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Hunting affects dry season habitat selection by several bovid species in northern Benin

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Multiple land uses including tourism, hunting, and agriculture around protected areas can be a serious complication for wildlife management. We calculated habitat selection indices (Manly's alpha) for 10 bovid species in the Pendjari Biosphere Reserve in Benin, west Africa, to assess if habitat use differed in each bovid species between hunting and non-hunting zones. Presence/absence data was used in resource-selection functions based on a generalized linear mixed effect model to examine factors that explained bovid species distribution. We observed stronger avoidance of open habitat types in the hunting zone than in the non hunting zone for the hartebeest *Alcelaphus buselaphus*, oribi *Ourebia ourebi*, roan *Hippotragus equines*, kob *Kobus kob*, waterbuck *Kobus ellipsiprymnus defassa* and reedbuck *Redunca redunca*. In contrast, in grey duiker *Sylvicapra grimmia*, red-flanked duiker *Cephalophus rufilatus*, bushbuck *Tragelaphus scriptus* and buffalo *Syncerus caffer* we found no differences in habitat use between hunted and non-hunted areas. This may indicate that the latter species show more pronounced ecological and behavioural plasticity. Further, resource selection of bovid species on a small scale was influenced by other factors such as habitat structure, landscape characteristics, and human disturbance. This preliminary assessment of bovid habitat relationships in west Africa suggests that human hunting activities may cause species to alter their habitat selection. We therefore suggest habitat models may need to incorporate this source of variation if they are to accurately predict habitat use or distribution of a species.

Understanding the process animals follow to select habitat, rather than just documenting the habitat they use is a central topic in ecology. Over the last two decades, studies about the underlying mechanisms that drive species abundance and distribution have increased and improved our ability to predict how the animals use habitat in other locations and how they will respond to changes in habitat (Guisan and Thuiller 2005).

Bovid species are common and widely distributed ungulates throughout the African savanna (Estes 1991). The majority of research on African bovid species has been conducted in east and South Africa. Little empirical data are available from west Africa (Schuette et al. 1998) and thus information for management in that area is lacking. In addition, bovid species experience a variety of anthropogenic influences such as hunting, disturbance from other human activities, and habitat alteration, which have the potential to detrimentally affect populations.

In African wildlife conservation, protected areas play a major role. Protected areas in west Africa and elsewhere commonly comprise a fully protected core zone surrounded by multiple-use areas. However, the consequences of this zonation concept and its various human land uses on habitat use of mammal species such as bovids are little understood. In multiple-use areas in semi-arid landscapes of west Africa, such as those occurring in the north of Benin, it is not known which factors most shape the distribution of wildlife.

In this study, we used bovids as model species to investigate if the habitat selection of wildlife populations can be used as indicators of human exploitation (Averbeck et al. 2012).

Our study took advantage of a unique opportunity to analyze several bovid species at the edge of their ranges with regard to past and present human pressures and conservation management (Kassa et al. 2007). We expected the distribution of bovid species to be influenced by habitat and environmental characteristics, and by human activities (Fritz et al. 2003, Setsaas et al. 2007, Stankowich 2008). In particular, we hypothesized that bovids would avoid open habitat where hunting occurs. We use a strictly protected area (i.e. a National Park) as a comparison to partially protected areas (i.e. two hunting reserves) to analyze bovid occurrence and habitat selection in a semi-arid multiple-use landscape. We endeavored to provide managers in west Africa with much-needed information required for a more informed assessment of the effects of protected area management practices on those ecologically and economically important species.

Material and methods

Study site

The Pendjari Biosphere Reserve (PBR) is situated in northwestern Benin (10°30′ to 11°30 N, 0°50′ to 2°00′E, Fig. 1). It was declared a Game Reserve in 1954 and upgraded to the National Park of Pendjari (NPP) in 1961. Today, it is comprised of a strictly protected core area (named 'National Park' covering 2660 km²) and two adjacent hunting zones named 'Konkombri' and 'Pendjari' hunting zones, which are on the eastern and southwestern sides of the National Park, respectively. These two hunting zones together cover 1971 km². The PBR is bordered by the foothills of the Atacora massif in the east and by the river Pendjari in the north and the west sides. PBR is located in the Sudanian zone with one rainy season (April/May to October) and one dry season (November to March). The total annual rainfall averages 1000 mm with 60% falling between July and September.

