Species-Packing of Grazers in the Mole National Park, Ghana

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Abstract

Hutchinson's body weight ratio (WR) theory was used to determine the degree of species-packing of 22 species of grazers in Mole National Park (MNP). The hypotheses, which suggest that facilitation is more likely to occur at a WR greater than 2.0, competition at WR less than 2.0, and coexistence at WR equals 2.0 were tested by regressing the natural logarithm of the body mass of a grazer against its rank number in the grazer assemblage. The results indicated competition in the grazer assemblage at MNP as its WR is 1.40 and therefore grazers are tightly packed. However, as several species with similar body weight coexisted at MNP, the Hutchinson's Rule could not be supported. Habitat heterogeneity rather than the size of conservation area related to species-packing and MNP with its low habitat heterogeneity showed a low degree of species-packing. Possible explanations have been advanced for existing ecological holes within the assemblage. Species-packing could still be a reasonable measure of the characteristics, dynamics, interactions and the patterns of assemble in animal communities. It could also be used to predict the effect of animal species loss or arrival on the stability of a natural ecosystem and provide useful guidelines in planning herbivore conservation measures in protected areas.

Introduction

Hutchinson (1959) proposed the weight ratio theory after studying character displacement among similar species of animals. In this theory the mass of each species is almost twice the mass of the next species in a size-ordered assemblage of animals. Since then, body size has been widely used to predict animal abundance and patterns of assemble (Damuth, 1981; Schmidt-Nielsen, 1984; Fa & Purvis, 1997; Bonyongo & Harris, 2007) and define resource use (Cousins, 1991). Several authors working with different taxa, e.g. fish (Brown, 1975), wandering spiders (Uetz, 1977), lizards (Schoener, 1970), birds (Schoener, 1974; Brown, 1975), bats (McNab, 1971; Fleming, Hooper & Wilson, 1972) and mammals (Brown, 1973, 1975) agreed on a constant ratio for sizes of adjacent species in a sequence. Since then the weight ratio theory has been inferred as an index to determine if facilitation, competition or coexistence occurs in the assemblages of sympatric species in an area.

Mole National Park (MNP) has significant biodiversity typical of guinea savanna ecosystem and best for protecting representative savanna wildlife in Ghana. The park is considered a preserve for antelope species including kob (*Kobus kob*), Defassa waterbuck (*Kobus defassa*), roan antelope (*Hippotragus equnus*), hartebeest (*Alcelaphus bucelaphus*), oribi (*Ourebia ourebi*), bushbuck (*Tragelaphus scriptus*), the red duiker (*Cephalophus natalensis*) and the yellow-backed duiker (*Cephalophus sylvicutor*) (Dakwa, 2016a). Whether it has sufficient representation of the diversity of species in terms of the fauna, especially herbivorous mammals in the park, which are morphologically diverse and ecologically similar is unknown. Also, whether the capacity and resources of the park will allow a sustainable coexistence of those sympatric species are unknown, which are the bases for this study. It is expected that, as so many species share the same natural pastures, there will be overwhelming competition for their common food resources. Early community ecologists (e.g. Hutchinson, 1959; MacArthur & Levins, 1967) proposed that competition prevents co-existence of species that are morphologically too similar and that the weight ratio determines whether facilitation or competitive displacement will occur within a given guild of grazers.

The objectives of this study were to: (i) determine how closely packed grazers of MNP are (the degree of species-packing); (ii) determine whether there is facilitation, competition or coexistence among the grazers in the MNP's assemblage and, (iii) identify and explain possible causes and implications of ecological holes in the grazer species assemblages at MNP. Accordingly, the hypotheses suggesting that facilitation is more likely to occur at a weight ratio (WR) > 2.0, competition at WR < 2.0, while coexistence will occur at WR = 2 (Prins and Olff, 1998) were tested. Grazers here refer to species, which use substantial amount of grasses as forage, including mixed feeders such as elephant (*Loxodonta africana*) and baboon (*Papio anubis*). Herbivorous mammals weighing at least 2 kg were considered in this study.

