Seasonal Variation in the Selection and Use of Habitats by Large Herbivores at Mole National Park, Ghana

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Abstract

There is scanty information on herbivore habitat ecology at Mole National Park (MNP) despite the fact that understanding habitat interactions, such as habitat selection and use, by large herbivores is fundamental for its management. Our aim was to determine the effects of seasonal variation on habitat selection and use by large herbivores at MNP, Ghana. Eight large herbivores were counted within transects, located in six habitat types, over one year and Jacobs' selectivity index was used to calculate their selectivity of the habitat types. Six of the eight herbivores maintained their preferred habitats throughout all seasons or showed unpredictable seasonal pattern of habitat selectivity, but a seasonal change was clear for elephant (*Loxodonta africana*) and buffalo (*Syncerus caffer*). Elephant shifted from riverine forest to swamp habitats in the dry season but preferred both riverine and swamp in other seasons. Buffalo selected and used *Anogeissus* in all seasons but used swamp in the rainy season and riverine forest in the fire season. Kob (*Kobus kob*), warthog (*Phacochoerus africanus*) and bushbuck (*Tragelaphus scriptus*) appeared to minimise predation risk by avoiding the open savanna, waterbuck (*Kobus defassa*) preferred swamp in all seasons, whereas roan antelope (*Hippotragus equinus*) and hartebeest (*Alcelaphus bucelaphus*) avoided swamp. All eight herbivores were less selective in the rainy season and more selective in the fire season. Shrinkage of habitat resources by fire increased selectivity, while post-fire regrowth in the rainy season increased forage resources and reduced selectivity. Of the factors that influenced the seasonal patterns of herbivore selectivity, only fire can be addressed by National Park management policies, particularly to determine which habitat types should be the focus of fire control operations.

Introduction

Landscape structure and plant community composition are key ecological factors that determine large-scale mammalian species distribution; these interact to produce the various habitat types that drive species' preferences. In particular, the extent and suitability of forage can determine the patterns of herbivore selection and habitat use which, in turn, influence the distribution and abundance of their predators (Fahrig, 2003). Therefore, the formulation of wildlife conservation and management strategies requires reliable data and information on herbivore habitat selection and use.

There has been little research into the ecology of mammals in Ghanaian national parks, such as Mole National Park (MNP). The limited data are on population trends and status of lions (Burton et al., 2010), the cost of raids caused by wildlife around MNP (Dakwa, 2016a), Allometry in sympatric grazers at MNP (Dakwa, 2016b), Climate and land cover changes at MNP (2018a), Abiotic and anthropogenic factors affecting the distribution of some herbivores (2018b) and Species-packing of large herbivores (Dakwa, 2019).

Thus, there is scanty information on herbivore habitat ecology despite the importance of understanding the role of landscape structure in determining herbivore distribution and abundance. Understanding how habitat selection is influenced by foraging requirements and predation risk is fundamental to evaluating the patterns of abundance and distribution of herbivores. This depends upon isolating and measuring vegetation characteristics in different habitats and relating them to the number of herbivores or the presence/absence of herbivores (Jacobs, 1974; Ben-Shahar & Skinner, 1988).

Our objective was to test the hypothesis that there are clear patterns of habitat selection and use because of habitat heterogeneity and the impact of distinct seasonal variation in the habitats, and that patterns of habitat selection and use differ with the seasons because of variation in forage availability.

