Scientific Research Publishing

Open Journal of Ecology, 2023, 13, 525-535
https://www.scirp.org/journal/oje
ISSN Online: 2162-1993
ISSN Print: 2162-1985

Flight Behavioural Responses for African Ungulates across Species and Vegetation Covers in a Trophy Hunting Ecosystem: A Case Study from Selous Game Reserve, Tanzania

Ezra Peter Mremi[1*], Felister Michael Mombo[2], Michael Muganda[1], Peadar Brehony[3], Michael Honorati Kimaro[4,5]

[1]Department of Wildlife Management, Sokoine University of Agriculture, Morogoro, Tanzania
[2]Department of Forest and Environmental Economics, Sokoine University of Agriculture, Morogoro, Tanzania
[3]Department of Zoology, University of Oxford, Oxford, United Kingdom
[4]Tanzania Research and Conservation Organization, Morogoro, Tanzania
[5]GELIFES Institute, University of Groningen, Groningen, Netherlands
Email: *mremiezra@gmail.com

How to cite this paper: Mremi, E.P., Mombo, F.M., Muganda, M., Brehony, P. and Kimaro, M.H. (2023) Flight Behavioural Responses for African Ungulates across Species and Vegetation Covers in a Trophy Hunting Ecosystem: A Case Study from Selous Game Reserve, Tanzania. *Open Journal of Ecology*, **13**, 525-535.
https://doi.org/10.4236/oje.2023.138032

Received: June 15, 2023
Accepted: July 31, 2023
Published: August 3, 2023

Abstract

Trophy hunting has severe consequences on wild animals' behaviors, which in return has implications for affecting wildlife populations. The Selous Game Reserve is a protected area in Tanzania that has been subjected to commercial trophy hunting for decades, and information about the effects of trophy hunting on animals' welfare is still scarce. The Flight Initiating Distance (FID) can be a good measure to evaluate the welfare of animals and the level of risk perception towards anthropogenic disturbances, including trophy hunting. The study used linear mixed models to assess the flight responses of twelve commonly hunted species in the Selous game reserve (S.G.R.). The study compared animal vigilance between species, vegetation types, and group size. The FID varied between species, with which more vigilance was observed in zebras, elands, wildebeests, and sable antelopes. The study found a significant influence of vegetation cover on individual species' FID. Further, the study found a significant influence of group size on animals' vigilance (L. M. M., 95% CI = 0.590 - 4.762), in which there was a decrease in FID with an increase in group size for wildebeests. At the same time, other species, such as buffaloes, eland, hartebeests, and zebras, had their FIDs increasing with the increase in group size. We conclude that the impact of trophy hunting on savannah ungulates varies between species, vegetation covers, and group size of individual species. Regulatory authorities should consider minimum approach

distances by trophy hunters in different vegetation cover to reduce animal biological disturbances.

Keywords

Trophy Hunting, Animal Behavior, Flight Initiating Distance, Vegetation Types, Wildlife Species

1. Introduction

In the ecosystem where trophy hunting is conducted, the hunters interact with animals in different ways, including walking on foot, driving vehicles, shooting animals, and camping [1]. Human activities/disturbances that are highly lethal to wildlife influence the movement pattern of wild animals, home ranges, foraging costs, resting, and level of vigilance [2] [3] [4]. The effects of these human disturbances can have long-lasting impacts on wild animals in various ways including reduction of reproductive success [3], changing home ranges, activity patterns [4], and physical (fitness) health of animals [1] [5].

Trophy hunting is one of the anthropogenic stressors that affect the flight-initiating behavior of hunted animal species, increasing trophy searching efforts which possibly affects hunting success. Flight initiation distance (FID) is the distance at which an animal or prey flees from an approaching threat, and it has been used to study the optimal escape theory and risk assessment [6]. The animals' decision to flee is influenced by several factors, and they would normally flee when the costs of staying exceed the benefits [7]. It is also normally used to reflect the amount of danger perceived by an animal and has been used to study factors prompting the decision to flee [7] [8] [9]. FID can be a very suitable tool for wildlife managers in developing buffer and setback distances between animal nesting or feeding areas and human visitors [10], and it can be used in the assessment of animal welfare states as an indicator of fear or distress [11].

