 1.15,  $p = 0.284$ ), and thus this predictor was not included in the final models. To test our hypothesis that FID would decrease in 2018 in the PPAs but not in SNP, we modelled the interactive effects of year and area on FID. We included SD and alertness as covariates to control for biases, because SD limits the potential range of response in FID by the focal animal(s), while animals that are alert prior to the approach may choose to escape earlier (Holmern et al., 2016). Therefore, the basic model was  $FID \sim year * area + SD + alert$ . However, not only management regimes, and changes therein, can cause changes in behaviour. Previous research has shown that various covariates might influence FID (Stankowich and Blumstein, 2005; Setsaas et al., 2007; Stankowich, 2008), including (1) vegetation (open or closed vegetation); (2) group size (number of individuals); (3) group type (bachelor, female, or single male); and (4) calf presence (calves present in group or not). We tested whether these covariates improved the fit of the model by adding them one by one to the basic model – and used model selection criteria to compare models. We used GLMs with negative binomial distributions (Table 2). Model selection was based on AICc (Burnham and Anderson, 2002). The most parsimonious model (i.e., with  $\Delta AICc < 2$ ) was selected as best fitting the data. Model residuals were normally distributed and no pattern (i.e., heteroscedasticity) was observed. No collinearity between predictors was found.

### 3. Results

#### 3.1. Demography

##### 3.1.1. Population density

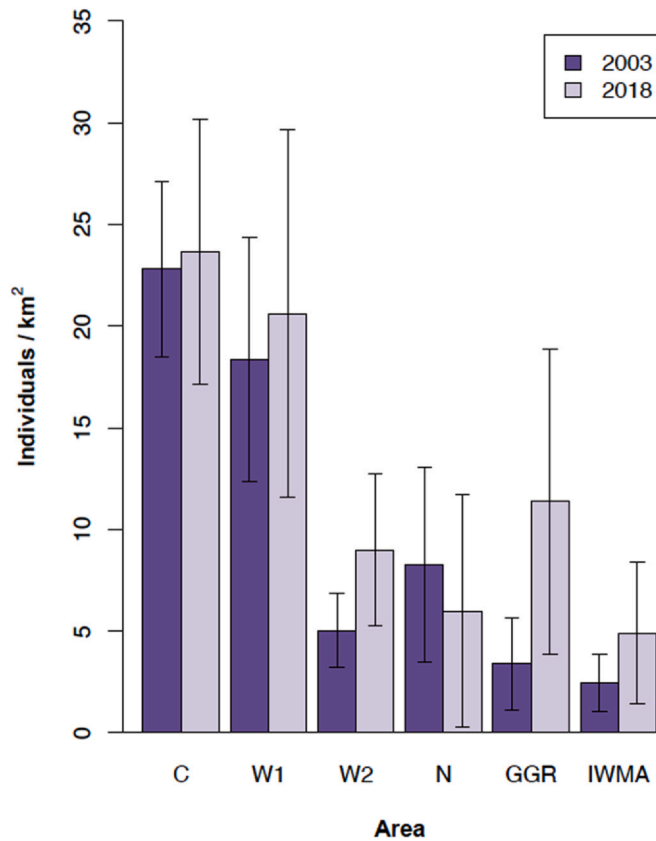
We found that the hazard rate key detection function fitted the data from both 2003 and 2018 best, when compared to the half-normal or exponential key functions ( $\Delta AICc < 2$ ). We determined that the best model for both datasets included area as covariate for both detection and abundance. The number of impala individuals per km<sup>2</sup> (Fig. 2) was significantly higher in 2018 than in 2003 in W2 (2003: 5.0 ind/km<sup>2</sup>; 2018: 9.0 ind/km<sup>2</sup>) and GGR (2003: 3.4 ind/km<sup>2</sup>; 2018: 11.4 ind/km<sup>2</sup>). The densities in the other areas did not differ significantly between the two periods (Fig. 2).