Materials and Methods

Study Area

MNP (Figure 1a) is located in northwest Ghana (9° 11'' and 10° 10'' N ; 1° 22'' and 2° 13'' W); and covers a land area of about 4,840 km^2 (Anon., 2011). There are six main habitat types: (i) *Anogeissus* with *Vitellaria paradoxa* (*Anogeissus*), (ii) boval vegetation (*Loudetiopsis kerstingii-Polycarpaea tenuifolia* community on rocky substrates (Boval), (iii) *Burkea-Terminalia* with *Detarium microcarpum* (BTD), (iv) *Burkea-Terminalia* with *Vitellaria paradoxa* (BTV), (v) riverine forest (Riverine), and (vi) swamp (Swamp) (Schmitt & Adu-Nsiah, 1993) (Figure 1b and Table 1). We refer to *Anogeissus*, BTD and BTV collectively as Open Savanna. MNP has >93 mammal species: the main large mammals are elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*), kob (*Kobus kob*), bushbuck (*Tragelaphus scriptus*), warthog (*Phachocoerus africanus*), Defassa waterbuck (*Kobus defassa*), roan (*Hippotragus equinus*)

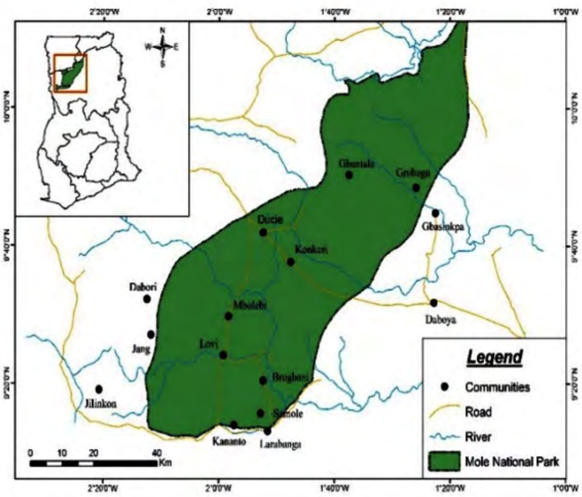

Figure 1a. Location of Mole National Park in Ghana showing some communities
Source: Dakwa (2016c)

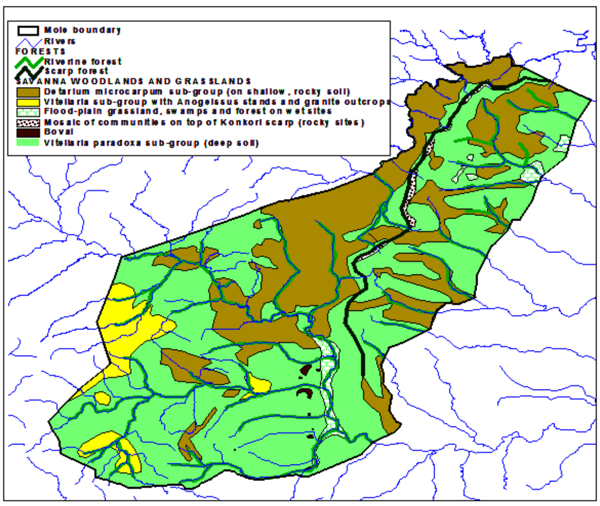

Figure 1b: Mole National Park showing key habitat types
Source: Anon (2011)

TABLE 1
Descriptions of the habitat types in the study areas

Habitat	Description
Anogeissus	Open savanna woodland found on granite outcrops. Dominant species is *Anogeissus* sp.
Boval	All plant communities on flat iron pans with patches of shallow soil. Mainly annuals when flooded and species-rich during the rains and subject to extreme water-stress during the dry season. Dominant species are *Loudetiopsis kerstingii* and *Polycarpaea tenuifolia*
BTD	Open savanna woodland confined to shallow and rocky soils. Dominant species are *Burkea* sp. and *Terminalia* sp., with *Detarium microcarpum*
BTV	Open savanna woodland comprising all savanna woodland on well-drained and often deep soils. Dominant species are *Burkea* sp. and *Terminalia* sp., with *Vitellaria paradoxa*
Riverine	Found along most of the rivers. It often forms bands of generally dense and species-rich forests of up to 38m in height
Swamp	Waterlogged areas, usually lowlands

Source: Anon. (2011)

TABLE 2
Different seasons at Mole National Park

Season	Description	Period
Dry	Harmattan* with low humidity	October - December
Fire	Dry harmattan* with low humidity; windy	January - April
Rainy	Heavy rains with lightning and thunder	May - July
Flood	Light rains; lowlands are flooded.	August - September

*Harmattan is a seasonal dry, dusty easterly or north-easterly wind.
Source: Dakwa (2016c)

and hartebeest (*Alcelaphus bucelaphus*). The park has an annual seasonal cycle of dry, fire, rainy and flood seasons (Table 2).