The mean annual daily temperature is 27°C. During the rainy season numerous small ponds in the vicinity of the large natural ones named Tiabiga, Fogou, Mondri, Diwouni, Yangouali and Bali in the centre of the National park are full of water. During the dry season, the natural ponds attract a variety of animal groups, especially large mammals searching for water. The vegetation cover of the PBR is made up of a mosaic of shrubs, trees, woodland savannas and grassland (Sokpon et al. 2001) which are burned in both National Park and hunting zones, every year to provide fresh pasture to herbivores that dominate the reserve, increase visibility to wildlife tourists and hunters (who visit mostly during the dry season), and avoid the uncontrolled mid and late dry season fires that spread from surrounding villages or that are lit by poachers to mask illegal activities. Bovid species are among the most targeted species by sport hunters in the Pendjari Biosphere Reserve.

Study species

We collected data on eleven bovid species from different feeding categories inhabiting the Pendjari Biosphere Reserve (Sinsin et al. 2002). These included two large bovid species weighing more than 300 kg: African buffalo *Syncerus caffer* and roan antelope *Hippotragus equinus*; two medium-sized highly gregarious obligate grazers: topi *Damaliscus lunatus korrigum* and kob *Kobus kob*; three mixed feeders: waterbuck *Kobus ellipsiprymnus defassa*, oribi *Ourebia ourebi* and hartebeest *Alcelaphus buselaphus*; reedbuck *Redunca redunca*, a savanna-dwelling small grazing antelope; and three primarily solitary forest-dwelling small browsing antelopes: bushbuck *Tragelaphus scriptus*, red-flanked duiker *Cephalophus rufilatus* and grey duiker *Sylvicapra grimmia*.

Survey design and data collection

We conducted field work from December 2010 to March 2011 covering four months during the dry season. We assigned 1330 quadrats of 30 × 30 m each for sampling. Quadrats were placed every 200 m along 38 transects of 7 km each. The 38 transects were randomly distributed and

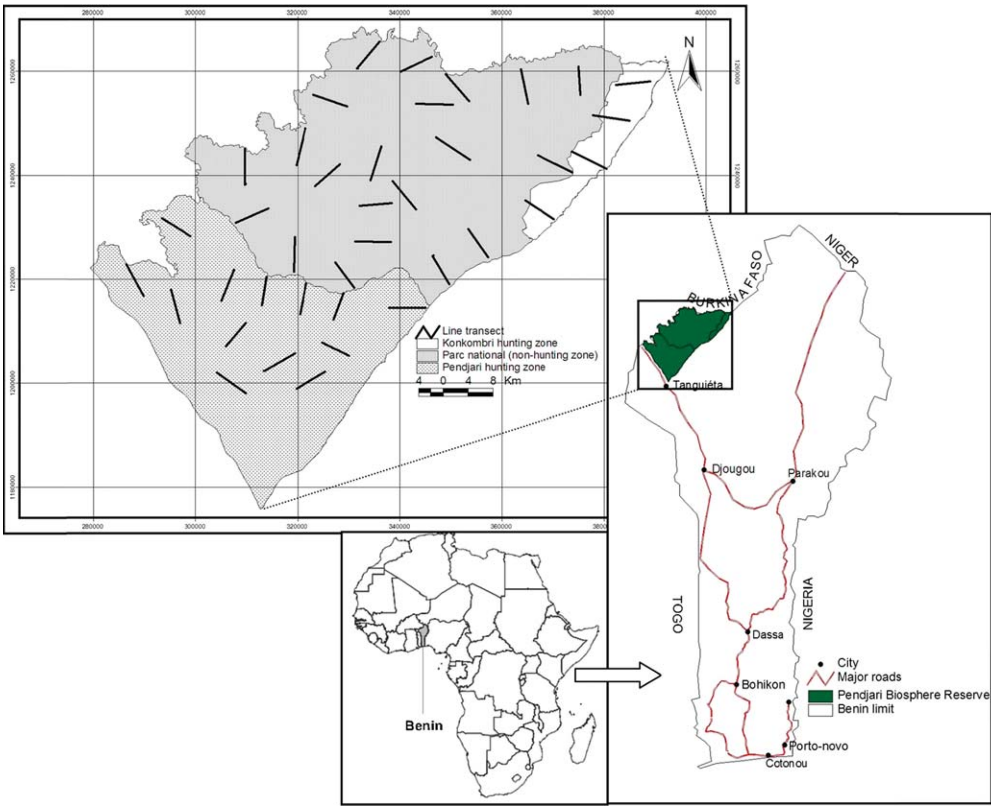

Figure 1. Study area showing the different hunting and non-hunting zones with the distribution of the transects within the study area.

