Fire and grazers in the West African savanna
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Citation
Klop, L. F. (2009, September 3). *Fire and grazers in the West African savanna*. Retrieved from https://hdl.handle.net/1887/13947

Chapter 4

Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna

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Published in:

Wildlife Research 34: 77–83 (2007)

ABSTRACT

The preference of grazing herbivores to feed on grass regrowth following savanna fires rather than on unburned grass swards is widely recognised. However, there is little information on which factors govern patterns of resource selection *within* burned areas. In this study, we attempted to disentangle the effects of different habitat and grass sward characteristics on the utilisation of post-fire regrowth by nine species of ungulates in a fire-dominated woodland savanna in north Cameroon. We used resource-selection functions based on logistic regression. Overall, the resource-selection functions identified the time elapsed since burning as the most influential parameter in determining probability of use by ungulates, as most species strongly selected swards that were recently burned. This pattern is most likely related to nutrient levels in the grass sward. In addition, most species selected areas with high grass cover and avoided grass swards with high amounts of dead stem material. This is likely to increase bite mass and, hence, intake rates. The avoidance of high tree cover by some species may suggest selection for open areas with good visibility and, hence, reduced risk of predation. Body mass seemed to have no effect on differential selection of post-fire regrowth, irrespective of feeding style.

4.1 INTRODUCTION

Burning of savanna grasslands is a widespread phenomenon throughout Africa. Up to 50% of the African savannas are burned annually (Hao & Liu 1994), comprising a total burned area of 5 – 10 million square kilometres (Van de Vijver 1999). One of the main purposes of burning grasslands is to stimulate new regrowth for wildlife and livestock (Whelan 1995, Kull 2004). Various studies have shown that herbivores are attracted to post-fire regrowth (e.g., Moe *et al.* 1990, Wilsey 1996, Moe & Wegge 1997, Gureja & Owen-Smith 2002; Tomor & Owen-Smith 2002, Archibald & Bond 2004, Archibald *et al.* 2004), which is likely to be the result of improved quality of the grass sward.

Since fires can significantly alter forage quality and availability, the intensity and spatial distribution of grazing is likely to be affected (Archibald & Bond 2004). Fires may have a homogenising effect on the vegetation (Hobbs *et al.* 1991), by replacing the mosaic of grazed and ungrazed patches in the grass sward by a more homogeneous sward of post-fire regrowth (Hobbs *et al.* 1991, Archibald & Bond 2004). Because of the relative uniformity of the burned grass sward, Archibald and Bond (2004) suggested that grazing herbivores utilize burned areas more evenly than unburned grass swards. Their hypothesis was supported by a more dispersed pattern of grazer sightings on burned areas compared to unburned areas in a South African savanna (Archibald & Bond 2004). However, the generality of their findings is far from clear, as many different factors may be responsible for the selection of post-fire regrowth by herbivores. Firstly, burned areas may show local heterogeneity in the structure and nutrient contents of the grass sward as a result of e.g. differences in fire intensity or local topography (Klop & Van Goethem, unpubl. data). Spatial variation in forage quality may be reflected in resource selection patterns of herbivores (e.g., Edwards *et al.* 1994), which may lead to uneven patterns of foraging intensity (Drescher 2003, Derry 2004). Secondly, besides the effects of forage quality, the extent to which burned grasslands are selected by herbivores may also be influenced by habitat factors such as distance to water sources, landscape region, and vegetation cover (Gureja & Owen-Smith 2002; Tomor & Owen-Smith 2002). Thirdly, the selection of post-fire regrowth by herbivores may be governed by species-specific parameters such as body mass, whereby selection of burned grassland may decrease with increasing size (Wilsey 1996; but see Tomor & Owen-Smith 2002). Finally, factors like increased visibility and predator avoidance may play a role in the use of burned grasslands (Moe & Wegge 1997). All these factors may act independently or interact with each other.

Understanding the response of grazers to fires is essential for the conservation and management of savannas and other rangelands. However, although the preference of herbivores for post-fire regrowth compared to unburned vegetation is well documented (see references above), there is little information on which factors govern patterns of resource selection *within* burned areas. This lack of information is especially apparent for the Guinea-Sudan savanna zone of West Africa. The goal of our study is to identify those factors that correlate with patterns of resource selection within burned areas. Thus, we attempt to answer the following questions: a) which factors may govern resource selection patterns by ungulates on post-fire regrowth, and b) what is the influence of body mass on these selection patterns?