**Table 2**  
FID model selection.

Model	df	AICc	$\Delta AICc$	$\omega_i$
<b>FID ~ year*area + SD + alert + group type</b>	<b>16</b>	<b>3137.9</b>	<b>0</b>	<b>0.718</b>
FID ~ year*area + SD + alert	14	3141.6	3.65	0.116
FID ~ year*area + SD + alert + group size	15	3142.6	4.62	0.071
FID ~ year*area + SD + alert + calf presence	15	3143.2	5.26	0.052
FID ~ year*area + SD + alert + vegetation	15	3143.6	5.65	0.043

GLMs explaining the variation in flight initiation distance (FID), with and without potential confounding factors. The models were ranked according to AICc (Akaike's Information Criterion adjusted for small sample sizes). df = degrees of freedom,  $\Delta AICc$  = the difference in AICc between the given model and the model with the lowest AICc value.  $\omega_i$  = Akaike's weights, i.e., normalised likelihood of the models. SD = starting distance.

The most parsimonious model (i.e., with  $\Delta AICc < 2$ ) is marked in bold.



**Fig. 2. Estimated impala densities.** Number of individuals per km<sup>2</sup> in each study area in the Serengeti ecosystem, for years 2003 (dark) and 2018 (light). Error bars represent 95% confidence intervals. C = Central area, W1 = Western corridor 1, W2 = Western corridor 2, N = Northern area, GGR = Grumeti Game Reserve, and IWMA = Ikona Wildlife Management Area.

### 3.1.2. Sex ratio

The OSR (Table 1) was significantly more female-skewed in 2018 than in 2003 in C ( $\chi^2 = 22.81$ ,  $df = 1$ ,  $p < .001$ ), and in W1 ( $\chi^2 = 12.52$ ,  $df = 1$ ,  $p < .001$ ). No significant changes in OSR were found in the GGR, IWMA, W2, and N ( $p > 0.148$ ).

### 3.1.3. Group size

Likelihood ratio test of the negative binomial model indicated that the model including year, area, their interaction, and group type significantly improved the explained variation in group size compared to the null model (LR stat = 261.94,  $df = 12$ ,  $p < 0.001$ ). Group size was significantly larger in 2018 than 2003 in IWMA ( $z = 2.147$ ,  $p = 0.032$ ) and in W2 ( $z = 2.257$ ,  $p = 0.024$ ; Table 1). Bachelor groups (mean  $\pm$  SE =  $7.1 \pm 0.4$ ) were significantly smaller than female groups (mean  $\pm$  SE =  $20.79 \pm 1.068$ ;  $z = -17.206$ ,  $p < 0.001$ ).

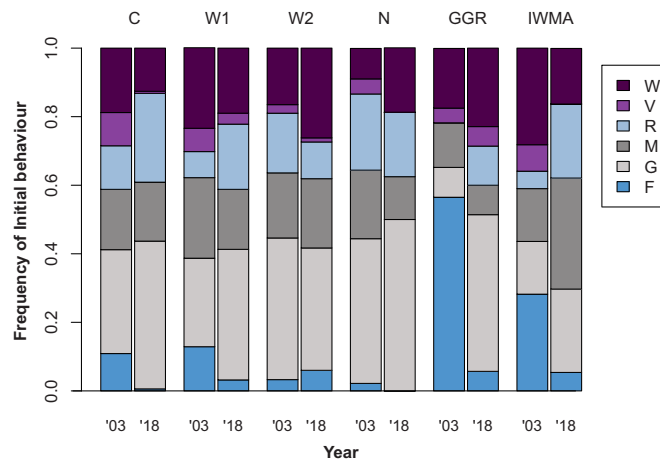
## 3.2. Behaviour

### 3.2.1. Initial behaviour

The frequency distribution of initial behaviours differed significantly between 2003 and 2018 in the different study areas ( $\chi^2 = 59.34$ ,  $df = 5$ ,  $p < 0.001$ ; Fig. 3). Specifically, there was a significant difference between years in C ( $p < 0.001$ ), W1 ( $p = 0.022$ ), GGR ( $p < 0.001$ ), and IWMA ( $p = 0.005$ ).