all habitat types were represented (Fig. 1). These transects covered the whole study area from north to south. Each sampling quadrat was visited by one well-trained observer who could reliably identify bovid dung to species. In each sampling quadrat, we examined which bovid species were present by identifying tracks and by counting the number of dung pellet groups per species (required for calculating habitat selection indices). For subsequent analysis, presence/absence data of the species in each sampling quadrat were generated by coding 0 for absence and 1 for presence.

The shape and size of most dung is species-specific and errors of identification are not common for most species. However, the pellets of certain bovid species may be misidentified, particularly between hartebeest and topi pellets, and between reedbuck and bushbuck (Hibert et al. 2008, 2011). Therefore, we used additional information such as hoof prints, animal vocalizations, and when possible, direct observations to enhance accuracy (Djagoun et al. 2013). The habitat type was recorded for each sampling quadrat. For practical reasons and prior to analysis, available habitat categories were aggregated into five general land cover types using Pendjari Biosphere land use/land cover database shape files: 1) grassland, 2) gallery forest, 3) wood savanna, 4) woodland, 5) outcrop vegetation. We used the spatial analysis function in ArcView GIS ver. 3.1 to create feature maps that also estimated the total coverage of each habitat type throughout the study area.

Multiple scales should be considered in habitat use studies (Rotenberry et al. 2006). Therefore, we used ecological descriptors that ranged from patch to landscape scales: we measured micro-habitat variables in the field, and derived landscape-scale variables using GIS. In total, we selected 10 environmental variables that could potentially influence the distribution of bovid species in arid and semi-arid ecosystems based on previous studies (Averbeck et al. 2009, Augustine 2010) and our own predictions (Table 1). These variables were classified with respect to habitat structure, human disturbance and topography.

Habitat structure

Micro-habitat variables recorded in the sampling quadrats included 'wood density', 'fire', 'grass' and 'canopy cover'. For the variable 'wood density', all the trees inside the sampling quadrat were counted. The binary factor 'fire' described whether the place had been recently burned or not. This variable is often important in habitat use studies because many herbivores are attracted by post-fire regrowth due to the superior forage quality and more favourable sward structure (Klop et al. 2007). Burning can also attract browsers by stimulating the sprouting of forbs and trees (Klop et al. 2007). However the response of herbivores to fires depends on the feeding guild.

Human disturbance

The presence of humans ('human disturbance' hereafter) can influence bovid species distribution and may be considered analogous to predation risk (Frid and Dill 2002). We used the 'distance to the nearest hunting zone', the 'distance to roads' and 'distance to the closest river' of each sampling quadrat as indicators of different levels of human disturbance.

Table 1. Variables used to model different bovid species distribution, at patch and landscape scales, in Pendjari Biosphere Reserve.

Variables/codes	Description
Habitat structure	
FIR	fire (recently burned sign (FIR_1) or not (FIR_0) inside the sampling quadrat)
WOD	wood density (Number of trees at dbh > 30cm inside the sampling quadrat)
GRC	grass cover (estimated % of grass inside the sampling quadrat)
CAC	canopy cover (estimated % of trees cover inside the sampling quadrat)
Human disturbance factors	
DIR	distance of sampling quadrat to the nearest river (m)
DIRO	distance of sampling quadrat to the nearest road (m)
DIH	distance of sampling quadrat to hunting zone (m)
Topographic factors	
ROC	rockiness (estimated % area covered by rocks)
SLP	slope: the sampling quadrat slope (°)
DIP	distance of sampling quadrat to the nearest pond (m)

Topography

We recorded 'distance to the closest pond', 'slope' (Suunto clinometer PM-5/1520 D), and 'rockiness' as the percentage area covered by rocks in each sampling quadrat.