Study area

Mole National Park (MNP) (Figure 1) lying between 9° 11" and 10° 10" N and between 1° 22" and 2° 13" W (Anon., 2011, Dakwa, 2018a) covers an area of about 4,840 km^2 (Anon., 2011) as Ghana's largest wildlife protected area. The park is located in northwest Ghana on grassland savanna and riparian ecosystems, with sharp escarpment forming the southern boundary of the park (Anon., 2011). There are six main habitat types in MNP, namely, the *Burkea-Terminalia* open savanna woodland with *Vitellaria paradoxa*, the *Burkea-Terminalia* open savanna woodland with *Detarium microcarpum*, the *Anogeissus* with *Vitellaria paradoxa*, the boval vegetation (*Loudetiopsis kerstingii- Polycarpaea tenuifolia* community on rocky substrates, riverine forest along most of the rivers in the park, and swamp (Schmitt & Adu-Nsiah, 1993). The climate of MNP is undergoing gradual changes that significantly affect its land cover (Dakwa, 2018a). In the 1930s some 2,300 km^2 of the present park was designated as a Game Clearance Area in an effort to control tsetse flies. The aim was to clear the area of

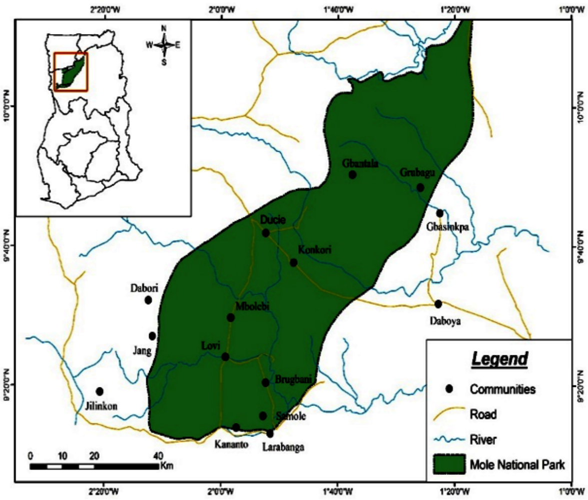

Figure 1: Map of Mole National Park. Source; Dakwa (2018a)

wildlife so that the tsetse flies would have no food and die out. Large numbers of mammals were eliminated but fortunately the policy of game clearance was abandoned in 1957. In 1958 Mole Game Reserve was established and was re-designated a national park in 1971 (Anon., 2011). The park is home to over 93 mammal species including the savanna elephant, hippopotamus (*Hippopotamus amphibius*) and buffalo (*Syncerus caffer*). It is bordered by 33 communities, with a total estimated population of about 35,000-40,000 people (Dakwa, 2016b; Anon., 2011).

Materials and methods

The list of grazers in MNP was obtained from the current management plan (Anon., 2011) and these were confirmed by driving or walking 36 transects in MNP (Dakwa, 2018b) to produce a checklist of all the grazers weighing at least 2 kg over a period of five months from January to May, 2014 in both rainy and dry seasons. Unit masses of species were obtained from Stuart and Stuart (1993), Kingdon (1997) and Prins and Olff (1998). Body weight ratio (WR) was used to determine the degree of species-packing of the MNP grazers based on Hutchinson (1959) following the methods of Prins and Olff (1998) and Bonyongo and Harris (2007).