Data Collection

We used 16 strip transects 200 m wide, 100 m either side of the central line and of varying lengths, along existing roads and paths traversing the main habitat types and 20 point transects, measuring 500 x 500 m to count eight large herbivores - elephant, buffalo, roan antelope, waterbuck, hartebeest, kob, warthog and bushbuck – in the dry, fire, rainy and flood seasons at MNP. The point transects were distributed to ensure as much spatial representation as possible in the study area. A non-parametric Mann-Whitney test found no significant difference between strip and point count methods (Dakwa, 2016b) and so selectivity estimates derived from the two methods were treated as equivalent.

The large herbivores were counted by driving strip transects at a speed of 20 km/hr, or walking point transects, between 07.30-10.30 GMT and 16.00-18.00 GMT, when herbivores are active, at least twice each season (Table 2) between September 2013 and August 2014. There was no significant difference between morning and evening counts and this is consistent with previous studies (Groom & Harris, 2010; Dakwa, 2016b) and so both were used to estimate selectivity and use of the various habitat types.

Selectivity of habitat use by the large herbivores

Selectivity of the six habitat types by herbivores was calculated using Jacobs (1974) selection index, E, as described by Gordon (1989):

$$E = (U_i - A_i) / \{(U_i + A_i) - 2 (U_i \times A_i)\} \quad \ldots\ldots\ldots (1)$$

where, U_i is the proportion of sightings in habitat *i* and A_i is the proportion of the study area occupied by habitat *i*. *E* is defined as the relative difference between use and availability of a habitat type. The value of *E* ranges from -1 to +1; values between -1 and 0 imply the species avoided the habitat type and values between 0 and +1 indicate selection (Gordon, 1989). It was assumed that values ≤ 0 represented avoided, > 0 to < 0.5 weakly selected, ≥ 0.5 but < 0.7 used in proportion to availability, ≥ 0.7 to < 0.9 strongly selected, and ≥ 0.9 very strongly selected.

It was not possible to calculate statistical significance for Jacobs' selectivity index by conventional methods and so "Monte Carlo" random resampling was used in R version 3.2.2 (R Core Team, 2015). For each species and season, and for each row of data (i.e. count of the number of herbivores of a given species), a habitat type (*Anogeissus*, Boval, BTD, BTV, Riverine, Swamp) was randomly picked in proportion to its area within all the transect samples and then summed. The selectivity index for the randomized (with respect to habitat type) counts was calculated 10,000 times and the proportion of times that the magnitude of the observed selectivity index was greater than the 10,000 random selectivity indices gave a p-value, i.e. the probability of getting the observed selectivity index. This had the advantage of using the observed counts of animals as it allocated those numbers to a habitat randomly, in proportion to the area of the habitat. We tried to model the number of animals as a known statistical distribution by using the negative binomial and a zero-inflated negative binomial but neither fitted the data well. Using the observed counts, rather than trying to model them statistically, addressed the issue of count events not being independent. For example, in one transect there were 21 warthogs (compared to an average of <1): the randomization method did not assume that the 21 warthogs were independent and so significant preferences were likely to be real.