There are other factors that influence animals' flight decisions which include group size, [12], environmental conditions [1], habitat cover [2] [11], and level and types of anthropogenic stressors [13]. The number of times the hunting group or observer comes into contact with the hunted animal species provides an encounter rate [14]. The encounter rate of different species in the hunting blocks may help to explain the search effort, which is the amount of time in hours or days used to find a certain trophy animal. Assuming that other factors remain constant, an increased search effort to harvest a particular species of the same trophy quality may indicate a declining population of that species [14].

Having a better understanding of how hunting pressure is accounted for by animals, wildlife conservation and management should consider ways of managing wildlife through monitoring of flight initiating distances between species [15]. It is important to know whether animal species therefore habituate or sensitize (perceive greater risk) to regular exposure to human disturbance in the

protected area [11] [16]. Several studies have used the FID to measure the short-term effects of human disturbances on wild animals [1] [9] [11] [17] [18] [19] [20]. The aim of this study was to assess the impact of trophy hunting on wild animals' behaviour in Selous Game Reserve, where hunting has been in practice for many years, and a recent assessment of behaviour of hunted animals is lacking. The study also aimed to assess how animals respond to human encounters across different vegetation covers.

2. Study Area and Methods

2.1. Study Area

Selous game reserve (SGR) is located in central south-eastern Tanzania between 130 and 500 km southwest of Dar-es-Salaam at 7˚20' to 10˚30'S, and 36˚00' to 38˚40'E (**Figure 1**). The study was conducted at the three hunting blocks within the game reserve which are LR2, LR3, and LL2 found in the Kingupira sector. The LL2 hunting block was without a trophy hunting investor for almost five years before being reinstated in 2020, while the LR2 and LR3 hunting blocks were in continuous operation. The combined size of the hunting blocks is 3562 km^2. The hunting blocks receive 1300 millimeters of average rainfall annually, and a temperature ranging between 23.1˚C in July and 37˚C in December [21].