Data analysis

All data were entered into Microsoft Excel tables (version 2013), before being exported into R statistical software package version 3.1.2 (R core team, 2014) to do all the analyses. A regression model was used to evaluate species-packing by regressing the natural logarithm of body mass *w*, against rank number *r*, for the grazers weighing at least 2 kg known to permanently inhabit MNP. The slope is expected to be ln 2 (=0.6933) considering a sequence in a coexisting assemblage where each species is exactly twice as heavy as the next (Prins and Olff, 1998). Therefore, $wr = e^{\ln 2} = 2$, and thus the natural logarithm of body mass of the ith species (*wi*) is expected to depend on the rank number (*ri*) where the regression line follows the function:

$$ln\ (w_i) = ar_i \quad \text{……….…………} (1)$$

and *a* is the coefficient of *ri* (Prins and Olff, 1998). The weight ratio, WR is then obtained by the function.

$$WR = e^a \quad \text{…….……}(2)$$

Results

Species-packing

The list of grazers weighing at least 2 kg confirmed to be permanently inhabiting MNP and the ranking of those grazers in the sequence are shown in Table 1. The species richness for MNP is 22 and the MNP's habitat heterogeneity is very low with only six habitat types (Dakwa, 2018b).

The F-ratio obtained by regressing the natural logarithm of body mass against rank number is significant {F (1, 19) = 459.9; $p<0.001$; $R^2 = 0.96$}. With such a high R^2 value and the fact that only 4% of the variation in the natural logarithm of body mass cannot be explained by its sequence rank, the regression model is a good fit that results in a significantly good degree of prediction. This validates WR (a measure of the degree of species-packing) obtained from the coefficient of the models parameter. A plot of body mass ranks against ln *w* showed that the slope of the regression

TABLE 1
List of grazers larger than 2 kg known to be inhabiting MNP

Species	Scientific name	BW	ln BW	Rank number
Whyte's (Togo) hare	*Lepus victoriae*	2	0.693	1
Scrub hare	*L. saxatilis*	2.5	0.916	2
Rock hyrax	*Procavia capensis*	3.6	1.281	3
Colobus	*Colobus vellerosus*	4.4	1.482	4
Cane rat	*Thryonomys gregorianus*	4.8	1.569	5
Green monkey	*Cercopithecus aethiops*	5.2	1.649	6
Patas monkey	*Cercopithecus patas*	9.4	2.24	7
Grey duiker	*Sylvicapra grimmia*	12	2.485	8
Red-flanked duiker	*Cephalophus rufilatus*	13.8	2.625	9
Oribi	*Ourebia ourebi*	14.1	2.646	10
Anubis baboon	*Papio anubis*	26	3.258	11
Giant pangolin	*Manis gigantean*	33	3.497	12
Yellow-back duiker	*Cephalophus silvicultor*	59	4.078	13
Bush buck	*Tragelaphus scriptus*	60	4.094	14
Warthog	*Phacochoerus aethiopicus*	73.5	4.297	15
Kob	*Kobus kob*	78.5	4.363	16
hartebeest	*Alcelaphus buselaphus*	171.7	5.146	17
Defassa water buck	*Kobus defassa*	211	5.352	18
Roan antelope	*Hippotragus equinus*	270	5.598	19
Buffalo	*Syncerus caffer*	631	6.447	20
Hippopotamus	*Hippopotamus amphibius*	1900	7.55	21
Elephant	*Loxodonta africana*	3550	8.175	22

w is the body mass in kg while ln w is the natural logarithm of body mass. Nomenclature follows Kingdon (2013).

line was 0.339 (ln w =0.339R - 0.054; R^2 = 0.96; t = 21.45, df =19, p<0.001) and therefore the WR of the grazers of the MNP was 1.40. This implied that the average increment in body size between species adjacent in size at MNP was 40%. Bonyongo and Harris (2007) evaluated the average increment in body size between species adjacent in size. The average increment for Etosha National Park in Namibia measuring 23,175 km^2 was 36%; Hwange National Park in Zimbabwe (14,621 km^2), 28%; Okavango Delta Conservation Area in Botswana (22,000 km^2), 25%; Kafue National Park in Zambia (24,000 km^2), 25%; and Kruger National Park in South Africa (19,633 km^2), 21%. MNP had higher WR and therefore lower degree of species-packing than any of the conservation areas studied by Bonyongo and Harris (2007), and though all these conservation areas compared are larger in size and have more habitat diversities, their grazers are more tightly packed than MNP.