Results

Seasonal Variation in Habitat Selectivity and Use

Figures 2 and 3 show seasonal variations in habitat selectivity by the eight species of large herbivores. Boval was only selected by elephant and warthog and avoided by the other six species. Elephant strongly selected Boval in the dry and fire seasons and avoided it in the rainy and flood seasons (Figure 2), whereas warthog only avoided Boval in the

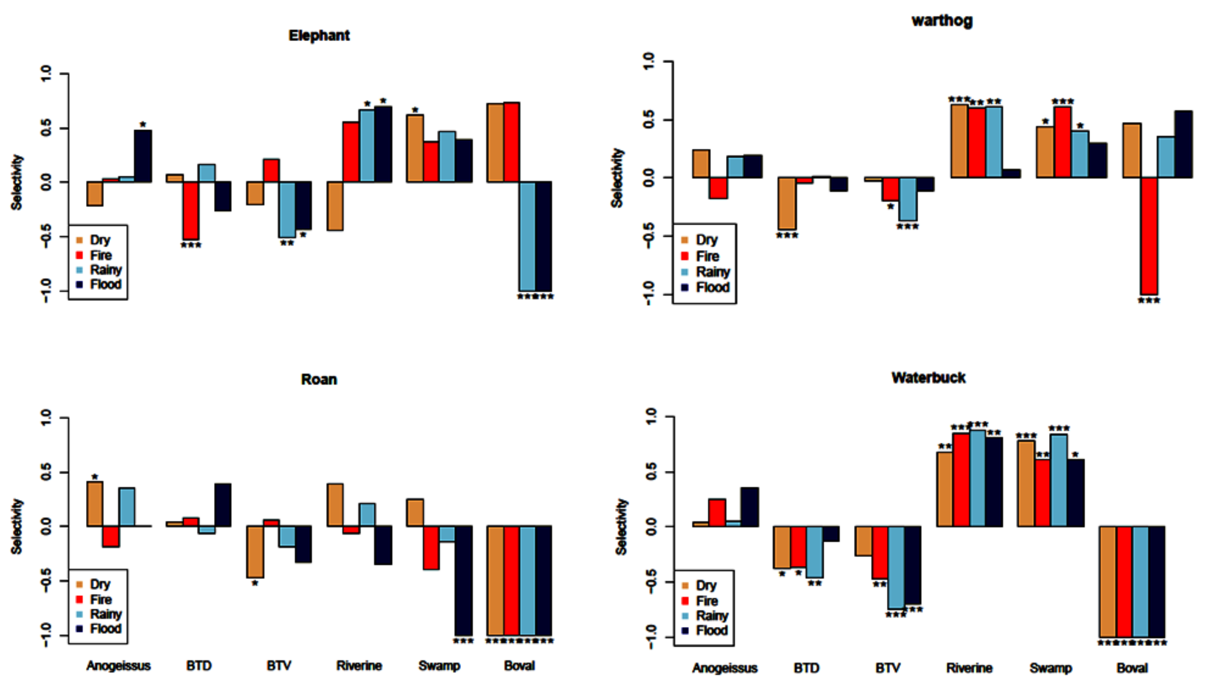

Figure 2 Selectivity indices for the elephant, warthog, roan antelope and waterbuck (* - $p < 0.05$, ** - $p < 0.01$ and *** - $p < 0.001$) Source: Data collected between September 2013 and August 2014