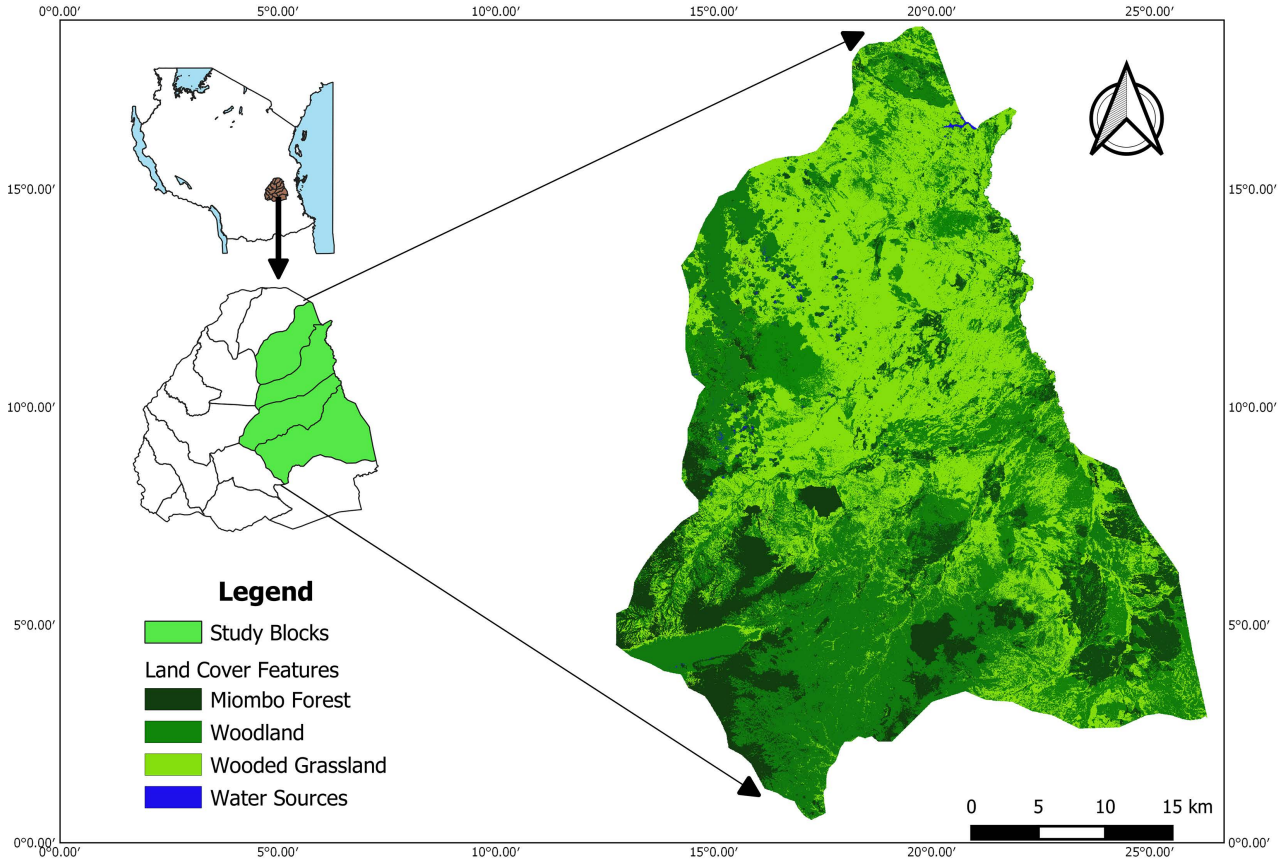

Figure 1. Map showing major vegetation zones from the selected hunting blocks in SGR.

The vegetation is dominated by Brachystegia spp. found in miombo woodland that covers most part of the game reserve [22].

2.2. Study Species

The study incorporated twelve (12) hunted species that were more encountered during the road transects survey in the Selous game reserve. The names of the selected species are; Cape buffalo (*Syncerus caffer*), bushbuck (*Tragelaphus sylvaticus*), common duiker (Sylvica pragrimmia), eland (*Taorotragus oryx*), greater kudu (*Tragelaphus strepsiceros*), impala Southern (*Aepyceros melampus*), Liechtenstein hartebeest (*Alcelaphus buselaphus*), Nyasaland wildebeest (*Connochaetestaurinus johnstoni*), sable antelope (*Hippotragus niger*), warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymnus*), and plains zebra (*Equus quagga*).

2.3. Methods

2.3.1. Study Design

The study applied a cross-sectional study design for primary data collection, where data were collected at a one-time point [23] The hunting blocks were selected because of their varied vegetation cover, good accessibility through roads, and border one another (landscape homogeneity). We surveyed all roads available that are used by trophy hunters and management during patrol operations because of their good accessibility. Data were collected during the dry season when the majority of the roads were accessible and trophy hunting was at its peak in August and September 2022.

2.3.2. Data Collection Techniques

All animals observed along the transects were recorded. The principal investigator (PI) selected six (total of 230 Km) accessible road transects during the hunting season which cross different vegetation types. The distances covered between transect roads varied. As conducted by Tarakini *et al.* (2014) [11], a vehicle was driven along road transects at a low speed of 25 - 30 km/hr., allowing easy animal detection for the two observers on top of the vehicle. When a solitary or herd of study species was detected, the vehicle was immediately stopped and the engine switched off. The PI recorded the type of animal species encountered, and the unit size (number of individuals observed). From the field observations, the vegetation cover was classified as follows; 1) Miombo forest: trees with height above 5 meters and a canopy cover of >70%; 2) Woodland: trees covering between 25% - 69% of an area; and 3) wooded grassland: Scattered trees covering between 5% - 24% of an area.

For flight initiation distance (FID) following the procedure of Setsaas (2007) [24] a rangefinder was used to measure the starting distance (SD) measured as the distance from the vehicle to the animal(s). The PI accompanied by an armed ranger walked on foot slowly toward the animal/herd, and then record the distance where the animal/herd starts moving away (flight), and the distance from the PI to the original position of the animals was defined as the FID.

2.3.3. Data Analysis

The analysis for variation of FID between species, the influence of vegetation types and group size on wild animals' behaviour were performed by using R software (R Core Team, 2021) [25], and the linear mixed model (LMM) was used with the utilization of the lme4 package from R. The FID was treated as a response variable, while the species name was treated as an explanatory variable. Since the transect length was not uniform, transect length was treated as a random variable. A similar model was used to assess the influence of vegetation types on the behaviour of animals in which FID was treated as a response variable, while vegetation type was treated as an explanatory variable. To assess the influence of group size, a similar model was used, in which FID was treated as a response variable, while the group size of the animals encountered was treated as an explanatory variable.