Grazer weight structure

Table 2 shows the distribution of grazers' species richness within body weight ranges in the grazer assemblage of MNP and Figure 2 shows the contributions of the different weight ranges to the total biomass of the MNP herbivorous mammals' assemblage. The highest number of species was found within the 2–50 kg weight range, accounting for nearly half of the total number of species within the MNP assemblage yet all these contributed only 2% to the total biomass of the MNP grazer assemblage. By reference to Bonyongo and

Harris (2007), each of Etosha, Hwange, Kafue and Okavango Delta had a deficit of species within the 2–50 kg body weight range as compared to MNP with slightly more species within that range and Kruger that had exactly half the total number of species. There were generally very low numbers of species heavier than 300 kg. For example, between 301–1000 kg weight range; Etosha, Hwange and MNP had only buffalo; and Kafue, Kruger, and Okavango Delta have two species, i.e. buffalo and eland. Above 1000 kg, there are only hippopotamus and elephant in the MNP and the other conservation areas compared except Kruger, which has the rhino (*Ceratotherium simum*) in addition. Therefore, it can be inferred that lower weight ranges have higher species richness and higher weight ranges have lower species richness, though this is to be expected. Grazers beyond 1000 kg alone contribute 76% to the total biomass (Figure 2) despite their low species richness.

Discussion

Species-packing

It appears that the low habitat heterogeneity of MNP, rather than its relatively small size, plays a part in its high species-packing (low WR). Dakwa (2016c) showed that size differences among conservation areas have no significant effect on species-packing but areas of high habitat heterogeneity support high species richness, and areas of low habitat heterogeneity show low species richness. These are consistent with the hypothesis (May, 1973) that complex or highly heterogeneous systems

TABLE 1

Weight ranges of grazers and their frequencies of occurrence in MNP

Weight Range (kg)	Frequency of grazers
2-50	12
51-100	4
101-300	3
301-1000	1
>1000	2

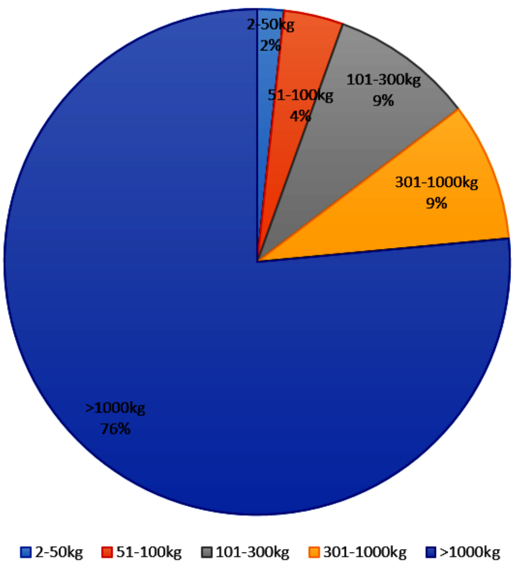

Figure 2: Weight ranges of herbivorous mammals in MNP and their biomasses

are expected to support a higher diversity and hence high degree of species-packing, while simple or homogeneous systems are likely to support low species diversity (low degree of species-packing). Therefore, habitat diversity might be the decisive factor in allowing coexistence in a grazer community. Thus, the greater the habitat diversity the less the possibility of competition and the lower the habitat diversity the greater the possibility of competition.

