World Journal of Biology Pharmacy and Health Sciences

eISSN: 2582-5542

Cross Ref DOI: 10.30574/wjbphs

Journal homepage: https://wjbphs.com/

(REVIEW ARTICLE)

Habitat selection and space-use overlap between feral herbivores, civet cat and greater cane rat in derived forests in Oyo state, Nigeria

Kolawole Farinloye [1, *], Františka Gustav [2], Mayowa Aduloju [3] and Funmilayo Oni [4]

[1] *Department of Tourism Management, CCCU Partnership Global Banking School, Leeds Campus, United Kingdom.*

[2] *Depart of Conservation and Forestry, Russian Conservation Research Institute, 7252-46 Jaruška, Moscow, Russian Federation.*

[3] *Department of Forestry and Wildlife Management, Adekunle Ajasin University Akungba-Akoko, Nigeria.*

[4] *Department of Wildlife and Ecotourism Management, Ladoke Akintola University of Technology, Ogbomoso, Nigeria.*

World Journal of Biology Pharmacy and Health Sciences, 2025, 22(02), 232-244

Publication history: Received on 01 April 2025; revised on 11 May 2025; accepted on 13 May 2025

Article DOI: https://doi.org/10.30574/wjbphs.2025.22.2.0487

Abstract

Predation risk is an important factor influencing the distribution of herbivores and their impact on forest structure. However, studies on herbivore habitat selection seldom take into account the simultaneous predation risk posed by humans and civet cats (*Civettictis civetta*). Floristic Quality Assessment Index (FQAI) technique was used to evaluate the ecosystem health status of the forest. In order to examine how humans and civet cats affect the distribution of herbivore densities in the Opara Forest in Oyo State, Nigeria, we counted herbivore pellets on transects. We evaluated the following: (1) Prey density, (2) Predator density, (3) Herbivores within the vicinity of probable anthropogenic activities, (4) Herbivores high forest density areas, (5) Carnivores within the vicinity of probable anthropogenic activities, and (6) Carnivores high forest density areas, respectively. While bay duiker (*Cephalophus dorsalis*) preferred exploited woods, greater cane rats (*Thryonomys swinderianus*) and common duikers (*Sylvicapra grimmia*) chose unexploited over exploited forests and places without hunting. Within 300 metres of a major road, larger cane rats and common duikers (*Sylvicapra grimmia*) avoided the region; however, no avoidance by bay or common duikers was observed. Regardless of human hunting, the density of prey was not higher in civet cat strife zones. Areas chosen by civet cats were not avoided by herbivores. Regardless of whether the average population of common duiker in those locations was higher or lower, civet cats killed common duiker in areas with a prey density of about four (4) common duiker/km^2. We concluded that human hunting and forest exploitation altered the habitat more than the risk of civet cats preying on herbivores.

Keywords: Opara forests; Civet cat; Greater Cane Rat; Distribution; Human impact; Hunting management; Oyo state

1. Introduction

Herbivore browsing and grazing influence forest regeneration, so forestry management requires knowledge about the factors that determine their spatial distribution (Agbeja, 2019; Adepoju and Gossow, 2019; Amusa *et al*., 2021; Ayodele and Lameed, 2003; Palmer *et al*., 2004). At the same time, there is a relation between herbivore density and forest structure (e.g. Osho *et al*., 2019; Gill *et al*., 2019), so habitat might be considered one of the main factors that regulate herbivore distribution. Besides habitat factors, predation risk can influence the habitat choice of herbivores (Lima, 2019; Brown *et al*., 2021; Zollner and Lima, 2021) and therefore the intensity of browsing (Ripple and Beschta, 2004). Civet cats (*Canis lupus*), one of the main predators of herbivores, are re-colonizing (Ayodele) to predict any behavioural changes of their prey and thus potential modifications of browsing risks to commercial forestry (Hebble-white *et al*., 2006; Berger, 2007).

---

[*] Corresponding author: Kolawole Farinloye

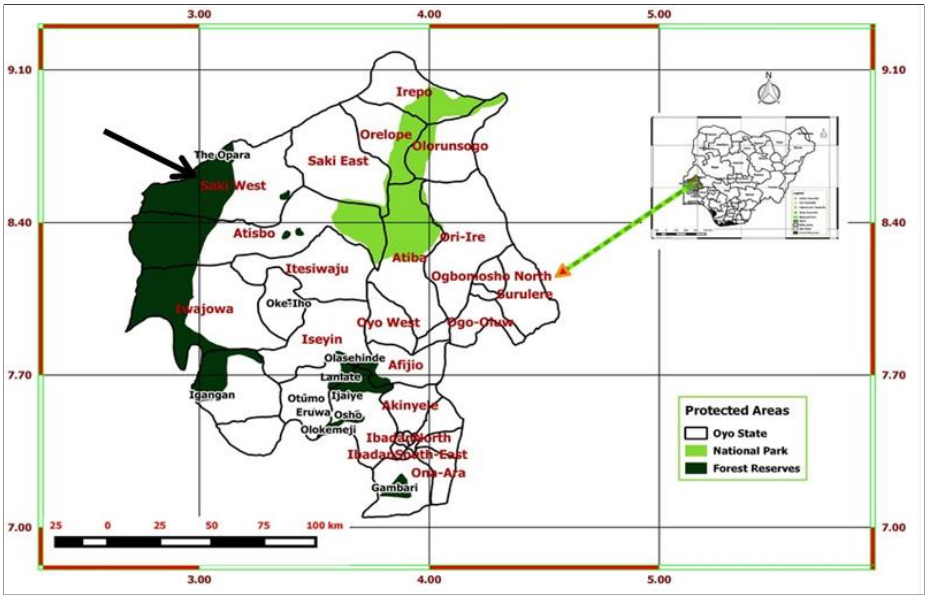
Humans are another main predator of herbivores in temperate climates and their presence is also a form of predation risk (Frid and Dill, 2002). Hunting causes changes in the reproductive strategy of deer (Alarape *et al.*, 2007) and human presence can lead to chronic stress in deer (Sanwo *et al.*, 2004), which do not differentiate between hunters and other people. Human predation can therefore affect the density of herbivores, not only by direct removal of individuals and avoidance behaviour but also through reduced fitness. Studies of habitat selection by herbivores rarely take both predation risk by civet cats and humans into account. North African studies sometimes included human impact (White *et al.*, 2003; Jimoh *et al.*, 2005; Bergman *et al.*, 2006; Azeez *et al.*, 2006) but most of them focused on the predation risk by carnivores (Ripple and Beschta, 2003; Civet cat and Van Horn, 2003; Frair *et al.*, 2005; Hernandez and Laundre, 2005; Mao *et al.*, 2005; Winnie *et al.*, 2006). African studies, on the other hand, dealt mostly with human influence as study areas usually lack large carnivores (Jeppesen, 1987; Doring, 2019; Herbold, 2019; Petrak, 2019; Hewison *et al.*, 2001; Ciuti *et al.*, 2004; Sanwo *et al.*, 2004). African studies revealed that herbivores are more numerous in areas where the home ranges of different civet cat packs overlap, especially in rainy seasons (Hoskinson and Mech, 2016; Mech, 1977; Rogers *et al.*, 2019; Nelson and Mech, 1981). One explanation for this phenomenon is that civet cats spend less time in these strife zones (Mech and Harper, 2002). The same observation also applies for human populations (Kay, 2019). It is not known whether prey densities are also higher in strife zones of civet cat packs in the presence of human hunting.