3. Results

3.1. Variation of Flight Initiating Distances (FID) between Species

A total of 12 species were mostly encountered in different road transect surveys which are waterbuck, zebra, wildebeest, hartebeest, common duiker, buffaloes, sable antelopes, bushbuck, eland, Greater kudu, impala, and warthog. For all species, the minimum flight initiating distance was approximately 33 meters. The study found that FID varied significantly between species (LMM, 95% CI = 52.339 - 103.744). Species that appeared to have higher flight initiating distances were Zebra, Eland, Sable antelopes, and Wildebeests (**Figure 2**).

3.2. The Influence of Vegetation Types on Wild Ungulates' Behavior

Through observation and image analysis, three major vegetation or habitat types identified were wooded grassland, woodland, and miombo forests. The study significant variation of animal species FID with vegetation types (LMM, 95% CI = 9.197 - 54.190). Species had high flight distances in wooded grassland vegetation than woodland and miombo forest vegetation types (**Figure 3**).

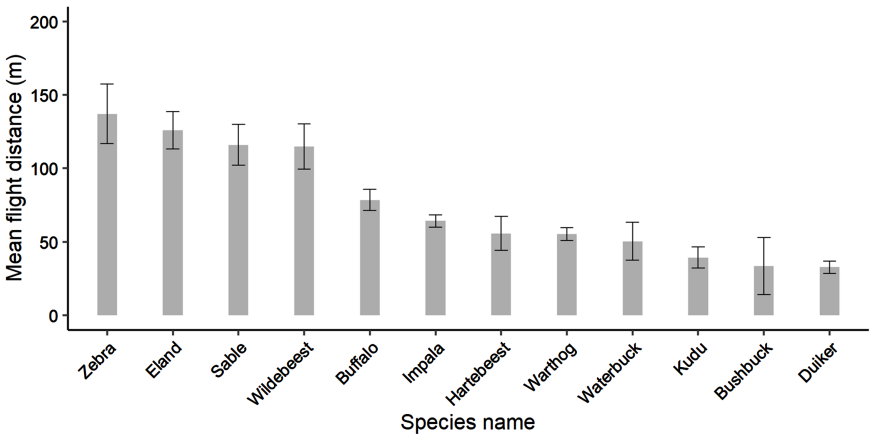

Figure 2. Mean FID between different species. The arrows indicate standard error.

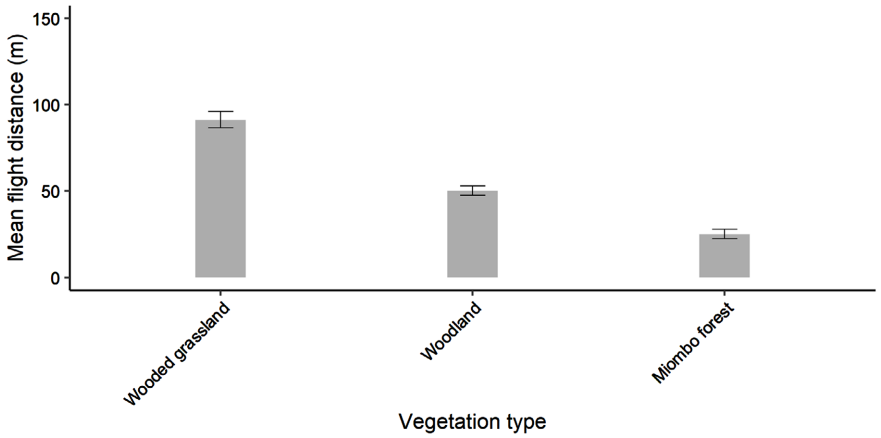

Figure 3. Mean FID of species in different vegetation types. The arrows indicate standard error.

Instead of assessing all species encountered during the survey, this study used four species that had the highest FID as species of focus to assess the variation of their FID in different vegetation types. These four species are zebra, eland, sable antelopes, and wildebeests. The study found that the selected species were encountered in wooded grassland and woodland only, indicating that these selected species were not observed in the miombo forest vegetation. Generally, the FID for all four selected species varied significantly between wooded grassland and woodland vegetation types (LMM, 95% CI = −76.513 - −1.251). Sable antelopes were observed in woodland vegetation only, while other three species were encountered in both wooded grassland and woodland vegetation types (**Figure 4**). Significant higher flight distances were observed for both zebra (LMM, 95% CI = −150.688 - −11.561) and wildebeest (LMM, 95% CI = −125.076 - −5.713) in the wooded grassland than in woodland vegetation types (**Figure 4**). Contrary to zebra and wildebeest, there was no significant difference of FID for elands in relation to vegetation types (LMM, 95% CI = −37.176 - 58.307).