4.2 METHODS

Study area

This research has been carried out in Bénoué National Park (1,800 km^2), north Cameroon. Annual rainfall ranges from 1,200 to 1,500 mm with a dry season from November to April. The vegetation can be classified as Guinea-Sudan savanna where major vegetation types include *Isoberlinia doka* woodland savanna, open savanna with dominance of *Terminalia laxiflora*, *T. macroptera*, *Burkea africana* and *Detarium microcarpum*, and *Anogeissus leiocarpus* riparian forests (Stark & Hudson 1985). Management burning is restricted to the dry season, with most fires occurring from November to February. A total number of 20 fires were recorded during the dry season of 2003 – 2004, burning about 85% of the park area (Klop & Van Goethem, unpubl. data).

Data collection

The collection of data followed a standardised resource selection study design (see Manly *et al.* 2002). Habitat characteristics have been randomly sampled for the entire study area and used resource units were measured at population level (i.e., sampling protocol A, design I; *sensu* Manly *et al.* 2002). In this study only animal observations and randomly sampled habitat characteristics on post-fire regrowth are considered. The data were collected by driving transects, ranging in length between 24 and 36 km. Care has been taken to select routes covering different areas and habitats, and at different distances from the Bénoué river, which is the main water source in the park. Transects were traversed by car using two observers and a driver. Data collection started in December 2003 and ended in May 2004. All transects were traversed at regular 18-day intervals, each transect being sampled nine times.

For each animal or group of animals observed along a transect, the species, sex, herd size, and behaviour were recorded. We classified the observed animals as a) grazers with more than 80% grass in their diet, b) mixed feeders with 20-80% grass in their diet, and c) browsers with less than 20% grass in their diet. Global Positioning System (GPS) bearings were taken on the location where the animals were observed. In addition, the following habitat characteristics were estimated: position along the catena (flat terrain, lower slope, middle slope, upper slope, hilltop), cover of trees (>6 m), cover of shrubs (<6 m), grass cover, and grass sward height. All cover data were measured as the vertical projection onto the ground and were visually estimated by one observer. The height of the burned grass sward was calculated as the average height of ten randomly chosen individual grasses at the place where the animals were seen.

For each animal observation the date of burning and the amount of dead grass stems remaining after the fire were recorded. The burning dates were obtained from the park management and were later transformed into the time elapsed since burning (measured in days) for each observation. The amount of dead grass stems remaining gives an *a posteriori* indication of the fire intensity, since fires of low intensity remove less vegetation biomass than fires of high intensity. Thus, after a low intensity fire, the grass sward will be a mix of new regrowth and old grass stems which were not properly burned by the fire. In contrast, after a high intensity fire, the grass sward will mainly consist of regrowth, with very few dead stems remaining. The amount of dead stem material in the sward was estimated using a board of 1 m^2 on which a checkerboard pattern of white and red squares of 20 x 20 cm was painted. The board was placed vertically on the ground at the place where the animals were observed. At a distance of 10 m the percentage of the board covered by dead stems was estimated. Three height classes were distinguished: 0-20 cm, 20-60 cm and 60-100 cm from ground level. All GPS locations were projected onto a satellite image using a geographic information system in order to calculate the distance to the Bénoué river (in km) for each observation. All distances were rounded to 10 m.

Besides measuring the abovementioned resource characteristics for each animal observation, the same parameters were also measured on randomly chosen locations on burned areas in the study area, independent of the presence of animals (following sampling protocol A, see Manly *et al*. 2002). For each transect during each field period, three sets of randomly generated numbers (between zero and one in six decimals) were generated using a spreadsheet program. The number of these random numbers was chosen to be equal to the number of animal observations recorded before along that same transect. The random numbers in the first set were multiplied by the length of the transect in order to obtain the place (distance from starting point) along the transect line for recording the data. The numbers in the second set were converted into either 'left' or 'right' (each having a 50% possibility) to indicate at which side of the transect the habitat characteristics should be measured. Finally, the numbers in the third set were multiplied by 100 to obtain the distance from the transect line where the measurements should be taken. A maximum distance of 100 m was chosen, based on the visibility in the habitats of Bénoué N. P. since most animals were recorded within 100 m from the transect line. No random locations were measured during the periods of December and January.