Data analyses and model construction

Bovid species habitat selection indices (Manly's alpha) for the five different habitat types were calculated following the method of Manly et al. (1972) using the following formula:

$$\alpha_i = \frac{r_i}{n_i} \frac{1}{\sum\left(r_i / n_i\right)}$$

where α_i is Manly's α for habitat i, r_i is proportion of habitat type i used by a given species (based on the pellet group count; $i = 1, 2, 3, \ldots, m$), n_i is the proportion of habitat type i available in the study area and m is the highest number of habitat types (i.e. five in this study). When there is no preference in habitat selection $\alpha_i = m^{-1}$. If $\alpha_i > m^{-1}$, habitat type i is preferred while $\alpha_i < m^{-1}$ indicates avoidance of habitat type i. This analysis allows investigating change in habitat selection across hunting and non hunting zones.

We estimated resource-selection functions (RSF's: Manly et al. 2002) following mixed-effects logistic regression (generalized linear mixed effect model, GLMM) to identify which habitat and environmental factors were associated with the occurrence of bovid species. Transects were included in the model as random factors, to control the lack of independence of sampling quadrats within them, arising from the spatially nested data structure. Estimation of parameters was carried out using the function lmer in the R software package lme4 (Bates 2007). The goodness-of-fit of the overall regression model was examined by comparing the log-likelihood of the full model to that of the reduced model. The significance of the individual coefficients was calculated on the basis of Wald statistics (Quinn and Keough 2002). We used a backward stepwise procedure for model simplification and selected the model with the lowest AIC (Akaike information criterion) values. Models with ΔAIC scores within 2 units from the most parsimonious model were included as alternative models. Co-linearity among the predictor variables was investigated by examining the Pearson correlation coefficients between the measured variables. Only one of a pair of variables that were strongly correlated i.e. $\rho > 0.7$, after Fowler and Cohen (1992), was included. Consequently 'wood density' was discarded from the model because of the high correlation with 'canopy' ($\rho = 2.44$). Separate analyses were conducted for each species. Few observations of topi were made, so we did not model topi distribution in this study. All analyses were performed in the statistical program R ver. 2.14.0.

Results

Habitat preferences across hunting versus non hunting zone

Lacking enough data for topi, we calculated the habitat selectivity index of Manly's alpha for the 10 remaining bovid species in the hunting and non hunting zone (Fig. 2). We found a preference for grassland for buffalo, waterbuck, hartebeest, roan, kob and reedbuck in both hunting and non hunting zones. However, except for roan, this preference was stronger in the hunting zone than the non-hunting. Eight species avoided outcrop vegetation independently of land use type: red-flanked duiker, grey duiker, bushbuck, buffalo, waterbuck, roan, kob and reedbuck. Hartebeest and oribi showed a preference for the outcrop vegetation in the hunting zone and avoidance in the non hunting zone. Oribi, grey duiker, bushbuck and red-flanked duiker avoided wood savanna, while waterbuck avoided this habitat in the non-hunting zone, but showed a preference for it in the hunting zone. Preference for wood savanna was significantly higher in the hunting zone for hartebeest, roan and kob. Buffalo, however showed a higher preference for wood savanna in the hunting and non-hunting zone. Except buffalo, all bovid species preferred woodland habitat in the non-hunting zone, however, in the hunting zone, avoidance of woodland was recorded for reedbuck, kob, hartebeest and waterbuck. Only buffalo, bushbuck, grey duiker and red-flanked duiker showed a preference for the gallery forest both in the hunting zone and in the non-hunting zone, which for the bushbuck was significantly higher in the hunting zone.