3.3. The Influence of Animal Group Size on Flight Behaviour

Six species were selected to assess the effect of group size on ungulates' behaviour as their encounters were enough for this analysis. These species are buffaloes, elands, hartebeests, waterbucks, wildebeests, and zebras. The study found a significant influence of group size animals' vigilance (LMM, 95% CI = 0.590 - 4.762), in which the FID decreased with an increase of group size for wildebeests, while for other five species (buffaloes, eland, hartebeests, and zebra) their FID increased with an increase of group size (**Figure 5**).

4. Discussion

The results suggest that Plains zebras had the highest FID, with a mean FID of 140 m, followed by three other species that were elands, wildebeests, and sable antelopes (**Figure 2**). In all observations, three species (zebra, elands, and sable

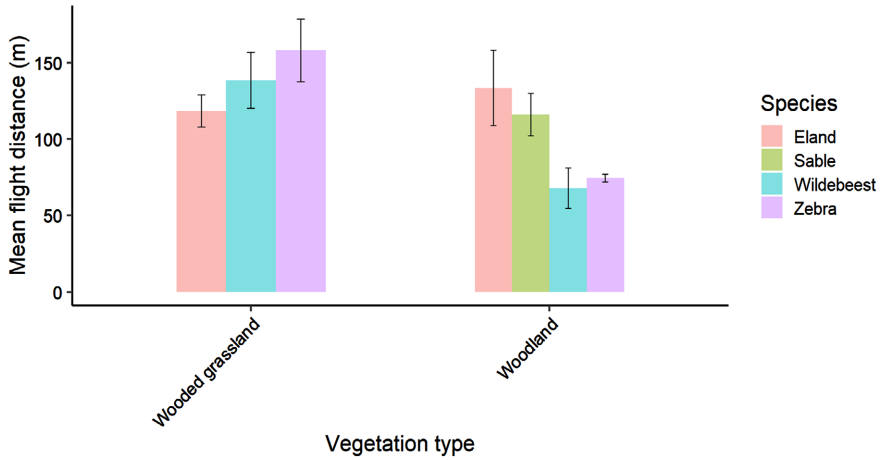

Figure 4. Mean FID for the four key selected species in different vegetation types. The arrows indicate standard error.

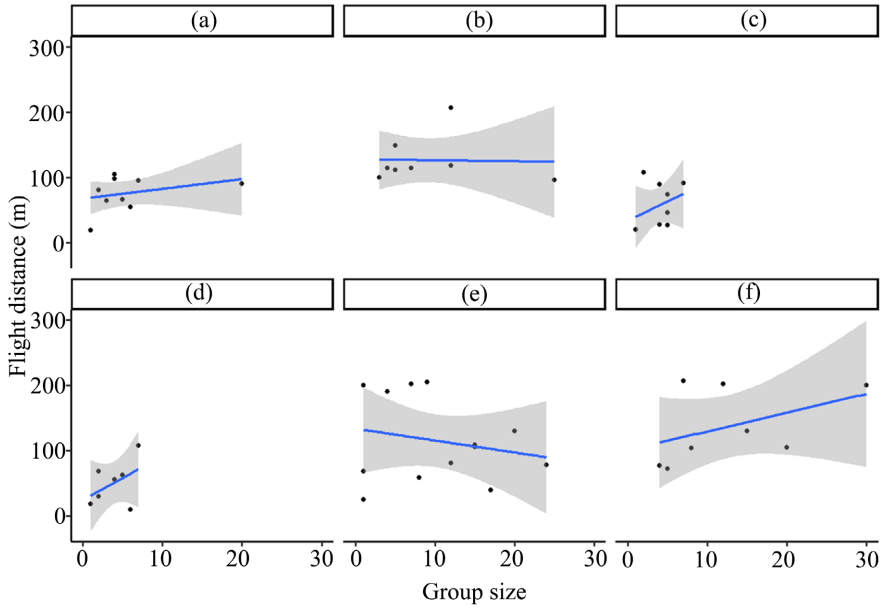

Figure 5. The FID of the six key selected species in different group sizes. The shadow indicates a 95% confidence interval. (a) Buffalo, (b) Eland, (c) Hartebeest, (d) Waterbuck, (e) Wildebeest, (f) Zebra.

antelopes) were encountered in groups rather than solitary, and the higher FID can be explained by Tammie *et al.* (2005) [26] hypothesis called the 'many eyes' hypothesis, which proposes that there is a greater chance of predators (in this case refers to humans) being detected earlier by individuals in a larger group. This hypothesis has been assessed and verified with a study that used FID as a proxy [11].