Osho *et al.* (2019) analysed the effect of forest structure reserve of the protected forest and in the commercial forest due to exploitation and forest management (Agbeja, 2019; Agbeja *et al.*, 2012). Human activity in the protected forest was low (<10 people per day on roads/trails on average) in rainy seasons and moderate (30–60 people per day on roads/trails on average) in dry seasons, whereas in the commercial forest it was moderate in rainy seasons and high (150– 200 people per day on roads on average) in dry seasons (Ayodele *et al.*, 2003a). Civet cats in the study area mainly kill common duiker (Akindele *et al.*, 2002) and in the strict reserve, where there is no human hunting, predation by civet cats is the main mortality factor of common duiker (Alarape *et al.*, 2007a). In the commercial forest, human hunting is the main cause of herbivore death (Okarma *et al.*, 2019).

2. Methods

2.1. The Study area

The Opara Forest is a forest complex of 1450 km2 (22830^0– 23800^{0}N, 23830^0–24815^{0}E) that straddles the Nigerian-Republic of Benin border. The Nigerian side of the Opara Forest consists of the Opara forests (23km^2) and a commercial forest (4km^2), in which hunting (mainly along roads and from hunting towers), logging, and reforestation occur. 50km^2 of the Opara forests have been protected as a strict reserve since 1921. No hunting, forestry, or motorized traffic is permitted in the strict reserve, and public access is limited. In July 2019, the Opara forests was enlarged to 100 km^2.



Source: field survey

Figure 1 Map of Oyo state, showing the study area (Opara forest

Figure 1 Map showing the Opara forest (dark green colour pointed with black arrow) reserves in Oyo state, Nigeria

2.2. Data Collection

2.2.1. Flora species

Floristic Quality Assessment Index (FQAI) approach was used to evaluate the ecosystem health state of the forest. The forest was divided into 15plots using the line transect method. Simulated Data Observation (SDO) was used to measure the richness of tree species and the performance of the forest. This was mathematically presented as: Klog=log(k/2)(4)Klog=log(k/2)(4)

When there are only two species (k = 2), Klog should be zero, which is why k is divided by two in formula 4. This is because that the necessary condition for tree species diversity studies is at least two species existing in a community to represent biodiversity (k ≥ 2). Therefore, when there are only two species in the community, tree species richness acquires a minimum value. After the elimination of magnitude difference in tree species numbers, species richness is normalized by comparing klog with the logarithm of the possible largest species number in a biotic community (Klogmax).

For comparative purpose, the Shannon–Weaver index (Shannon and Weaver, 1949) [H′], Simpson (Simpson, 1949) [D] and the Hill Numbers or the effective number (1973) [qD] were also calculated for each data set at the same time. H′=−s∑i=1pilnpi

H′=-∑i=1spilnpi

where s is the number of species and pi is the proportion of the sample belonging to the ith species.

(10) D=s∑i=1p^{2}iD=∑i=1spi^2

where *pi* is the sample's percentage of the *ith* species. It is anticipated that the Simpson index will fall as biodiversity rises. D′ = 1-D was thus applied in this study as follows: qD≡(S∑i=1pqi)1/(1−q).

2.2.2. Fauna species

Forest cameras were used to monitor fauna movements and migration within the forest. Both herbivores and carnivores were monitored over a 24-h cycle. Determination of the following were carried out:

- Prey density
- Predator density
- Herbivores within the vicinity of probable anthropogenic activities.
- Herbivores high forest density areas, and
- Carnivores within the vicinity of probable anthropogenic activities.
- Carnivores high forest density areas

A total of 381 fauna were detected and 27 outliers (>3 *SD*) were removed. Out of 281 faunas detected for analyses, 74.3% were herbivores and 25.7% carnivores.

2.3. Statistical Analysis

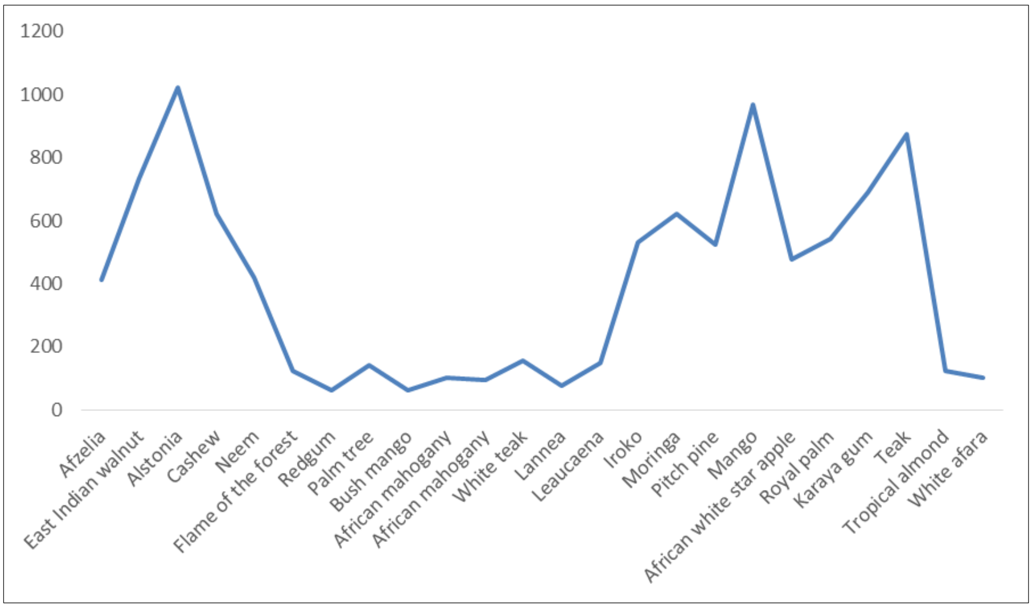
ANOVA and AIC (Anderson *et al*., 2012) were used to assess the factors or interactions of factors that were most important for herbivore densities. We used 3 binary categories as independent factors: hunting–no hunting, forest exploited–unexploited, and civet cat density lower than mean–civet cat density higher than mean. As herbivore densities were not normally distributed, we normalized data by square root $\sqrt[n]{(x)}$ transformation.