The structure and quality of the burned grass sward were monitored in a separate study in the same area. At regular 18-day intervals, the grass on five randomly located squares (4 m^2) was clipped on a burned site in the study area. Grass samples were air dried, separated into leaf and stem material, and live (green) and dead (yellow) material, and subsequently weighed. Green leaf material was analyzed for nutrient concentrations after a modified Kjeldahl destruction. Digestibility was measured according to the method of Tilley and Terry (1963).

Data analyses

The relative importance of each habitat characteristic on the use by a particular species has been analysed using resource selection functions (RSF; Manly *et al*. 2002) based on logistic regression. Here the response variable is binary (i.e., used or not used), and the probability that a resource unit is used by a particular species is modelled as:

$$g(x) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \dots$$

where $g(x)$ is the probability of use, β_0 is the constant (intercept), and β_i is the partial regression coefficient for variable X_i, holding all other remaining predictors constant (Quinn & Keough 2002). The predictor variables are the habitat characteristics mentioned above. The categorical variable 'position along the catena' was converted into dummy variables, using the first dummy variable (i.e., flat terrain) as reference category to which the other categories are compared. Since g(x) is not guaranteed to be proportional to true probability of use in use-availability designs (Keating and Cherry 2004), we do not intend to model resource selection using g(x). Rather, as stated in the introduction, we use logistic regression to identify those factors that are most strongly correlated with the selection of burned areas. 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 (i.e., with the constant only). Significance of the individual coefficients was calculated based on Wald statistics (see Quinn & Keough 2002). The relative importance of each predictor variable is quantified by the odds ratio, i.e., the change in utilization probability with respect to a one unit change in a specific predictor variable. The odds ratio is calculated as e^{β} where β is the coefficient for an individual predictor variable. Although interpretation of the odds ratio may assume a linear response to the measured variable, which may not always be realistic in our study, it is a good indicator of relative importance of a specific variable (Quinn & Keough 2002).

Collinearity among the predictor variables was investigated by examining the Pearson correlation coefficients between the measured variables (see Table 1). Only the first height class (i.e., 0-20 cm) of the amount of dead stem material was incorporated in the analyses because of high correlations between the height classes (i.e., with $\rho > 0.60$). The correlations between all other variables are very low (i.e., mostly with $\rho < 0.20$) (see Table 1).

Table 1. Correlation between the measured variables. Pearson's correlation coefficients are shown, with associated significance levels where * significant at 0.05 level, ** significant at 0.01 level.

	Time since	**Place along**	**Dead stems**	**Dead stems**	**Dead stems**	**Grass cover**	**Shrub cover**	**Tree cover**	**Grass height**
Distance to river	-0.23	-0.109**	0.037	0.046	0.063*	0.026	0.107**	0.122**	0.315**
Time since burning		0.141**	-0.118**	-0.021	0.027	0.120**	0.029	0.088**	0.201**
Place along catena			-0.038	-0.038	-0.020	-0.032	-0.061*	0.087**	-0.036
Dead stems 0-20 cm				0.816**	0.636**	-0.014	-0.024	0.040	0.159**
Dead stems 20-60 cm					0.819**	-0.025	-0.025	-0.001	0.131**
Dead stems 60-100 cm						-0.034	0.003	0.006	0.109**
Grass cover							-0.039	-0.187**	0.226**
Shrub cover								0.047	0.079**
Tree cover									0.211**

4.3 RESULTS

The transects resulted in a total of 767 observations for eleven mammal species (see Table 2), and an additional 467 random observations. The goodness-of-fit of the RSF models for these eleven species is presented in Table 2. For all species except waterbuck and Derby's eland the RSF models are significant. In Table 3 the logistic regression coefficients are presented for all measured parameters.

The coefficients for the parameter 'position along the catena' are not presented because of space constraints. However, the position along the catena is generally not of much influence, as we found no significant effect of this parameter for any of the species. The data for waterbuck and Derby's eland are omitted since the RSF models are not significant for these species.

Table 2. The 11 species of ungulates recorded during the transects. Body mass data are taken from Kingdon (1997) and refer to the average weight of male and female. Note that the Hartebeest subspecies *major* can reach much higher body mass (228 kg; Estes 1991) than the nominate. Guild refers to grazer (G) or browser (B). *n* refers to the number of observations during the transects. Goodness-of-fit refers to the significance of the RSF functions for each species (see text for details).