The effect of vegetation type on the FIDs of animals cannot be overshadowed as this study suggests that it plays a role in animals' vigilance. As Stankowich & Blumstein (2005) [18] suggested, the decreased FIDs in closed habitats may be caused by the limited ability to detect incoming threats at longer distances. It is

noted that the perceived risk of animals increases by 43% when they are far from their potential refuge, and they are expected to have higher FIDs from the potential threat [18]. This has been observed in our findings, in which higher FIDs in wooded grassland than in woodland for four species (zebras, elands, wildebeests, and sable antelopes) that were recorded to have the highest FIDs occurred. Elands however showed higher FIDs in both vegetation covers, and as study by Furstenburg, (2012) [27] suggests that elands are shy animals but they would remain still if approached, and they would move away quickly only when alert to danger. The high FIDs of elands in both vegetation covers in this study could suggest that the animals are sensitized by the human presence from years of trophy hunting and flee at great distances.

Waterbucks, greater kudus, bushbucks, and common duikers were mostly encountered in the closed vegetation (miombo woodland and miombo forest) and they could be detected at shorter distances (**Figure 2**). The greater kudu in our study had approximately 40 m FID, and are comparative to 59 m and 64 m from Muposhi *et al.* (2016) [1] and Tarakini *et al.* (2014) [11] studies respectively. There are limited studies to relate to waterbucks, bushbucks, and common duikers' FIDs. This study however suggests that the closed vegetation cover influenced their shorter FIDs as the animals could not detect an incoming threat at long distances, and also, they felt more secure in the potential refuge (vegetation cover) as suggested by Stankowich & Blumstein (2005) [18].

For animals encountered at shorter distances, the approacher was expected to move a short distance before the animals move away because animals have less time to assess risk at shorter encountering distances according to Cooper & Frederick (2010) [6]. In this study, six species (hartebeest, warthog, waterbuck, kudu, bushbuck, and duiker) showed tolerance towards the researcher's vehicle and fled at the sight of approaching observers walking on foot. The trophy hunting guidelines in Tanzania do not allow hunting to be conducted from vehicles. The FIDs of animals in closed habitats after detecting the observer while showing tolerance towards the vehicle could be explained as relating the direct human approach with danger compared to vehicles, as argued by Muposhi *et al.* (2016) [1] and Stankowich (2008) [2] studies.

Our results further showed the effect of group size on the FID of different animal species (**Figure 5**). The wildebeests' FID decreased with an increase in group size, which can be explained by a model of predation risk assessment by Samia *et al.* (2015) [28], which predicts a declining risk of predation as group size increases and individuals in larger groups might thus tolerate closer approach. The FIDs of buffalo, hartebeest, waterbuck, and zebra increased with an increase of the group size (**Figure 5**). The earlier detection of incoming threats (in this case humans) may influence the high FID of animal species in groups as those who detect the threat could alert the other group members [19] [26] [29]. In our study, however, group size did not affect elands as their FID was similar in both small and large groups. This suggests that the FID variation differs between individual species, and elands were more vigilant to human presence.

5. Conclusions

This study provided an empirical summary of the impact of trophy hunting on the hunted animals' behaviours across different vegetation types in the Selous Game Reserve (SGR). The selected hunting blocks have been used to conduct trophy hunting for many decades, and most hunted animal species have become more vigilant toward encounters with humans. Trophy hunting is mostly conducted during the dry season, and approximately 83% of the study species were encountered in groups while 17% were encountered solitarily. These ungulate species have a herding behaviour in which they form permanent herds, moving herds, territorial herds' bachelor groups, and harem groups as described by Walther (1991) [30]. The groups/herds move together in search of pastures and water, also individuals in the group increase their chances of survival through early risk detection and predator confusion [26]. The herding behaviour can also be explained as behavioural adaptations and the "dilution effect" of the prey species, in which the animals reduce their chances of being preyed on or hunted by staying in groups [18].