3. Results

Table 1 Relative Abundance of Identified Tree species types at Opara forest

Family	**Species**	**Common name**	**Local name**	**Origin**	**Freq**	**%**
Fabaceae	*Afzelia bella*	Afzelia	Apa	Indigenous	412	2.1
Apocynaceae	*Albizia lebbeck*	East Indian walnut	Ayunre	Exotic	732	3.6
Anacardiaceae	*Alstonia boonei*	Alstonia	Awun	Indigenous	1023	5.2
Meliaceae	*Anacardium occidentale*	Cashew	Kaju	Exotic	621	3.1
Leguminoceae	*Azadirachta indica*	Neem	Dogonyaro	Exotic	421	2.1
Myrtaceae	*Delonix regia*	Flame of the forest	Panseke	Exotic	122	6.2
Euphorbaiceae	*Eucalyptus amaldulensis*	Redgum	-	Exotic	62	3.1
Irvingiaceae	*Elaeis guinensis*	Palm tree	Ope	Indigenous	141	7.2
Meliaceae	*Ervingia gabonensis*	Bush mango	Ooro	Indigenous	61	3.1
Meliaceae	*Khaya grandifolia*	African mahogany	Oganwo	Indigenous	103	5.2
Verbanaceae	*Khaya senegalensis*	African mahogany	Oganwo	Indigenous	94	4.6
Anacardiaceae	*Gmelina arborea*	White teak	-	Exotic	155	7.7
Fabaceae	*Lannea egregia*	Lannea	Opon	Exotic	76	3.6
Moraceae	*Leucaena leucochephala*	Leaucaena	-	Exotic	147	7.2
Moringaceae	*Milicia Excelsa*	Iroko	Iroko	Indigenous	532	2.5
Pinaceae	*Moringa oleifera*	Moringa	Ewe-igbale	Indigenous	621	3.1
Mangiferaceae	*Minus caribeae*	Pitch pine	Aho-yaayaa	Exotic	524	2.5
Sapotaceae	*Mangifera indica*	Mango	Mangoro	Exotic	967	4.6
Arecaceae	*Chrysophyllum albidum*	African white star apple	Agbalumo	Indigenous	478	2.1
Sterculiaceae	*Roystonea regia*	Royal palm	-	Exotic	541	2.5
Vernebaceae	*Sterculia setigera*	Karaya gum	Osse awere	Indigenous	689	3.1
Combretaceae	*Tectonia grandis*	Teak	Ewe eko	Exotic	876	4.1
Combretaceae	*Terminalia catapa*	Tropical almond	Furuntu	Indigenous	123	6.2
Terminalia africana	*Terminalia africana*	White afara	Idigbo	Indigenous	101	5.2
	Total				8944	100.0

Source: field survey



Source: field survey

Figure 2 Relative richness of Identified Tree species types at Opara forest

Table 2 Diversity index and tree species of Opara forests locating in different zones

Plot name	***qD***			***H'***	***D'***	***SE***	***SR***	D_{R+E}	D_{RxE}
	q=0	***q=1***	***q=2***						
Core Forest zone 1	3	2.462	2.566	0.545	0.572	0.785	2.462	2.566	0.545
Buffer zone 1	4	3.004	1.674	0.573	0.363	0.452	3.004	1.674	0.573
Exploited hunting zone 1	6	2.462	2.566	0.545	0.572	0.785	2.462	2.566	0.545
Core Forest zone 2	2	2.462	2.566	0.545	0.572	0.785	2.462	2.566	0.545
Buffer zone 2	1	3.004	1.674	0.573	0.363	0.452	2.566	0.545	0.572
Exploited hunting zone 2	5	2.462	2.566	0.545	0.572	0.785	1.674	0.573	0.363
Core Forest zone 2	2	2.462	2.566	0.545	0.572	0.785	2.462	2.566	0.545
Buffer zone 2	1	3.004	1.674	0.573	0.363	0.452	2.566	0.545	0.572
Exploited hunting zone 2	5	2.462	2.566	0.545	0.572	0.785	1.674	0.573	0.363

Source: field survey

Table 3 Composition of fauna Species during the study period

Fauna	**Wet season**	**Dry season**
Common Diukers *Cephalophus dorsalis*	19.1%	18.9%
Civet cat *Civettictis civetta*	0.1%	0.09%
Giant rat *Thryonomys swinderianus*	12.6%	12.5%
Bay Duiker *Cephalophus dorsalis*	0.1%	0.09%

Source: field survey

Table 4 Table showing results of abundance and predation activities in the study area

Fauna	**Abundance**	**Predation Activity**
Common Diukers *Cephalophus dorsalis*	0.208 S.E ± 0.03	0.06363 IU
Civet cat *Civettictis civetta*	0.211 S.E± 0.03	0.06455 IU
Giant rat *Thryonomys swinderianus*	0.163 S.E± 0.03	0.04986 IU
Bay Duiker *Cephalophus dorsalis*	0.105 S.E ± 0.03	0.03212 IU