Modelling bovid species distribution

The sampling quadrats resulted in a total of 1986 observations for 10 bovid species (Table 2). We achieved significant GLMMs (Table 2) for all species except buffalo and oribi, so the data for these two species were omitted. In Table 3, the three most parsimonious candidate models are presented for each bovid species with the ΔAIC indicating the 'best-model' (i.e. lowest AIC value) and the alternative models at $\Delta AIC < 2$. Of the initial set of 10 variables, the 'best-model' included only three or four variables. Our results show that in the Pendjari Biosphere Reserve the 'distance from river' parameter was significantly negatively selected in bushbuck ($\beta = -0.354$, $p = 0.025$), red-flanked duiker ($\beta = -1.030$, $p < 0.001$), grey duiker ($\beta = -0.563$, $p = 0.048$) and reedbuck ($\beta = -2.267$, $p = 0.007$), indicating that these species preferred areas close to water. On the other hand, avoidance of areas close to natural ponds was found for the bushbuck ($\beta = 0.081$, $p = 0.031$) (Table 4). In contrast, the kob ($\beta = -0.264$, $p = 0.041$) and waterbuck ($\beta = -0.826$, $p = 0.034$) selected shorter 'distance from the natural ponds'. We found a selection for greater 'canopy cover' for waterbuck ($\beta = 5.133$, $p = 0.018$) and for red-flanked duiker ($\beta = 2.145$, $p = 0.008$) and grey duiker ($\beta = 1.125$, $p = 0.002$). The effects of 'distance to hunting zone' varied among species. In the final model retained for grey duiker, a significant negative selection ($\beta = -1.045$, $p = 0.037$) was found for this parameter, suggesting preference for areas close to the hunting zone. In contrast, the roan, kob and waterbuck showed significant positive selection for 'distance from the hunting zone' (Table 4) indicating an increase in the probability of occurrence with increasing distance from the hunting zone. A positive selection for the 'grass cover' parameter was found for roan, kob and waterbuck. The 'distance from the Pendjari River' parameter was positively correlated with hartebeest ($\beta = 2.073$, $p = 0.063$) and roan ($\beta = 1.015$, $p = 0.032$) distributions, suggesting habitat occupancy of areas further away from water sources. The 'rockiness' parameter was significantly positively selected by the hartebeest. A preference for recently burned areas was shown by the roan and hartebeest distribution model as shown by the significant positive estimates calculated for both species in the GLMM. A significant negative selection of the 'slopes' parameter was found for the red-flanked duiker and reedbuck indicating the steeper the habitat, the lower the probability of use by these species. An opposite effect was noted in grey duiker distribution with an increase in the selection probability with sloping habitats.

Discussion

This is the first study analyzing bovid species' habitat use and distribution in the semi-arid landscape of west Africa. Our analysis reveals how the distribution of bovid species in this savanna environment is shaped by habitat structure, landscape characteristics and sources of human disturbance, and topographic factors.

We observed differences in habitat selection of 6 of 10 species between the hunting vs. non hunting areas: reedbuck, roan, kob, oribi, hartebeest and waterbuck had a stronger avoidance of open habitats in the hunting zone than in the non-hunting zone. In the hunting zone, habitat use of reedbuck, roan, kob, oribi, hartebeest and waterbuck was tightly linked to woodland and gallery forest, presumably because these animals perceived these more closed habitat types as more secure. Similar patterns were recorded in the western Tanzanian woodlands by Waltert et al. (2009), where roan, reedbuck, and waterbuck were observed to have a stronger preference for open areas in the national park than in a game reserve where hunting activity occurred.