Encountering hunted species in different road transects suggests low searching efforts for trophies in the hunting blocks, and also the ungulates' populations are still sustainable. This conclusion however needs to be justified by either monitoring hunted species populations in longer terms or conducting the annual animals' population census before the start of the hunting season, which would help to accurately determine the viable hunting quotas. Our study emphasizes professional hunters abide by the hunting guidelines and ethics and prohibit hunting of species in groups/herds with young/infants, as it will create biological stresses to these animals which may affect their well-being and reproductive success.

6. Recommendations

Our study emphasizes professional hunters abide by the hunting guidelines and ethics and prohibit hunting of species in groups/herds with young/infants, as it will create biological stresses to these animals which may affect their well-being and reproductive success. This study recommends more studies of the same nature to be conducted in the same ecosystem but in areas primarily used for photographic tourism like the nearby Mikumi national park, so as to compare the anthropogenic impacts on wild animals' behaviours. We recommend the use of the FID method to assess behaviour of animals over time as it is a quick and cost-effective technique

Acknowledgements

We are grateful to the Sokoine University of Agriculture (SUA), the Tanzania Wildlife Research Institute (TAWIRI), and the Tanzania Wildlife Authority (TAWA) for their permission to undertake this study. We also sincerely thank the Selous game reserve's management for their support and assistance during

data collection. Finally, we would like to thank Dascot Limited Company for funding this research.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

[1] Muposhi, V.K., Gandiwa, E., Makuza, S.M. and Bartels, P. (2016) Trophy Hunting and Perceived Risk in Closed Ecosystems: Flight Behavior of Three Gregarious African Ungulates in a Semi-Arid Tropical Savanna. *Austral Ecology*, **41**, 809-818. https://doi.org/10.1111/aec.12367

[2] Stankowich, T. (2008) Ungulate Flight Responses to Human Disturbance: A Review and Meta-Analysis. *Biological Conservation*, **141**, 2159-2173. https://doi.org/10.1016/j.biocon.2008.06.026

[3] Ciuti, S., Northrup, J., Muhly, T., Simi, M.M., Pitt, J. and Boyce, M. (2012) Effects of Humans on Behavior of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *PLOS ONE*, **7**, e50611. https://doi.org/10.1371/journal.pone.0050611

[4] Gaynor, K., Hajnowski, C., Carter, N. and Brashares, J. (2018) The Effects of Human Disturbances on Wildlife Nocturnality. *Science*, **360**, 1232-1235. https://doi.org/10.1126/science.aar7121

[5] Frid, A. and Dill, L. (2002) Human-Caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, **6**, Article No. 11. https://doi.org/10.5751/ES-00404-060111

[6] Cooper, W.E. and Frederick, W.G. (2010) Predator Lethality, Optimal Escape Behavior, and Autotomy. *Behavioural Ecology*, **21**, 91-96. https://doi.org/10.1093/beheco/arp151

[7] Ydenberg, R.C. and Dill, L.M. (1986) The Economics of Fleeing from Predators. *Advances in the Study of Behavior*, **16**, 229-249. https://doi.org/10.1016/S0065-3454(08)60192-8

[8] Blumstein, D.T. (2003) Flight-Initiation Distance in Birds Is Dependent on Intruder's Starting Distance. *The Journal of Wildlife Management*, **67**, 852-857. https://doi.org/10.2307/3802692

[9] Dumont, F., Reale, D., Pasquarettta, C., Hardenberg, A. and Bogliani, G. (2012) Flight Initiation Distance and Starting Distance: Biological Effect or Mathematical Artefact? *Ethology*, **118**, 1051-1062. https://doi.org/10.1111/eth.12006

[10] Fernandez-Juricic, E., Venier, M.P., Renison, D. and Blumstein, D.T. (2005) Sensitivity of Wildlife to Spatial Patterns of Recreationist Behavior: A Critical Assessment of Minimum Approaching Distances and Buffer Areas for Grassland Birds. *Biological Conservation*, **125**, 225-235. https://doi.org/10.1016/j.biocon.2005.03.020