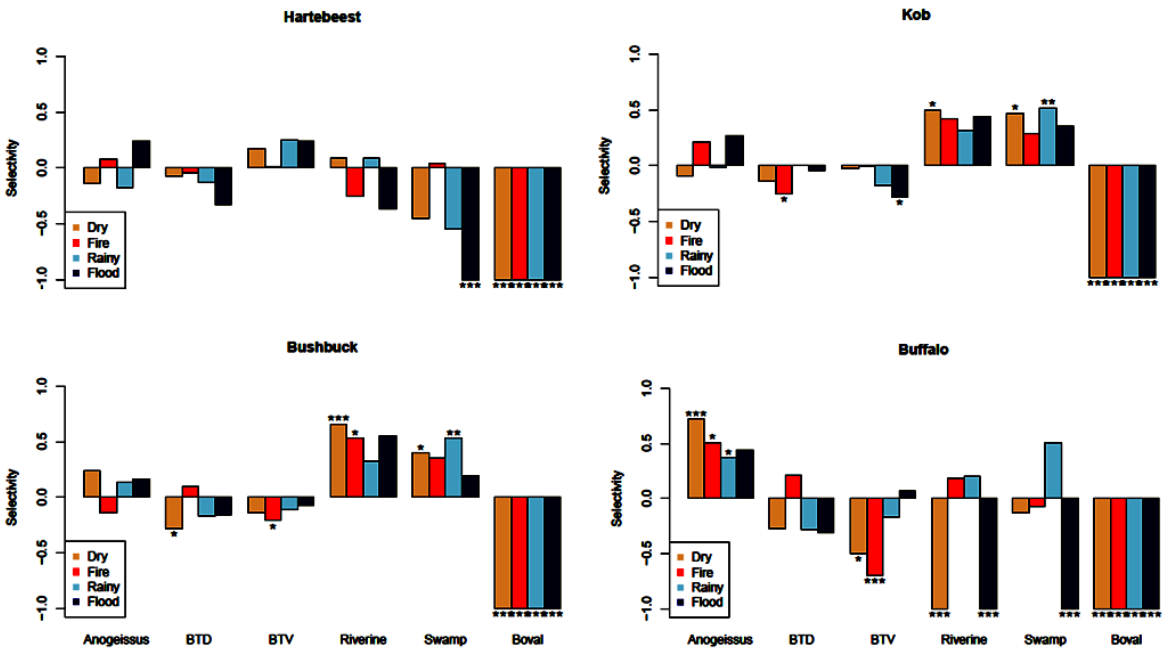

Figure 3 Selectivity indices for the hartebeest, kob, bushbuck and buffalo. (* - p < 0.05, ** - p < 0.01 and *** - p < 0.001) Source: Data collected between September 2013 and August 2014

fire season (Figure 2).

Elephant always selected Swamp, albeit weakly (Figure 2). They avoided Riverine in the dry season but selected it strongly in the flood season and weakly in the fire and rainy seasons. Elephant also selected *Anogeissus*, though weakly, and avoided it in the dry season; they selected BTD weakly in the dry and rainy seasons but avoided it in the two other seasons; and selected BTV weakly only in the dry and fire seasons (Figure 2). Thus elephant did not show a clear habitat preference.

Warthog avoided BTV in all seasons (Figure 2); they avoided *Anogeissus* in the fire season but selected it weakly in all other seasons; they selected BTD weakly in the rainy season; they also selected Riverine weakly in the flood season but used it in proportion to availability in the other seasons; and used Swamp in proportion to availability in the fire season but selected it weakly in the other seasons (Figure 2). Warthog selected Riverine and Swamp and avoided open savanna in all seasons.

Roan antelope avoided *Anogeissus* in the fire season but selected it weakly in other seasons (Figure 2); they avoided BTD in the rainy season but selected it weakly in other seasons; they selected BTV weakly in the fire season but avoided it in other seasons; they weakly selected Swamp in the dry season but avoided it in other seasons; and weakly selected Riverine in the dry and rainy seasons and avoided it in the other seasons (Figure 2). Thus roan antelope did not show any clear habitat preferences but avoided wet habitats.

Waterbuck always selected *Anogeissus*, riverine and swamp; they selected *Anogeissus* weakly and Riverine and Swamp very strongly. They avoided the other habitats in all seasons: they preferred Swamp and Riverine habitats to others in all seasons (Figure 2).

Hartebeest selected BTV weakly and avoided Boval and BTD in all seasons (Figure 3), and did not show a clear pattern of seasonal habitat selectivity. Kob selected Riverine and Swamp in all seasons though weakly (Figure 3); they avoided *Anogeissus* in the dry and rainy seasons but selected it weakly in the fire and flood seasons, avoided BTD in all but the rainy season, and avoided BTV in all seasons. Kob selected Riverine and Swamp and avoided open savanna, especially in the dry and fire seasons. Bushbuck avoided *Anogeissus* in the fire season but selected it weakly in all other seasons, and weakly selected BTD in the fire season (Figure 3); they avoided BTV in all seasons, and selected both Riverine and Swamp weakly in all seasons. Bushbuck avoided open savanna.