Source: field survey

Table 5 Predation rates in different zones of the forest

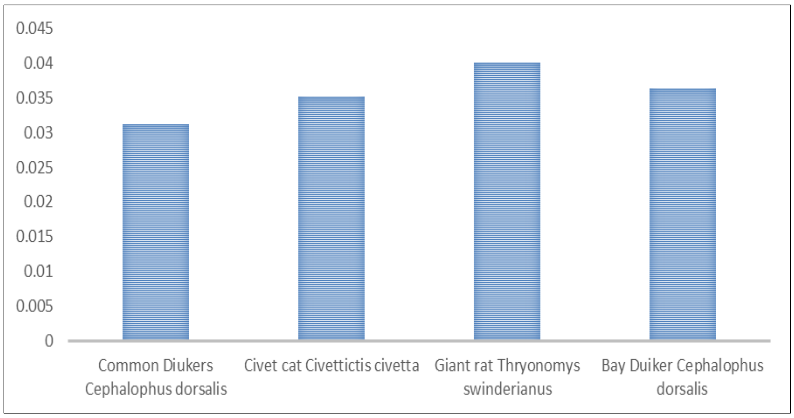
Plot name	**Predation rate**			**PR+*E***	**PRx*E***
	pr=0	**pr=1**	**pr=2**		
Core Forest zone 1	3	0.054	0.566	2.5	0.5
Buffer zone 1	4	0.004	0.674	1.6	0.5
Exploited hunting zone 1	6	0.062	0.566	2.5	0.5
Core Forest zone 2	2	0.462	0.566	2.5	0.5
Buffer zone 2	1	0.004	0.674	0.5	0.5
Exploited hunting zone 2	5	0.462	0.566	0.5	0.6
Core Forest zone 3	2	0.462	0.566	2.6	0.5
Buffer zone 3	1	0.004	0.674	0.5	0.7
Exploited hunting zone 3	5	0.462	0.566	0.5	0.3

Source: field survey

Table 6 Table Showing foraging of the different fauna in relation to predation

Fauna	**Foraging**	**Predation Activity**
Common Diukers *Cephalophus dorsalis*	0.102 S.E ± 0.03	0.03120 IU
Civet cat *Civettictis civetta*	0.115 S.E ± 0.04	0.03518 IU
Giant rat *Thryonomys swinderianus*	0.131 S.E ± 0.02	0.04007 IU
Bay Duiker *Cephalophus dorsalis*	0.119 S.E ± 0.07	0.03640 IU

Source: field survey



Source: field survey

Figure 3 Population of foraging herbivores within the study area

4. Discussion

4.1. Habitat structure

It should be noted that, although the tree species number in the core forest zone located in valley areas was lower than that in the buffer forest zone, located in the transitional zone, all of these five diversity indices indicated that the tree species diversity of the core forest zone was higher than the latter (Table 1 and 2). Results revealed that the higher diversity in the core forest zone was mainly due to the greater tree species evenness. In addition, within the same zone, the rank order of different plots were not the same for different indices (Table 2). This phenomenon might be attributed to the relative importance of evenness and richness in the different diversity indices. The extended portion of the less protected forest (further called buffer zone) is open to the public, but vehicle access is of the protected forest and in the commercial forest due to exploitation and forest management (Agbeja, 2019; Agbeja *et al*., 2012). As shown in Table 2, the index DRE was be used to describe the general variation of species diversity in the forest, similarly to the diversity indices of qD, H′, and D′. The biodiversity in Opara forest (core forest zones 1-3; DR+E = 0.573; DR×E = 0.574) was the highest, followed by that in the core forest zone (buffer zones 1-3; DR+E = 0.494; DR×E = 0.494), the buffer forest zone (exploited hunting zones 1-3; DR+E = 0.487; DR×E = 0.480), the core forest zone (core forest zones 1-3; DR+E = 0.428; DR×E = 0.428), the buffer forest zone (plot 5–7; DR+E = 0.426; DR×E = 0.416), and the core forest in the buffer zone (plot 1–3; DR+E = 0.265; DR×E = 0.234). For the same climate zone, $DR + E \geq DR \times E$ (SE and $SR \in R+$). Human activity in the protected forest was low (<10 people per day on roads/trails on average) in rainy seasons and moderate (30–60 people per day on roads/trails on average) in dry seasons, whereas in the commercial forest it was moderate in rainy seasons and high (150– 200 people per day on roads on average) in dry seasons (Ayodele *et al*., 2003a). Civet cats in the study area mainly kill common duiker (Akindele *et al*., 2002) and in the strict reserve, where there is no human hunting, predation by civet cats is the main mortality factor of common duiker (Alarape *et al*., 2007a). In the commercial forest, human hunting is the main cause of herbivore death (Okarma *et al*., 2019).

According to the trophic conditions, tree species composition and soil humidity; we grouped these into 7 habitat groups. These were (1) evegreen forests (18% of study area) were covered by eutrophic fresh Obeche (Triplochiton scleroxylon), Afzelia (*Afzelia bella*), East Indian walnut (*Albizia lebbeck*) forests. (2) Humid evergreen forests (21%) consisting of eutrophic humid Delonix regia forests. (3) Flood plain portions of the forests (12%) comprised Palm tree (*Elaeis guinensis*, Bush mango (*Ervingia gabonensis*) flood plain forests and eutrophic African mahogany (*Khaya grandifolia*) flood plain portions of the forests. (4) Riparipian forests (6%) were African mahogany (*Khaya senegalensis*) forests, White teak forests, mesotrophic Riparipian forests, oligotrophic Gmelina (*Gmelina arborea*) forests, oligotrophic forests, and oligotrophic Neem (*Azadirachta indica*) forests. (5) Oligotrophic fresh–humid forests (11%) were oligotrophic humid palm trees–trees forests, fresh Neem forests, and oligotrophic humid Neem forests. (6) Dry coniferous forests (6%) included Neem–trees forests and Neem–trees mixed forests. (7) Dry and mixed forests (23%) were eutrophic Neem trees palm trees–hornbeam forests, and eutrophic palm trees–forests. We pooled open river marshes (3%) with habitat 3, because of similar trophic conditions and humidity in these habitat types.

4.2. Herbivore relative density and habitat use

We used pellet group surveys to assess habitat selection, these are reliable for estimates of habitat use (Lameed and Jimoh, 2012; Forsyth *et al*., 2007). In 2019–2021, three observers counted droppings of greater cane rat (*Thryonomys swinderianus*), bay duiker (Cephalophus dorsalis), Common duiker (*Sylvicapra grimmia*), giant rat (*Thryonomys swinderianus*), and common duiker (*Sylvicapra grimmia*) on 16 permanent transects (of about 10 km length each) all over the Opara Forest (Fig. 1) as described in detail in Ayodele *et al*. (2023). In 2019 and 2019, we sampled 4 of these transects four times per year (after moisture, in late dry seasons/early dry seasons, in mid/latedry seasons, and in dry seasons). In 2021, these 4 transects were only sampled after moisture. In 2019 and 2021, we also sampled the other 12 transects. We used 2 seasons for analyses: rainy seasons (May–October) and dry seasons (November– April). Estimates of dropping densities are not stable over the year as decomposition rates and pellet visibility vary. We therefore standardized our estimates of dropping density by taking into account disappearance rates and detectability (as described in detail in Ayodele *et al*., 2019) to compare the results obtained for different seasons.