[11] Tarakini, T., Crosmary, W.G., Fritz, H. and Mundy, P. (2014) Flight Behavioral Responses to Sport Hunting by Two African Herbivores. *South African Journal of Wildlife Research*, **44**, 76-83. https://doi.org/10.3957/056.044.0110

[12] Stankowich, T. and Coss, R.G. (2006) Effects of Predator Behaviour and Proximity on Risk Assessment by Colombian Black-Tailed Deer. *Behavioral Ecology*, **17**, 246-254. https://doi.org/10.1093/beheco/arj020

[13] Reimers, E. and Colman, J. (2006) Reindeer and Caribou (*Rangifer tarandus*) Re-

sponse towards Human Activities. *Rangifer*, **26**, 55-71. https://doi.org/10.7557/2.26.2.188

[14] TAWA (2020) Tanzania Wildlife Management Authority—Tawa United Republic of Tanzania. 121(April), 0-19.

[15] Cooper, W.E. and Frederick, W.G. (2007) Optimal Flight Initiation Distance. *Journal of Theoretical Biology*, **244**, 59-67. https://doi.org/10.1016/j.jtbi.2006.07.011

[16] Rodriguez-Prieto, I., Fernández-Juricic, E., Martín, J. and Regis, Y. (2009) Antipredator Behavior in Blackbirds: Habituation Complements Risk Allocation. *Behavioral Ecology*, **20**, 371-377. https://doi.org/10.1093/beheco/arn151

[17] Miller, S.G., Knight, R.L. and Clinton, K.M. (2001) Wildlife Responses to Pedestrians and Dogs. *Wildlife Society Bulletin*, **29**, 124-132.

[18] Stankowich, T. and Blumstein, D. (2005) Fear in Animals: A Meta-Analysis and Review of Risk Assessment. *Proceedings of the Royal Society B*, **27**, 22627-2634. https://doi.org/10.1098/rspb.2005.3251

[19] Brubaker, A. and Coss, R.G. (2016) Effects of Single- and Mixed-Species Group Composition on the Flight Initiation Distances of Plains and Grevy's Zebra. *Ethology*, **122**, 531-541. https://doi.org/10.1111/eth.12500

[20] Tarlow, E.M. and Blumstein, D.T. (2007) Evaluating Methods to Quantify Anthropogenic Stressors on Wild Animals. *Applied Animal Behaviour Science*, **102**, 429-451. https://doi.org/10.1016/j.applanim.2006.05.040

[21] Norwegian Meteorological Institute (2022) Weather Forecasting: Selous Game Reserve.

[22] Baldus, R. (2009) The Selous-Niassa Wildlife Corridor in Tanzania: Biodiversity Conservation from the Grassroots. Practical Experiences and Lessons from Integrating Local Communities into Transboundary Natural Resources Management. Budapest. 48 p.

[23] Levin, K.A. (2006) Study Design III: Cross-Sectional Studies. *Evidence-Based Density*, **7**, 24-25. https://doi.org/10.1038/sj.ebd.6400375

[24] Setsaas, T.H., Holmern, T., Mwakalebe, G., Stokke, S. and Røskaft, E. (2007) How Does Human Exploitation Affect Impala Populations in Protected and Partially Protected Areas? A Case Study from the Serengeti Ecosystem, Tanzania. *Biological Conservation*, **136**, 563-570. https://doi.org/10.1016/j.biocon.2007.01.001

[25] R Core Team (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org

[26] Tammie, M.A., Anne, W.G. and David, A.P. (2005) Factors Affecting the Vigilance and Flight Behavior of Impalas. *African Journal of Wildlife Research*, **35**, 1-11.

[27] Furstenburg, D. (2012) Elands Facts (*Tragelaphus oryx*) S.A Hunter 08067:32-34.

[28] Samia, D., Nakagawa, S., Nomura, F., Rangel, T.F. and Blumstein, D.T. (2015) Increased Tolerance to Humans among Disturbed Wildlife. *Nature Communications*, **6**, Article No. 8877. https://doi.org/10.1038/ncomms9877

[29] Testroote, E. (2018) Vigilance and Flight Behavior in Herds of Three Different Ungulate Species: Zebra, Wildebeest and Impala. Resource Ecology Group.

[30] Walther, F.R. (1991) On Herding Behavior. *Applied Animal Behavior Science*, **29**, 5-13. https://doi.org/10.1016/0168-1591(91)90235-P