English name	**Scientific name**	**Body mass (kg)**	**Guild**	***N***	**Goodness-of-fit**		
					χ^2	**df**	***P***
Red-flanked duiker	*Cephalophus rufilatus*	10.0	B	60	32.76	11	0.00
Oribi	*Ourebia ourebi*	17.0	G	86	56.17	11	0.00
Common duiker	*Sylvicapra grimmia*	17.5	B	44	41.51	11	0.00
Bohor reedbuck	*Redunca redunca*	47.0	G	9	36.05	11	0.00
Bushbuck	*Tragelaphus scriptus*	48.5	B	36	24.15	11	0.01
Warthog	*Phacochoerus africanus*	82.5	G	11	22.67	11	0.02
Kob	*Kobus kob*	85.8	G	437	215.66	11	0.00
Western hartebeest	*Alcelaphus bucelaphus major*	161	G	47	51.74	11	0.00
Defassa waterbuck	*Kobus ellipsiprymnus defassa*	215	G	11	12.29	11	0.34
Roan	*Hippotragus equinus*	261.3	G	22	34.78	11	0.00
Derby's eland	*Taurotragus derbianus*	539.3	B	4	9.95	11	0.54

The effects of the distance to the Bénoué river vary with the species. Kob show significant negative selection ($P<0.01$) for this parameter, or stated otherwise, kobs significantly prefer areas close to the river. In contrast, warthog, hartebeest and roan show significant positive selection for distance to river. The odds ratio for kob for distance to river is 0.88, indicating that for a one unit (i.e., 1 km) increase in distance to the river there is a decrease of 12% in probability of use by kob. The mean distance to the river where animals were observed is 4.6 km (SD=5.8).

Table 3. Results of the resource selection functions for the different species during the dry season. For each species, the regression coefficient ± 1 standard error are shown. The parameter 'position along the catena' has been omitted (see text). * significant at 0.05 level, ** significant at 0.01 level.

Species	**Distance to river**	**Time since burning**	**Dead stems**	**Grass cover**	**Shrub cover**	**Tree cover**	**Grass height**
Red-flanked duiker	-0.021 ± 0.023	-0.018 ± 0.005 **	-0.033 ± 0.013 **	0.032 ± 0.025	0.022 ± 0.012	0.016 ± 0.008	0.062 ± 0.034
Oribi	0.008 ± 0.020	-0.019 ± 0.004 **	-0.032 ± 0.011 **	0.046 ± 0.025	0.006 ± 0.012	-0.019 ± 0.011	-0.081 ± 0.040 *
Common duiker	0.030 ± 0.024	-0.023 ± 0.005 **	-0.012 ± 0.010	0.101 ± 0.026 **	-0.009 ± 0.017	0.007 ± 0.011	-0.055 ± 0.046
Bohor reedbuck	0.057 ± 0.069	-0.022 ± 0.014	-0.028 ± 0.035	0.141 ± 0.049 **	-0.049 ± 0.071	-0.188 ± 0.144	-0.084 ± 0.119
Bushbuck	-0.053 ± 0.032	-0.015 ± 0.006 *	-0.016 ± 0.012	0.008 ± 0.041	0.029 ± 0.014 *	0.032 ± 0.009 **	0.014 ± 0.045
Warthog	0.109 ± 0.046 *	0.017 ± 0.013	-0.082 ± 0.058	-0.061 ± 0.072	-0.002 ± 0.026	-0.006 ± 0.022	0.041 ± 0.056
Kob	-0.126 ± 0.018 **	-0.016 ± 0.002 **	-0.032 ± 0.006 **	0.071 ± 0.016 **	-0.017 ± 0.010	-0.017 ± 0.006 **	-0.055 ± 0.025 *
Hartebeest	0.086 ± 0.026 **	-0.021 ± 0.005 **	-0.026 ± 0.015	0.078 ± 0.026 **	0.020 ± 0.015	-0.037 ± 0.018 *	-0.066 ± 0.049
Roan	0.088 ± 0.034 **	-0.024 ± 0.008 **	-0.087 ± 0.038 *	0.017 ± 0.050	-0.001 ± 0.026	-0.032 ± 0.021	-0.059 ± 0.061

The mean time since burning for sites where animals were observed is 87.5 days (SD=44.4). However, nearly all species show strong negative selection for the parameter time since burning, i.e., most species significantly prefer grass swards that are recently burned. The avoidance of older regrowth is significant for bushbuck ($P<0.05$), red-flanked duiker, oribi, common duiker, kob, hartebeest and roan (all with $P<0.01$). For all these species a one-day increase in regrowth age corresponds to a decrease in probability of utilization of around 2%.