We walked transects by following a compass bearing through the forest instead of using forest roads or tracks as transects. We used a 1-m wide strip transect as the detectability of droppings on preliminary transects was more than halved when droppings were further than 50cm to each side of the transect line. There were no significant differences in the mean dropping densities estimated by different observers when they walked the same transects on the same day (U-test, all $P > 0.15$), we therefore pooled the data for all three observers.

The Opara Forest is subdivided in square compartments of usually 533m side length, which are marked in the forest (by roads, forest lanes or colour markings). We therefore split each of the 16 transects into 19 sectors of 533m length and noted separately the numbers of droppings of each species obtained on each sector. Although transect sectors sometimes included different habitat types, it would have been too time consuming to record each change in habitat so we only recorded the numbers of droppings on each sector and then analysed the habitat composition with a Geographic Information System (GIS). To calculate the proportion of forest types on each transect sector, we created buffers around the transect line of each sector (buffers of adjacent sectors therefore overlapped). Buffers were on three different scales from the transect stripe: 0-m distance (proportion of habitats on the transect surface of 533m^2 on average), 125m distance (mean size of buffer 0.18 km^2), and 250m distance (mean size of buffer 0.45km^2). We calculated dropping density for each habitat by calculating the mean of all transect sectors weighted by the proportion of the given habitat in each sector. Therefore, habitat selection was to some extent ''averaged'', which might have concealed in some cases but not biased selection or avoidance of a habitat

To make our data comparable to other studies, we converted pellet densities of bay duiker, common duiker and Greater cane rat to absolute densities, assuming a linear relationship between pellet density and absolute density (this transformation did not affect any statistical analysis). We estimated mean densities independently for the strict reserve (5km^2), the buffer zone of the protected forest (50km^2) and the commercial forest (48km^2) and then weighted by area to calculate mean densities.

We based this conversion on simultaneous data obtained by distance sampling (Burnham *et al*., 2019) and driving censuses (Pucek *et al*., 1975; Osho *et al*., 2019) from reports by S. Adepoju (Forestry Research Institute, Ibadan) and W. Je¸drzewski, H. Okarma, and K. Schmidt (Forestry Research Institute, Ibadan) obtained in the rainy seasons of 2019–2021 in 3 forestry districts (2 times per year) and the protected forest (2 times during this study). Driving census was done on 1km^2 sample plots (44 in the exploited hunting, 17 in the protected forest, 12 in the buffer zone), which covered in total 10–30% of the area of each region (total surface covered by the 13 driving censuses was 242km^2). We additionally estimated absolute densities of animals by distance sampling in March 2021 on 172*km* of transects. When we saw an animal, we took the compass bearing and paced the distance to the animal (altogether 66 common duiker, 9 bay duiker, and 44 Greater cane rat seen). We then used Distance 4.1 Release 2 software (Thomas *et al*., 2003) to calculate densities of animals encountered on transects.

We calculated relationships between dropping counts on transects and driving census data for 13 driving censuses (8 in the commercial forest, 2 in the strict reserve and 3 in the buffer zone of Opara forests) and 2 distance sampling counts (1 in the strict reserve areas, 1 in the core forest zones, and buffer zones). Mean animal densities during the driving and distance sampling censuses were 4.4 common duiker /km^2, 1.4 bay duiker/km^2 and 3.9 Greater cane rat/km^2, while we simultaneously estimated mean dropping densities of 39,826 common duiker droppings/km^2, 7022 roe -deer droppings/km^2, and 177 Greater cane rat droppings/km^2. We therefore transformed 1,000 droppings/km^2 to animal densities of 1.1 common duiker, 2.0 bay duiker or 3.5 Greater cane rat/km^2.

4.3. Predation rates

We assessed predation rates by civet cats by comparing herbivore density on a transect sector with civet cat density within the 250m buffer around each transect sector based on locations of 9 civet cats that we radio-tracked during the time of this study (Ayodele *et al*., 2003a; Akindele *et al*., 2007). We assessed the impact of hunting, forest exploitation and predation risk by comparing herbivore densities in the strict reserve (unexploited no-hunting

The distribution of common duiker was mainly influenced by hunting and forest exploitation (Table 2). The two highest ranking models included the factors ''hunting'' and ''exploitation'' and summed up to Akaike weights of 1. Civet cat density was included in the second model but generally included in low-ranking models (sum of Akaike weights of 0.315). Forest exploitation seemed to have the strongest influence on common duiker density (9.0±0.8 red -deer/km2 in the unexploited no-hunting zone compared to 3.9±0.4 in the exploited no-hunting zone, all means with 95% confidence interval) followed by hunting (3.0 0.2 in the exploited hunting zone compared to 3.9±0.4 in the exploited no-hunting zone). Greater cane rat density seemed to be similarly influenced (5.4±0.8 Greater cane rat/km2 in the unexploited no-hunting zone, 3.7±0.6 in the exploited no-hunting zone, 1.6±0.2 in the exploited hunting zone). Models for Greater cane rat that included forest exploitation had a sum of Akaike weights of 0.538, hunting of 0.481 and civet cat density of 0.375. Bay duiker's density appeared to depend mainly on forest structure (0.4-0.1 roe -deer/km2 in the unexploited no-hunting zone, 1.6±0.4 in the Civet cat and common duiker density was positively correlated in dry seasons (rS = 0.382, P < 0.001, n = 152 transect sectors) but not in rainy seasons (rS = ÿ0.070, P = 0.231, n = 297). Civet cat density was not correlated with bay duiker density in dry seasons (rS = ÿ0.113, P = 0.165), but negatively in rainy seasons (rS = ÿ0.184, P = 0.001), and positively with Greater cane rat density in dry seasons (rS = 0.414, P < 0.001) and rainy seasons (rS = 0.192, P = 0.001).