### 3.2.2. Flight behaviour

The most parsimonious model for FID was the model including group type ( $FID \sim year * area + SD + alert + group type$ ; Table 2). The model explained 71% of the variation in FID. FID was significantly shorter in 2018 (mean  $\pm$  SE =  $61.3 \pm 1.7$  m) than in 2003 ( $70.6 \pm 1.75$  m;  $z = -3.764$ ,  $p < 0.001$ ). Specifically, FID was significantly shorter in 2018 compared to 2003 in C (2018:  $57.3 \pm 1.99$  m, 2003:  $67.2 \pm 1.94$  m;  $z = -2.901$ ,  $p = 0.004$ ), and in IWMA (2018:  $55.2 \pm 3.68$  m, 2003:  $68.7 \pm 3.63$  m;  $z = -2.697$ ,  $p = 0.007$ ). There was no data collected in GGR in 2003. FID also increased significantly with increasing SD (Table 3), and single impala ( $61.9 \pm 1.67$  m) had significantly shorter FID compared to female groups ( $68.6 \pm 1.84$  m;  $z = 2.805$ ,  $p = 0.014$ ) and tended to have a shorter FID compared to bachelor groups ( $67.1 \pm 2.04$  m;  $z = 2.077$ ,  $p = 0.095$ ).



**Fig. 3. Frequency of initial behaviours.** Frequency of different initial behaviours in impala recorded during transects, divided into years and study areas in the Serengeti ecosystem. W = watching the observer, V = vigilant, R = resting, M = moving, G = feeding, F = fleeing. C = Central area, W1 = Western corridor 1, W2 = Western corridor 2, N = Northern area, GGR = Grumeti Game Reserve, and IWMA = Ikona Wildlife Management Area.

**Table 3**  
Estimates for the selected model explaining FID.

Coefficients	df	Deviance	Resid. df	Resid. Dev.	p
<b>NULL</b>			350	1223.51	
<b>Year (2018)</b>	1	6.76	349	1216.75	0.009
<b>Area (C)</b>	4	188.88	345	1027.86	< .001
<b>SD</b>	1	657.78	344	370.08	< .001
<b>Alert (No)</b>	1	2.96	343	367.12	0.085
<b>Group type (Bachelor)</b>	2	8.59	341	358.53	0.014
<b>Year: Area</b>	4	3.4	337	355.13	0.493

Analysis of Deviance of the most parsimonious GLM explaining flight initiation distance (FID) in impala for the different study areas in the Serengeti ecosystem in years 2003 and 2018. Model formula = FID ~ year \* area + SD + alert + group type. Reference levels are in brackets. C = Central area. SD = starting distance

#### 4. Discussion

Our results show that long-term changes in management practices had significant positive effects on the behaviour and demography of wild impala populations in the Serengeti ecosystem. After a 15-year period of increasing investment and effort in conservation management, including both anti-poaching enforcement and community outreach, impala in the GGR had higher population densities, tended to have larger group sizes, were more tolerant of vehicles, and were less flighty compared to before. These results are encouraging, indicating that a change in management practices can potentially improve impala population persistence rapidly.

Impala densities in 2018 were more than double those recorded in 2003 in GGR. This result is corroborated by aerial census surveys, which indicated that the impala population in the Grumeti Fund's concession area, which includes GGR, had doubled between 2003 and 2014 (Goodman, 2014). Impala densities were also higher in 2018 in W2, the part of SNP closest to GGR, while impala densities did not change significantly in the other study areas. In 2003, W2 was considered to be the most exploited area in SNP, experiencing the highest levels of illegal hunting (Holmern et al., 2002; Nuno et al., 2013). Given that many studies show that mammal population densities are generally higher in less exploited areas (Caro, 1999b; Topp-Jørgensen et al., 2009; Waltert et al., 2009; Wilfred and MacColl, 2016; Kiffner et al., 2020a, 2020b), our results indicate that exploitation in W2 and GGR has declined considerably. Wildebeest (*Connochaetes taurinus*) have also increased their utilisation of GGR and W2 over the last two decades, which is thought to be the result of strong patrolling effort (Veldhuis et al., 2019). Together, these results may indicate that the area has become safer for wildlife to utilise, resulting in increased population densities.