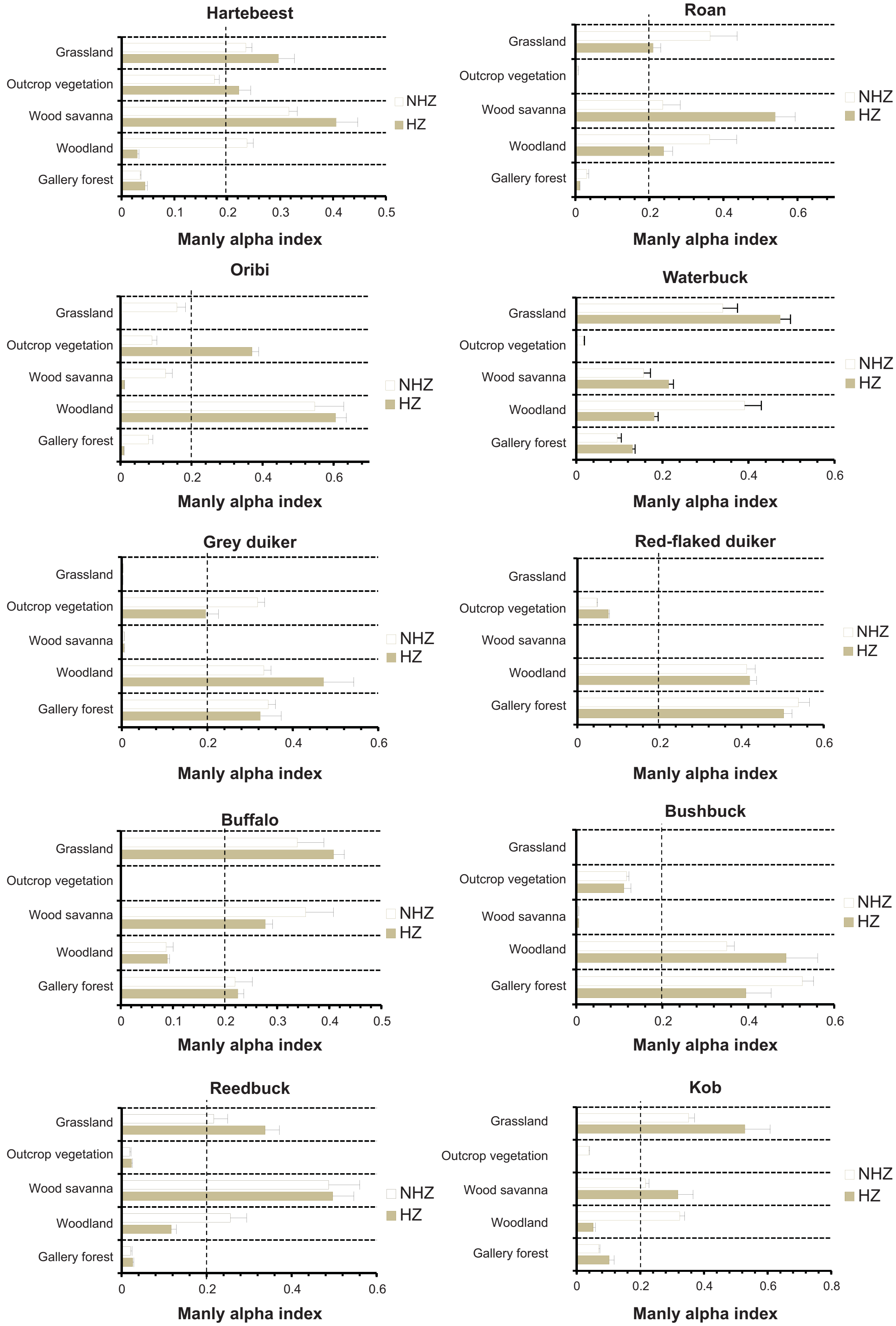

Figure 2. The habitat selectivity index of Manly's alpha was calculated for 10 bovid species in the hunting zone (HZ) and in the non hunting zone (NHZ). The dashed line at a value of 0.2 represents no preference for a habitat (this is the reciprocal of the number of available habitats).

Table 2. Goodness-of-fit of the generalized linear mixed model for the 10 species of ungulates recorded on the sampling quadrats. N refers to the number of the sampling quadrats where a given species was recorded as present. Goodness-of-fit refers to the significance of the model used for each species (see text for details). Distribution pattern of buffalo and oribi was not predicted by the GLMM (bold values).

			Goodness-of-fit	
English name	Scientific name	n	χ^2	p
Buffalo	*Syncerus caffer*	**489**	**245.35**	**0.097**
Roan	*Hippotragus equinus*	175	87.36	0.002
Bushbuck	*Tragelaphus scriptus*	82	38.94	0.001
Kob	*Kobus kob*	643	325.56	0.042
Waterbuck	*Kobus ellipsiprymnus defassa*	212	121.35	0.032
Oribi	*Ourebia ourebi*	**36**	**30.12**	**0.058**
Hartebeest	*Alcelaphus buselaphus*	145	58.78	0.023
Reedbuck	*Redunca redunca*	95	45.32	0.000
Red-flanked duiker	*Cephalophus rufilatus*	41	22.55	0.007
Grey duiker	*Sylvicapra grimmia*	68	35.61	0.006

As expected, grey duiker, red-flanked duiker and bushbuck didn't show any shift in habitat use among hunted and protected areas. Grey duiker and bushbuck are both known as flexible species, surviving in numerous anthropogenically-influenced habitats (Wilson 2001) and plasticity in habitat use may be a key to their survival, even in densely settled areas and urban surroundings (Wilson 2001).

We suggest that our analytical approach may be used to assess the extent to which a given management practice is affecting the habitat-relationships of wildlife by comparing changes in the habitat selectivity index of Manly's alpha among differently-managed areas. We suggest that this approach can be applied to study spatio-temporal changes in herbivore distribution in many other systems.