Most species strongly avoid areas with high amounts of dead stem material. This avoidance is significant for red-flanked duiker, oribi, kob (all with $P<0.01$), and roan ($P<0.05$). For kob, an increase in the amount of dead stem material by one percent results in a decrease in utilization probability of 3%. Similarly, the decrease in probability of use is 3% for both red-flanked duiker and oribi, and 8% for roan as the amount of dead stem material increases by one percent.

Grass cover is significantly selected for by common duiker, bohor reedbuck, kob and hartebeest (all with $P<0.01$). A one percent increase in grass cover results in an increase in probability of use of 7% for kob, 8% for hartebeest, 11% for common duiker and 15% for bohor reedbuck. Bushbuck is the only species for which shrub cover significantly contributes to model prediction ($P<0.05$). Tree cover is significantly avoided by kob ($P<0.01$) and hartebeest ($P<0.05$), but preferred by bushbuck ($P<0.01$). One percent increase in tree cover results in a decrease in utilization probability of 2% for kob and 4% for hartebeest, but an increase of 3% for bushbuck. Grass height is significantly negatively selected by oribi and kob (both with $P<0.05$). The decrease in probability of use by oribi is 8% and 5% by kob, given a one unit (i.e., 1 cm) increase in grass height.

No significant correlation between body mass and the odds ratios for distance to river (grazers: $\rho=0.23$, $P=0.71$; browsers: $\rho=-0.65$, $P=0.55$) or time since burning (grazers: $\rho=0.03$, $P=0.97$; browsers: $\rho=0.70$, $P=0.50$) could be found. Likewise, body mass did not correlate significantly with selection for grass height (grazers: $\rho=0.17$, $P=0.78$; browsers: $\rho=-0.10$, $P=0.94$) or any of the vegetation cover parameters, i.e., amount of dead stem material (grazers: $\rho=0.04$, $P=0.94$; browsers: $\rho=0.46$, $P=0.70$), grass cover (grazers: $\rho=-0.04$, $P=0.95$; browsers: $\rho=-0.54$, $P=0.64$), shrub cover (grazers: $\rho=0.48$, $P=0.42$; browsers: $\rho=0.50$, $P=0.67$), and tree cover (grazers: $\rho=0.24$, $P=0.70$; browsers: $\rho=0.86$, $P=0.34$).

4.4 DISCUSSION

Overall, the resource selection functions identify the time elapsed since burning as the most influential parameter in determining probability of use by ungulates. That is, seven out of nine species significantly select grass swards that are recently burned. In addition, the parameters distance to river, the amount of dead stem material in the grass sward, and grass cover all give significant results for four species, although the parameter distance to river has opposite effects on different species.

The selection of recently burned swards is probably due to a selection for high nutrient levels. Young regrowth is known to contain higher nutrient levels than unburned living vegetation (see e.g. Van de Vijver *et al*. 1999 and references therein). Levels of nitrogen (N) and other nutrients may decrease sharply, however, and fall back to the levels of unburned vegetation in 1.5 – 3 months time (Van de Vijver *et al*. 1999). This may be well below maintenance levels of the herbivores (see Prins 1996). Ruminants need a minimum of 5 – 7% crude protein in their food to maintain body weight, which corresponds with N concentrations of 0.8 – 1.1% (Prins 1996). Although no data on nutrient levels were directly incorporated into the RSF analyses, temporal trends in grass quality and structure were monitored in a separate study in the same area. To illustrate which grass sward parameters might relate to the decrease in probability of use as regrowth gets older, Figures 1a-d show the relation between the extent to which kob selects regrowth of a particular age, and temporal trends in nutrient levels, sward structure, and digestibility. There seem to be no clear relations between selection and parameters of sward structure (leaf:stem ratios, live:dead ratios, green leaf bulk density), digestibility, and the levels of phosphorus, calcium and magnesium. However, the patterns in Fig. 1a suggest that there might be a relation between selection and levels of nitrogen and potassium. Thus, the apparent avoidance of old regrowth may be related to lower levels of N and K in the grass sward.