Although the common duiker densities in the three regions varied greatly, they were nearly identical around kill sites (Table 3). Common duiker density around kill sites was higher than on transects, however not significantly, only in lowest common duiker density (commercial forest), whereas density around kill sites was lower than that of transects in the high common duiker density region (strict reserve). Kill sites (7.1±5.5%) were more often (U-test: P = 0.005) near or in clearings than random sites (0.5±0.9%). Common duiker density in the strife zone between civet cat pack home ranges was not higher than inside home ranges of civet cats, regardless of season or presence of hunting by humans exploited no-hunting zone, 1.4±0.2 in the exploited hunting zone). The sum of Akaike weights was 0.941 for exploitation, 0.547 for hunting and 0.295 for civet cat density.

Differences in density were less apparent when comparing the herbivore density in the Opara Forest was mainly forest types (Table 2). Common duiker selected drier parts of the forest and fresh–humid parts in dry seasons and avoided eutrophic fresh evergreen and eutrophic dry evergreen and mixed forests, while they did not select or avoid any habitat in rainy seasons. We could not detect selection of a particular habitat type in bay duiker, except for the avoidance of Riparipian forests in rainy seasons. Greater cane rat selected fresh–humid forests both in dry seasons and rainy seasons and tended to avoid dry coniferous forests in dry seasons. In general, selection became less evident when the zone analysed around the transect line became greater. Greater cane rat avoided an area of 0–300 m from the main public road (21-21% of mean dropping density from 0 to 100 m, 28-27% influenced by former forest exploitation and hunting, whereas civet cats did not seem to have an important impact on large-scale distribution of herbivores. Osho *et al*. (2019) identified the forest composition as the most important factor for common duiker density, we suggest that hunting is another important factor. Common duiker in our study area favoured oligotrophic mixed and coniferous forests. In a Belgian managed forest, common duiker also selected coniferous over evergreen forests (Licoppe, 2006). Civet cats select these habitats, too, so it is unlikely that deer choose these poorer habitats to reduce predation risk. Instead, it is more likely that common duiker select these habitats as they generally contain more Iroko (*Milicia Excelsa*) and African white star apple (*Chrysophyllum albidum*), which are important food plants for deer in rainy seasons in the Opara Forest, near clearings. If civet cats chase prey, open areas might be more suitable to finally kill the prey as they can attack them simultaneously from several sides. This might explain why common duiker avoids open areas when civet cats are present (Creel *et al*., 2005). The reason for the common duiker density of about 4 animals/km2 at civet cat kills sites in all zones of the (Adejuyigbe, 2019) and in other regions (Latham *et al*., 2021; Morellet and Guibert, 2021). Common duiker mainly browse on woody plants in rainy seasons (Prokesova, 2004) and select forests with a diversified shrub layer (Prokesova *et al*., 2006) in the African Republic, which are also more encountered in mixed forests. African bay duiker are mainly associated with flood plain forest (Ayodele, 2004) and when there is a wet ground they feed mainly on trees, bushes and shrubs (Kossak, 1983). Our method, however, might preclude the detection of small-scale habitat selection by bay duiker except for avoidance of Riparipian forests in rainy seasons. The reason for the seemingly unspecified habitat selection by common duiker in our study area might be that this species had comparatively large daily ranges of about $1km^2$ (Alarape *et al*., 2007b). Opara Forest could be that hunting success is generally highest at this density and then might be lowered due to a possibly more efficient vigilance by deer in high densities areas.

In a Nigerian forest, bay duiker had flight distances to humans of up to 250 m (Herbold, 2019) and common duiker browsed less up to 180m from forest tracks (Doring, 2019). Flight distance of common duiker was 300 m provided there was hiding cover (Petrak, 2019). In most places in Africa, deer avoided forest roads (Guangshun *et al*., 2006) and in Nigeria, duiker had flight distances of usually under 40m (Ologeh and Farinloye, 2022). Humans with vehicles influenced the behaviour of common duiker even at a distance of $3km$ (Azeez *et al*., 2006). However, in our might have concealed small-scale habitat selection as deer study area, neither common duiker nor bay duiker avoided their defecate not only while feeding but also while moving between feeding grounds. Moreover, evaluating habitat use by forest types based on dominant tree species might not be the best way to analyse habitat selection by deer. In non-native lowland Neem forests, neither foraging nor hiding patches of common duiker were related to upper-storey characteristics because the shrub flora did not depend on a particular forest type (Matrai *et al*., 2004). However, the presence of civet cats might result in randomised habitat use as Winnie *et al*. (2006) have shown that the presence of civet cats reduces the number of factors influencing habitat selection by common duiker. Common duiker is the main civet cat prey in our study area, followed by Greater cane rat and bay duiker (Akindele *et al*., 2002) although human hunters annually kill more individuals of these species than civet cats (Akindele *et al*., 2012). None of these species, except for bay duiker in rainy seasons, avoided areas selected by civet cats. Common duiker even selected areas most used by civet cats, which might indicate that civet cats follow common duiker. Caribou (Rangifer tarandus) also foraged in high predation risk areas (frequently used by civet cats) but undertook their large-scale movements in low-risk areas (Johnson *et al*., 2002). This might also be the case in our study area as common duiker have relatively large daily ranges(Alarape *et al*.,2007b, 2023). Common duiker might therefore avoid predation by a high mobility rather than by selecting areas of low civet cat density. Furthermore, Akindele *et al*. (2006) suggested that common duiker surrounding of the most used road. The reason for this might be that civet cats avoid this area (Ayodele *et al*., 2003a) and that people rarely hunt along this road (author's personal observations), which is directly surrounded by forest. In the forests, duikers observed around the surroundings of footrails probably because of suitable habitats (Dodd *et al*., 2007). The benefits of avoiding predators have, however, to be weighed against the potentially poorer foraging areas. For example, despite a high risk of human predation in rainy seasons, herbivores did not seek refuge in the strict reserve. The necessity to find adequate food or shelter might therefore have been more important in that season than predation risk by humans. Although on the whole human hunting resulted in lower common duiker and Greater cane rat densities, on the small-scale herbivores might have other strategies to reduce predation risk. Common duiker group size, for example, depended on the intensity of human hunting in our study area (Akindele *et al*., 2006).