Buffalo always selected *Anogeissus* but only strongly in the dry season and weakly in the other seasons (Figure 3); they selected BTD in the fire season, BTV in the flood season, Riverine in the fire and rainy seasons, but avoided it in the dry and flood seasons, and used Swamp in proportion to its availability in the rainy season (Figure 3). Thus buffalo preferred *Anogeissus* in the dry season but shifted to Riverine in the fire season and swamp during the rainy season.

Discussion

In the MNP, elephant and buffalo showed distinct seasonal patterns of habitat selection and use, whereas the other six herbivores we investigated did not respond to seasonal changes: they either maintained their preferred habitats throughout the year or showed no seasonal pattern of habitat selectivity. In the dry season, elephant shifted from Riverine to Swamp to enable them to utilize water holes created near swamp, but preferred both Riverine and Swamp in other seasons. Buffalo selected and used *Anogeissus* in all seasons but selected Swamp during the rainy season and Riverine in the fire season. The study observed that, generally, the large herbivores at MNP were less selective during the rainy season and more selective during the fire season. Fire caused a shrinkage of habitat resources and so selectivity increased in the fire season, while post-fire regrowth during the rainy season increased forage resources and reduced selectivity. This supported previous studies (Gordon, 1989; Fritz et al., 1996), and confirmed the hypothesis that there is low selectivity when forage abundance is high and high selectivity when forage abundance is low. Previous studies have shown inter-habitat shifts by herbivores in response to distinct resource diversities in different seasons (Western, 1975; Sinclair, 1985; Ben-Shahar & Skinner, 1988; Gordon, 1989; McNaughton, 1990; Ben-Shahar & Coe, 1992; Owen-Smith, 1992; Fritz et al., 1996; Omphile, 1997; Mwangi & Western, 1998; Bergström & Skarpe, 1999). The lack of clear patterns of inter-habitat shifts in habitat selection and use by six of the eight herbivores we studied suggested the effect of multiple factors, rather than just resource diversity, on habitat selection and use by the large herbivores. For example, forage diversity (such as the distribution of different plant communities), plant productivity and variations in the availability of different habitats could affect habitat selection and use by the herbivores. The fine-scale mosaics of habitats that characterized the MNP might have complicated the patterns of habitat selection and use for some herbivores. Furthermore, predation is likely to be an important factor in habitat selection. Kob, warthog and bushbuck avoided open savanna, possibly as a response to predation, whereas Swamp and Riverine provided abundant forage for these species.

This study is consistent with Kingdon (1997), that waterbuck strongly selected Swamp in all seasons. However, apart from Boval, the habitat least preferred by roan antelope was Swamp, which they only used when the ground was dry. It appears that the waterbuck is a lowland species and the roan antelope just avoids wet grounds but it is not necessarily a highland species, and as noted by Dakwa (2016c), ecological barriers such as altitude and wet grounds may restrict habitat selection and use by some of these herbivores.

In conclusion, the pattern of large grazers' selectivity and use of habitat resources in MNP has been complicated by abiotic factors including fire and altitude and biotic factors such as predation and the fine-scale mosaic of habitats, which are probably the result of fire and other ecological disturbances. However, fire is the only perturbation that can be addressed at the management level. Since habitat mosaics are ecologically important in creating or maintaining biodiversity by introducing variability in vegetation composition, future studies should explore the impact of habitat mosaics on selectivity of the herbivores. Understanding habitat selection and use by herbivores is fundamental for the management of MNP, and particularly to determine which habitat types should be the focus of fire control operations.

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