Areas with high amounts of dead stem material, which is a result of low fire intensity, are significantly avoided by four out of nine species. The presence of stems and dead material in the grass sward can negatively affect access and bite mass of a grazing herbivore (Prins 1996, Drescher 2003). Bite mass is one of the main determinants of intake rate (Spalinger & Hobbs 1992, Hobbs *et al*. 2003) and is determined by both morphology of the mouth (Illius & Gordon 1987, Gordon & Illius 1988) and characteristics of the grass sward (Laca *et al*. 1992, Jiang & Hudson 1994). The relation between structure of the grass sward and functional response has been studied extensively by Drescher (2003). Increasing the amount of dead stems in the sward depresses intake rates and may even change the shape of the functional response curve, i.e., from type I to type II (Drescher 2003). In contrast, an increase in grass cover can significantly increase bite size and hence, intake rates. Not surprisingly, the odds ratios are high for

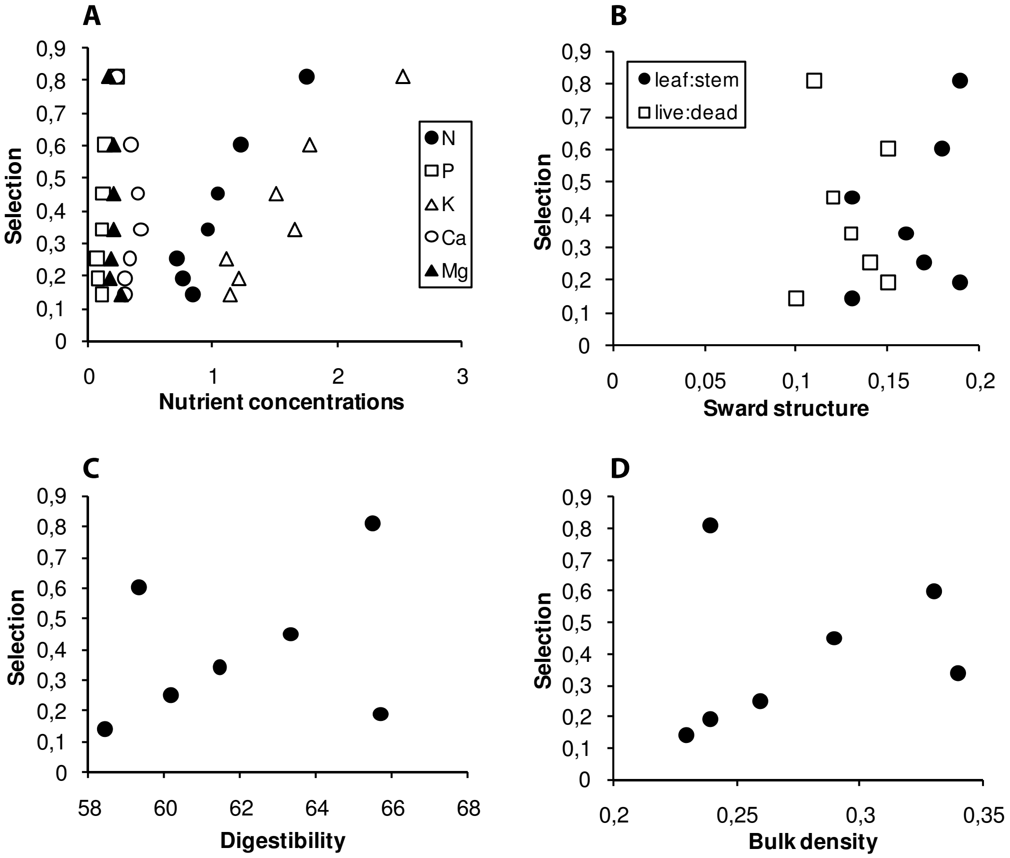

Fig. 1. Scatterplots showing the relationship between temporal patterns in regrowth quality and the extent to which kob selects regrowth of a specific age. Measurements of sward characteristics were taken on Days 13, 32, 49, 67, 85, 103 and 121 after burning. Each marker in the plots represents the degree of selection on one of these dates. Selection is calculated as $x = y^z$ where y = the odds ratio for time elapsed since burning, z = the number of days since burning, and x = degree of selection. (a) Selection versus concentrations (as a percentage) of nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg) and calcium (Ca). (b) Selection versus leaf:stem ratios and live:dead ratios. (c) Selection versus percentage dry matter digestibility. (d) Selection vs. green leaf bulk density, expressed as the amount of green leaf biomass per unit volume (g dm^{-3}).

grass cover. For example, an increase in grass cover by one percent increases the odds by about 7% in utilization by kob, and even 15% for bohor reedbuck.