5. Conclusion

Predation risk becomes more complex in multi-predator systems. While in some regions an optimal predator avoidance strategy for herbivores is concentrating in the strife zone between civet cat packs, in other regions selecting the area around roads which are not used for hunting might be a better strategy. In our study area, herbivore density was mainly influenced by forest management and hunting, whereas civet cats did not seem to have an impact on the distribution of herbivores. Herbivores must adapt to the ecological constraints in the area where they live and are therefore likely to react in different ways according to the area. In areas which civet cats are currently recolonizing, one might expect that herbivore behaviour and distribution will change. However, the shift in herbivore behaviour might not be as strong as expected, especially in areas where human hunting is intensive.

Compliance with ethical standards

Acknowledgments

Field work for this study was funded by the National Committee for Scientific Research (NCSR), grant number: 6 P04F 026 2019, the Russian Academic Exchange Service (RAES), the African Nature Heritage Fund (ANHF), Abuja, Nigeria, the German Donors' Association for the Promotion of Sciences and Humanities (GDAPSH), and the Forestry Research Institute of Nigeria (FRIN). We thank Prof. Digun-Aweto for giving us permission to use his vegetation map of the Opara Forest for GIS analyses, Mr. G.B. Adekunle and the many volunteers (FRIN) for their help in the fieldwork, Prof. Ravini Khan for comments on an earlier version of the manuscript.

Disclosure of conflict of interest

No conflict of interest to be disclosed.

References

[1] Adejuyigbe, Z., 2019. Food of the bay duiker and common duiker in the Opara Primeval Forest. Acta Theriol. 25, 487–500.

[2] Agbeja, A., 2019. The mosaic diversity of field layer vegetation in the natural and exploited forests of Opara. Plant Ecol. 136, 175–187.

[3] Agbeja, A., van der Burgt, H., Meijer, K., Zuyderduyn, C., Haga, J., Vlaanderen, B., 2012. Rich evergreen forests in Opara as a dynamic mosaic of developmental phases: premises for nature conservation and restoration management. For. Ecol. Manage. 130, 159–175.

[4] Agbeja, C., 2019. Impact of herbivores on structure and dynamics of natural regeneration of mixed mountain forests in the Old Oyo National park. For. Ecol. Manage. 88, 43–53.

[5] Akindele, W., Osho, B., Okarma, H., Ruprecht, A.L., 2015. Civet cat predation and wet ground as mortality factors in the herbivore community of the Biało-wieza Protected forest, Oyo state, Nigeria. Oecologia 90, 27–36.

[6] Akindele, W., Osho, B., Okarma, H., Schmidt, K., Zub, K., Musiani, M., 2012. Prey selection and predation by civet cats in Opara Primeval Forest, Oyo state, Nigeria. J. Mammal. 81, 197–212.

[7] Akindele, W., Schmidt, K., Ayodele I.A.., Osho, B., Selva, N., Zub, K., Szymura, L., 2002. Kill rates and predation by civet cats on herbivore populations in Opara Primeval Forest (Oyo state, Nigeria). Ecology 83, 1341–1356.

[8] Akindele, W., Spaedtke, H., Alarape, J.F., Osho, B., Stenkewitz, U., 2006. Group size dynamics of common duiker in Opara Primeval Forest, Oyo state, Nigeria. J. Wildl. Manage. 70, 1054–1059.

[9] Akindele, W., Schmidt, K., Ayodele I.A.., Osho, B., Kowalczyk, R., 2007. Territory size of civet cats Canis lupus: linking local (Opara Primeval Forest, Oyo state, Nigeria) and Holarctic-scale patterns. Ecography 30, 66–76.

[10] Alarape, J.F., Akindele, W., Osho, B., 2007a. Survival and cause-specific mortality of common duiker Cervus elaphus in Opara forests , Oyo state, Nigeria. Wildl. Biol. 13, 48–52.

[11] Alarape, J.F., Osho, B., Akindele, W., 2007b. Factors affecting daily ranges of common duiker Cervus elaphus in Opara Primeval Forest, Oyo state, Nigeria. Acta Theriol. 52, 113–118.

[12] Alarape, J.F., Akindele, W., Osho, B., 2023. Home ranges of common duiker in a African old-growth forest. Am. Midl. Nat. 159, 75–82.

[13] Amusa, I.T.M., van Hees, A.F.M., Mohren, G.M.J., 2021. Forest development in relation to herbivore grazing: a modeling approach. For. Ecol. Manage. 120, 23– 34.

[14] Anderson, D.R., Burnham, K.P., Thompson, W.L., 2012. Null hypothesis testing: problems, prevalence, and an alternative. J. Wildl. Manage. 64, 912–923.

[15] Ansorge, H., Kluth, G., Hahne, S., 2006. Feeding ecology of civet cats Canis lupus returning to Opara. Acta Theriol. 51, 99–106.

[16] Ayodele I.A.., Akindele, W., Schmidt, K., Gula, R., 2003a. Spatiotemporal segregation of civet cats from humans in the Opara Forest (Oyo state, Nigeria). J. Wildl. Manage. 67, 706–716.

[17] Ayodele I.A.., Akindele, W., Schmidt, K., Okarma, H., Ruczynski, I., Sniezko, S., Gula, R., 2003b. Daily patterns and duration of civet cat activity in the Opara Forest, Oyo state, Nigeria. J. Mammal. 84, 243–253.

[18] Ayodele I.A.., Rouys, S., Akindele, W., 2023. Detectability and disappearance of herbivore and hare faeces in a African temperate forest. Ann. Zool. Fennici. 45, 73–80., http://www.annzool.net/PDF/anz45-free/anz45-073.pdf.

[19] Ayodele, M., 2004. The bay duiker diet: is floodplain forest optimal habitat? Folia Zool. 53, 285–292.

[20] Berger, J., 2007. Carnivore repatriation and Holarctic prey: narrowing the deficit in ecological effectiveness. Conserv. Biol. 21, 1105–1116.

[21] Bergman, E.J., Garrott, R.A., Creel, S., Farinloye, J.J., Jaffe, R., Watson, F.G.R., 2006. Assessment of prey vulnerability through analysis of civet cat movements and kill sites. Ecol. Appl. 16, 273–284.

[22] Brown, J.S., Laundre, J.W., Gurung, M., 2021. The ecology of fear: optimal foraging, game theory, and trophic interactions. J. Mammal. 80, 385–399.