In addition to preferences exhibited by each bovid species for various habitat types, the resource selection by bovids was influenced on a small scale by factors such as habitat structure, landscape characteristics, and human disturbance. The distribution patterns of the smaller ungulate species (especially that of grey duiker, red-flanked duiker and bushbuck) were strongly affected by the habitat structure and landscape characteristics parameters, and by the variables 'canopy cover' and 'site humidity'. These results are consistent with previous findings suggesting that habitat features, particularly the amount of cover and proximity of water, have the potential to affect the habitat selection of small ungulates (Waltert et al. 2009). The smaller herbivores experience more predation pressure than larger herbivores (Sinclair et al. 2003), a likely explanation for their preference for more forested areas (poor forage but more secure habitats) than the open habitat (rich forage and risky habitats) as was noticed in the grey duiker, red-flanked duiker and bushbuck distribution. In addition, the parameter 'distance to hunting zone' was significantly negative in the best RSF model retained for grey duiker, suggesting their attraction to anthropogenically-influenced habitats. A similar result was found for the grey duiker in Kabo concession (northern Congo), suggesting the capability of grey duiker to change their behaviour in response to human disturbance (Mockrin 2009).

The distribution pattern of the large herbivores such as kob, hartebeest, reedbuck, roan and waterbuck was predicted by grass cover with preference for the open habitat, especially with low canopy cover. For these large species, predator avoidance (e.g. by hiding in dense vegetation or in higher grass) evidently played a lesser role (Creel and Winnie 2005). However, more detailed investigations are necessary to better understand the effect of vegetation coverage (grass and canopy) on the habitat preferences of ungulate herbivores. Not surprisingly, kob, waterbuck and reedbuck show a strong selection for areas close to natural ponds. These species are highly water-dependent and need to drink daily and forage close to sources of water (Estes 1991, Smitt 2011).

Table 3. Candidate models of 8 bovid species occurrence in the Pendjari Biosphere Reserve, with the number of parameters used (k), the Akaike information criterion (AIC) and the difference between each selected model (ΔAIC).

Species	Candidate models	k	AIC	ΔAIC
Bushbuck	CAC+ SLP+ DIR+ DIP	4	238.1	0
	CAC+ DIR+ DIRO+ SLP	4	238.2	0.1
	CAC+ SLP+ DIR+ DIP+ DIH	5	240	1.9
Kob	CAC+ GRC+ DIP+ DIH	5	1776.7	0
	CAC+ GRC+ SLP+ DIRO+ DIH	4	1779.0	2.3
	GRC+ SLP+ ROC+ DIR+ DIRO+ DIP	6	1780.1	3.4
Waterbuck	CAC+ GRC+ DIP+ DIH	4	658	0
	GRC+ DIRO+ DIP+ CAC	4	658.5	0.5
	CAC+ GRC+ SLP+ DIRO+ DIH	5	659.5	1.5
Roan	FIR_1 + GRC+ DIR+ DIH	5	554.1	0
	GRC+ SLP+ ROC+ DIR+ DIRO+ DIP	6	555.9	1.8
	CAC+ GRC+ SLP+ ROC+ DIR+ DIRO+ DIP	7	556.9	2.8
Hartebeest	GRC+ ROC+ DIR+ DIP	4	349.7	0
	CAC+ GRC+ DIP+ DIH	4	353.2	3.5
	CAC+ GRC+ SLP+ DIRO+ DIH	5	355.3	5.6
Reedbuck	GRC+ SLP+ ROC+ DIR	4	307.0	0
	GRC + DIP + DIH	3	308.1	1.1
	GRC+ CAC + DIP + DIH	4	309.6	2.6
Red-flanked duiker	CAC+ SLP+ DIR	3	140.4	0
	CAC+ DIR+ DIRO+ DIP	4	142.214	1.8
	CAC+ DIR+ GRC+ ROC+ DIP	5	4.3	3.9
Grey duiker	CAC + SLP+ DIR+ DIH	4	192.2	0
	CAC + SLP+ DIR	3	193.7	1.5
	CAC + SLP+ DIR+ DIRO	4	195.7	3.5

Table 4. Generalized linear mixed final model explaining bovid species distribution in Pendjari Biosphere Reserve, using the best model (AIC) with the levels of significance.