The negative selection for grass height by oribi and kob may be the result of the fact that a higher grass sward is also older and of lower quality. The animals may then select younger grass swards which still contain most of the nutrients at an acceptable level. However, only a weak (albeit significant) correlation was found between the parameters grass sward height and time since burning (see Table 1). Grazers like kob and oribi may also select shorter grass swards because of the effects of grazing itself on the quality and structure of the grass sward (see e.g. McNaughton 1984, Fryxell 1991). During the growing season, heavily grazed grass swards of low height and biomass have been shown to be nutritionally superior to ungrazed swards (Verweij *et al.* 2006). However, it remains unclear how grazing on burned swards during the dry season may affect sward quality and hence, herbivore resource selection.

In contrast to Gureja and Owen-Smith (2002), we did not find an effect of topography on resource selection patterns. In their study, the differential use of landscape regions seemed to be related to gradients in grass height along the catena (Gureja & Owen-Smith 2002). However, no relation between grass height and place along the catena was found in our study (Table 1). The selection of post-fire regrowth by browsers like red-flanked duiker and bushbuck may be explained by the fire-induced sprouting of several species of forbs and trees. During extensive observations of grazing behaviour in 2003, the two species of duikers and bushbuck have regularly been observed browsing on newly sprouted forbs in burned areas (Klop & Van Goethem unpubl. data). In addition, although bushbuck is classified as a browser, it is known to graze on regrowth following fires (Estes 1991).

Not surprisingly, kob show a strong selection for areas close to the Bénoué river. This species is highly water-dependent and needs to drink daily (Estes 1991). In contrast, warthog and roan select areas farther away from the river. Moving away from a water source, grazing pressure tends to decrease but the energetic costs associated with travel to that water source will increase (Derry 2004). Thus, animals may balance forage intake against energetic costs for travel (Derry 2004). It seems likely that this trade-off may be influenced by the water-dependency of a particular species, which might explain the patterns shown by kob versus warthog and roan. However, based on the results from computer simulations, Derry (2004) suggested that animals are not distributed according to their water requirements. In addition, the energetic costs of travel could not explain the spatial extent of the foraging range (Derry 2004). Instead, intake constraints and available foraging area might be more important in explaining the distribution of animals around water sources (Derry 2004).

Besides selection for high quality forage, ungulates may also select burned areas because of improved visibility and hence, reduced risk of predation (Moe & Wegge

1997). The data show avoidance of high tree cover by kob and hartebeest, which may be the result of selection for areas with high visibility. The strong avoidance of areas with high amounts of dead stem material may also to some extent be explained by anti-predator behaviour, since these dead stems obscure visibility. However, while the visibility on burned areas remains the same throughout the dry season, resource selection patterns are strongly influenced by time as regrowth is getting older. Thus although predator avoidance may be one of the determinants of post-fire regrowth use, it may be overridden by the selection for young regrowth.

Wilsey (1996) suggested that the selection of post-fire regrowth by herbivores may be governed by body weight. His hypothesis reflects the fact that larger species have longer gut retention times than smaller species, allowing better digestion of low quality food (Van Soest 1982, Demment & Van Soest 1985, Prins & Olff 1998; but see Gordon & Illius 1996). Since small herbivores need higher quality food than large species, it would be expected to find large species to be less restricted to recently burned sites or areas with low amounts of dead stem material. However, the body mass of neither grazers nor browsers seemed to have any effect on the selection of post-fire regrowth, as no significant correlation could be found between body mass and any of the odds ratios for the abovementioned parameters. However, any pattern may be obscured by low sample sizes (n=5 for grazers and n=3 for browsers).

Our results show that resource selection by herbivores on post-fire regrowth is not uniform, which was suggested by previous research (see Archibald & Bond 2004). Instead, local differences in regrowth age, amount of dead stem material, grass cover, and the distance to water sources may result in a patchy use of burned areas. Although in our study we focused on wild bovids, our results are likely to be valid for livestock in semi-natural environments as well. Knowledge of the response of grazers to burning is thus essential for the management and conservation of rangelands worldwide.

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