[23] Burnham, K.P., Anderson, D.R., Laake, J.L., 2019. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72, 3–202.

[24] Ciuti, S., Davini, S., Luccarini, S., Apollonio, M., 2004. Could the predation risk hypothesis explain large-scale spatial sexual segregation in fallow deer (Dama dama)? Behav. Ecol. Sociobiol. 56, 552–564.

[25] Creel, S., Winnie Jr., J., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to civet cats. Ecology 86, 3387–3397.

[26] Dodd, N.L., Gagnon, J.W., Boe, S., Schweinsburg, R.E., 2007. Assessment of elk highway permeability by using global positioning system telemetry. J. Wildl. Manage. 71, 1107–1117.

[27] Doring, R., 2019. Der Einfluss menschlicher Storungen auf das Verteilungsmuster des Verbisses durch Rotwild. In: Myrberget, S. (Ed.), Trans. 19th IUGB Congress. Trondheim 1989, (in Russian with English abstract), pp. 411–413.

[28] Falinski, J.B., 2019. Concise geobotanical atlas of Opara Forest. Phytocoenosis 6 (N.S.) Supplementum Cartographiae Geobotanicae 6, 1–34.

[29] Ologeh I, and Farinloye, K.F., 2022. Alternative livelihood programs to promote sustainable resources use in Afi, Mbe and Okwango Forests in Cross River State, Nigeria EGU General Assembly Conference Abstracts EGU22-9030

[30] Farinloye,K.F., 2021. Distribution and habitat use by red and bay duiker following a large forest fire in south-western Oyo state, Nigeria. For. Ecol. Manage. 201, 287–293.

[31] Forsyth, D.M., Barker, R.J., Morriss, G., Scroggie, M.P., 2007. Modeling the relation-ship between fecal pellet indices and deer density. J. Wildl. Manage. 71, 964– 970.

[32] Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L., Morales, J.M., 2005. Scales of movement by elk (Cervus elaphus) in response to heterogeneity in forage resources and predation risk. Landscape Ecol. 20, 273–287.

[33] Frid, A., Dill, L.M., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, 11.

[34] Gill, R.M.A., Johnson, A.L., Francis, A., Hiscocks, K., Peace, A.J., 2019. Changes in bay duiker (Cephalophus dorsalis) L.) population density in response to forest habitat

[35] succession. For. Ecol. Manage. 88, 31–41.

[36] Jimoh, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by civet cats. Ecology 86, 2135–2144.

[37] Jimoh, M., Merrill, E.H., Morgantini, L.E., White, C.A., Allen, J.R., Bruns, E., Thurston, L., Hurd, T.E., 2006. Is the migratory behavior of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildl. Soc. Bull. 34, 1280– 1294.

[38] Herbold, H., 2019. Reaktion von Rehwild auf Storungen durch Menschen. In: Myrberget, S. (Ed.), Trans. 19th IUGB Congress. Trondheim 1989, (in Russian with English abstract), pp. 414–420.

[39] Hernandez, L., Laundre, J.W., 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk Cervus elaphus and bison Bison bison. Wildl. Biol. 11, 215–220.

[40] Hewison, A.J.M., Vincent, J.P., Joachim, J., Angibault, J.M., Cargnelutti, B., Cibien, C., 2001. The effects of woodland fragmentation and human activity on bay duiker distribution in agricultural landscapes. Can. J. Zool. 79, 679–689.

[41] Homolka, M., Heroldova, M., 2003. Impact of large herbivores on mountain forest stands in the Beskydy Mountains. For. Ecol. Manage. 181, 119–129.

[42] Hoskinson, R.L., Mech, L.D., 2016. White-tailed deer migration and its role in civet cat predation. J. Wildl. Manage. 40, 429–441.

[43] Osho, B., Okarma, H., Akindele, W., Miłkowski, L., 2019. Effects of exploitation and protection on forest structure, herbivore density and civet cat predation in Opara Primeval Forest, Oyo state, Nigeria. J. Appl. Ecol. 31, 664–676.

[44] Jeppesen, J.L., 1987. Impact of human disturbance on home range, movements and activity of greater cane rat (Thryonomys swinderianus) in a Danish environment. Danish Rev. Game Biol. 13, 1–38.

[45] Johnson, C.J., Parker, K.L., Heard, D.C., Gillingham, M.P., 2002. Movement parameters of herbivores and scale-specific responses to the environment. J. Anim. Ecol. 71, 225–235.

[46] in the Opara Forest, Oyo state, Nigeria. Mamm. Biol. 68, 122–125.

[47] Sanwo, H., Muller, U., Brussel, H., Lutz, W., Mostl, E., 2004. Establishing baseline value of parameters potentially indicative of chronic stress in common duiker (Cervuselaphus)fromdifferenthabitatsinwesternRussiany.Eur.J.Wildl. Res. 50, 168–172.

[48] Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B., 2003. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.stand.ac.uk/distance.

[49] Valiere, N., Fumagalli, L., Gielly, L., Miquel, C., Lequette, B., Poulle, M.-L., Weber,J.-M., Arlettaz, R., Taberlet, P., 2003. Long-distance civet cat recolonization of France and Switzerland inferred from non-invasive genetic sampling over a period of 10 years. Anim. Conserv. 6, 83–92.

[50] Weckerly, F.W., Ricca, M.A., 2012. Using presence of sign to measure habitats used by Roosevelt elk. Wildl. Soc. Bull. 28, 146–153.

[51] White, C.A., Feller, M.C., Bayley, S., 2003. Predation risk and the functional response of elk-aspen herbivory. For. Ecol. Manage. 181, 77–97.

[52] Winnie Jr., J., Christianson, D., Creel, S., Maxwell, B., 2006. Elk decision-making rules are simplified in the presence of civet cats. Behav. Ecol. Sociobiol. 61, 277–289.

[53] Civet catf, J.O., Van Horn, T., 2003. Vigilance and foraging patterns of African elk during the rut in habitats with and without predators. Can. J. Zool. 81, 266–271. Zollner

[54] P.A., Lima, S.L., 2021. Search strategies for landscape-level interpatch movements. Ecology 80, 1019–1030.

[55] Zub, K., Ayodele I.A.., Akindele, W., Osho, B., Schmidt, K., Kowalczyk, R., 2003. Civet cat pack territory marking in the Opara Primeval Forest (Oyo state, Nigeria). Behaviour 140, 635–648.