Species	Parameters	Estimates (β)	Standard error (±SE)	p-value
Bushbuck	Intercept	−9.629	8.945	0.048
	CAC	5.133	3.004	0.018
	SLP	−5.971	3.901	0.086
	DIR	−0.354	0.055	0.025
	DIP	0.081	0.040	0.031
kob	Intercept	−0.021	0.016	0.946
	CAC	0.941	0.376	0.012
	GRC	3.260	0.760	p<0.001
	DIP	−0.264	0.078	0.041
	DIH	0.140	0.028	p<0.001
Waterbuck	Intercept	−15.681	9.054	0.411
	GRC	6.414	2.142	0.094
	CAC	−3.859	1.062	0.048
	DIP	−0.826	0.049	0.034
	DIH	0.334	0.066	0.020
Roan	Intercept	−12.600	8.576	0.040
	FIR_1	2.959	5.087	0.023
	GRC	3.971	2.735	0.014
	DIR	1.015	0.615	0.032
	DIH	1.012	0.913	0.025
Hartebeest	Intercept	−11.756	3.149	0.092
	GRC	3.066	2.846	0.081
	ROC	2.658	1.004	0.062
	DIR	2.073	1.566	0.063
	FIR_1	1.169	0.490	0.030
Reedbuck	Intercept	−10.177	4.186	0.169
	GRC	7.609	4.642	0.002
	SLP	−0.201	0.055	0.018
	ROC	−1.149	0.301	0.063
	DIR	−2.267	1.872	0.007
Red-flanked duiker	Intercept	4.213	2.542	0.021
	CAC	2.145	0.756	0.008
	SLP	−1.803	1.012	0.013
	DIR	−1.030	0.752	p<0.001
Grey duiker	Intercept	−9.619	4.125	0.367
	CAC	1.125	3.569	0.002
	SLP	1.235	0.356	0.036
	DIR	−0.563	1.024	0.048
	DIH	−1.045	0.460	0.037

In contrast, hartebeest and roan selected areas further away from sources of water. Similar resource selection behaviour was found for the hartebeest and roan (Klop et al. 2007, Tyowua et al. 2009). There is evidence that a decrease in grazing pressure tends to occur when moving away from a water source. Natural pond avoidance was clearly noticed for the bushbuck in Pendjari Biosphere, in spite of their preference for humid areas. One possible explanation is that all of the natural ponds in the Pendjari Biosphere Reserve are located in the grassland with low canopy cover, which may be too risky for the species to use. We suspect that the interaction between canopy cover and site humidity played an important role in bushbuck habitat selection, accounting for their preference for gallery forest. The distribution pattern of buffalo and oribi was not predicted by the GLMM. Buffalos are highly gregarious and nomadic (Kingdon 1982, Estes 1991) and appear to randomly use the entire study area. This contrasts with the findings of Averbeck et al. (2009) who reported the distribution pattern of buffalo in Uganda to be predicted by site humidity. Also, oribi are known to occupy two major habitat types, namely open grasslands and wooded grasslands (McCann et al. 2006). These results need to be taken with some caution and more research with other resource selection functions may help to reveal what factors affect the distribution of oribi and buffalo in the Pendjari Biosphere Reserve and other areas.

Most importantly, our results suggest different land-use practices and approaches to wildlife management may cause the responses of a species to habitat to vary substantially, and this effect may differ substantially among relatively similar areas in terms of biota and climate. The implication is that applications of models like RSFs for conservation and management – especially those extrapolating distributions (Boyce and McDonald 1999) – may be limited, unless factors contributing to model variation are recognized and accommodated. Although the use of pellet group counts as an indicator of habitat use has been criticized (Collins and Urness 1981), when specifically compared to other methods like radio-telemetry to infer the habitat use patterns of ungulate species, it has been found that the results are similar (Guillet et al. 1995). Furthermore, other authors (Loft and Kie 1988, Edge and Marcum 1989) have found that pellet group counts accurately indicate which habitats receive the greatest and least amount of use.

In conclusion, our results indicate that bovid species are influenced by a range of factors operating at different scales. In particular, they indicate that the risk of hunting may significantly alter habitat selection in African bovids. In line with Averbeck et al. (2012) who revealed monitoring grouping patterns as tool in detection of negative effects of human activities on gregarious species, this study also highlights that monitoring resource selection function of bovids can be a powerful tool to detect potentially-negative effects of human activities on those ecologically and economically-important species. As one of the first studies of bovid habitat relationships in west Africa, our results provide insights but there is a need for follow-up studies that explore the mechanisms behind these observed patterns. Future studies could attempt to use fine-scaled movement data (e.g. from GPS collars) combined with finer-scaled map data (data which was not available to us) to identify in detail the response to variation in habitat factors and the critical limits at which selection and avoidance occur.

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