The WR = 1.40 for grazers at the MNP is less than the expected WR = 2.0, implying that, in theory, the grazers at MNP are too closely packed or too similar in body weight to coexist and are supposed to be competing according to the Hutchinson's Rule. However, because there are several species with similar body weight coexisting within the MNP grazer assemblage, the results do not support the Hutchinson's Rule and so the hypothesis of competition in the MNP assemblage is rejected. Similar body weight coexisting is not much observed for larger grazers weighing more than 80 kg, but it is common to grazers less than 80 kg that accounted for about 71% of the species richness, which is most likely one of the reasons for coexistence of MNP's grazers. Owen-Smith (1992) and Tokeshi (1999) pointed out that species of similar weight are believed to have evolved distinct morphological, habitat selection and feeding patterns, thereby permitting differential resource use and clear ecological separation. For example, warthog (73.5 kg) and kob (78.5 kg) coexist despite similarities in body weight because warthog are mixed feeders while kob, strictly grazers, which make them ecologically separated at MNP. Roan antelope (270 kg) and waterbuck (211 kg) are similar in body weight but because roan prefer highlands while waterbuck prefer lowlands (Dakwa, 2018b), they are able to coexist at MNP. Ecological separation is well studied (e.g., Biggs, 1979; Bell, 1982; Kingdon, 1997; Voeten & Prins, 1999; Burns & Griffin, 2000; Dakwa, Monney and Ashie, 2018c), and many coexistence patterns have been explained for ecological assemblages. For example, species may compete for a common resource, without being limited simply by its availability, because they differ in the way they utilize the resource (resource partitioning). Though resource partitioning was not the focus of this study it is a possible phenomenon that allows grazers at MNP to coexist.

Grazer assemblage structure

MNP is deficient in species within the 80 – 260 kg body weight range but this is explained more in terms of climatic preference. Majority of African herbivores in this weight range live in the temperate zones (Bonyongo and Harris (2007). Potentially, Bohor reedbuck (*Redunca redunca*) may also be expected to occur in MNP. Report in the current Management Plan indicate few encounters with the Bohor reedbuck in MNP that remains unconfirmed officially but this may lend credence to a possible existence of a very low remnant population of the Bohor reedbuck that may have resulted from the historical massacre of mammals in MNP.

The absence of grazers weighing beyond 1000 kg, apart from the African elephant, has been traced to Pleistocene extinctions about 4000 years ago (Owen-Smith, 1992; Prins & Olff, 1998, Bonyongo and Harris, 2007), which also account for low species richness at MNP. The African giraffe (*Giraffa camelopardalis*), weighing 1010 kg could very well have fitted into this weight category but may have, additionally, suffered the historic massacre of mammals at MNP to cause its extirpation, a speculation that needs strong justification, though the habitats of MNP could have been favourable grounds for the giraffe. The distribution map of the giraffe (Furstenburg, 2007), indicates their abundance in the northern part of Ghana in the past, implying that MNP probably harboured the giraffe in times past. The map also indicates the presence of giraffe in areas beyond the northern borders of Ghana, including Burkina Faso and Mali, currently. This study supports Bonyongo and Harris (2007) that the African elephant (*Loxodonta africana*) likely lack potential competitors in grazer assemblages.

The occurrence of ecological holes in the grazer assemblages at the MNP suggests the possibility of a successful translocation plan for (i) Bohor reedbuck to augment its population and (ii) the giraffe, to establish a new population; for the purposes of conservation of the species and tourism.

Conclusion

The result of species-packing at MNP defies the Hutchinson's co-existence rule as the weight ratio (degree of species-packing) is less than the theoretically expected value of approximately 2.0. This is because there is co-existence of species of similar sizes involving, especially, species of small body weights. There also exists ecological holes due to the absence of species of similar body weights, especially in the large body weight category, believed to be partly due to climatic and habitat preferences, historic massacre of mammals and Pleistocene extinctions. Despite criticisms of the weight ratio theory, it can be a reasonable measure of the characteristics, dynamics, interactions and the patterns of assemble in animal communities. It can also be used to predict the effect of animal species loss or arrival on the stability of a natural ecosystem and provide useful guidelines for conservation planning and action in protected areas.

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