Sex-ratios in the PPAs were not different in 2018 compared to 2003 in all areas except C and W1. We predicted a less female-skewed sex ratio in the areas that were previously most disturbed (i.e. GGR, IWMA and W2), as both illegal and legal hunting, which are generally biased towards males, should have decreased since 2003 (Holmern et al., 2006; URT, 2015). However, in C and W1, sex ratio was significantly more female-skewed in 2018 compared to 2003. A female-skewed sex ratio in a polygynous species such as impala is not unexpected (Jarman, 1974). Males are expected to have higher mortality rates due to male-male competition and increased predation risk, as males are generally less vigilant and have more risk-prone behaviour (Jarman, 1974; FitzGibbon and Lazarus, 1995; FitzGibbon, 1998). However, it is important to note that GGR had a much higher female-skewed OSR (1:3.21) compared to the other areas (mean = 1:2.24) in 2018. Possibly, increasing predator populations in GGR



have increased male impala mortality. Indeed, the population densities of lions have increased 10-fold between 2003 and 2018 (Grumeti Fund, 2018), although lion predation on impala should be limited as impala are not their preferred prey (Hayward and Kerley, 2005). The small sample size in GGR in 2003 could also explain why we did not see a change over time.

Group sizes were significantly larger in 2018 than in 2003 in IWMA and W2. We expected larger group sizes in GGR, IWMA, and W2 as a response to lower hunting pressure (Manor and Saltz, 2003; Gude et al., 2006; Fischer and Linsenmair, 2007). Though the difference was not significant, average group size in GGR was nearly double in 2018 compared to 2003. Auerbeck et al. (2010) found that female impala groups were larger in a national park compared to an adjacent unprotected area, where hunting was permitted. Similarly, Manor and Saltz (2003) found that group size of mountain gazelles (*Gazella gazella*) decreased in response to human disturbance. Aggregating into larger groups may be advantageous when facing predators since increased group vigilance might decrease per capita predation risk, but not when facing human hunters (Fischer and Linsenmair, 2007). On the other hand, Caro (1999a) observed few significant differences in group sizes inside and outside Katavi National Park for a range of mammal species, including impala. Although impala groups have been found to be smaller during the dry season, indicating that group size and food availability may be correlated (Jarman, 1974, 1979; Murray, 1982), our study was conducted in the early and late dry season, well after the green flush of the wet season, and seasonality is therefore unlikely to affect our interpretation of the results.

Impala were less likely to flee in 2018 than in 2003 in GGR and IWMA, but also C and W1. Furthermore, impala had shorter FID from a human approach in 2018 than in 2003 in IWMA and C. Ungulate populations exposed to low levels of hunting pressure have been found to be less wary than populations that experience higher hunting activity (Caro, 1999b; Stankowich, 2008). Previous studies have also found impala specifically to be more likely to flee and have significantly greater FID in areas with greater hunting intensity (Caro, 1999a; Matson et al., 2005; Hariohay et al., 2018). Furthermore, impala habituating to human presence also become less wary and have shorter FID (Higham and Shelton, 2011). The amount of tourist activity in the Serengeti has increased considerably in the past years (Fyumagwa et al., 2013), and ungulates in areas with frequent non-lethal human contact show weaker flight responses compared to those in areas where human contact is rare (Stankowich, 2008). Therefore, the observed reduction in FID from 2003 to 2018 suggests that impala in several study areas, both inside and outside of SNP, are now exposed to less hunting and human disturbance than before.

## 5. Conclusion

The results of our study show several positive trends in the demography and behaviour of impala populations, suggesting that changes in management in the PPAs since 2003 have reduced negative human disturbances on impala. Management actions, such as increased anti-poaching efforts, are potentially underlying these positive changes, and are likely to have benefited numerous species in addition to impala. Indeed, most resident species surveyed in the PPAs have seen an increase in population size since 2003 (Goodman, 2014). We show that the combined monitoring of both demographic and behavioural proxies to assess the effect of human disturbances on wildlife can offer a more complete insight into the threats facing wildlife populations. Our study is encouraging for managers and reveals a conservation success story: if proper action is taken to increase the protection of wildlife within PPAs, wildlife populations can respond quickly and positively.

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## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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