Grazers species-packing in the Okavango Delta, Botswana

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Abstract

We used body weight ratio to determine the degree of species-packing of the Okavango Delta (22,000 km^2) grazers and compared it to that of four conservation areas of similar sizes but varying in the diversity of habitat types. They are Etosha National Park (23,175 km^2) in Namibia, Hwange National Park (14,621 km^2) in Zimbabwe, Kafue National Park (24,000 km^2) in Zambia and Kruger National Park (19,633 km^2) in South Africa. We considered possible ecological explanations for existing gaps within the assemblage. The weight ratio (measure of the degree of species-packing) of the grazers of the Okavango Delta was 1.25, with a total of 27 species which was far less than the theoretically expected 2.0. One-way analysis of covariance (ANCOVA) showed that there were significant differences in the degree of species-packing between the Okavango Delta and other conservation areas of similar size in southern Africa ($F_{1,5} = 166$, $P < 0.001$). Regressing habitat heterogeneity (expressed as number of different habitat types) on species-packing of the five conservation areas yielded a positive linear relationship with $R^2 = 0.76$ implying that 76% of the variation in the degree of species-packing in the five conservation areas is explained by variation in habitat heterogeneity. We conclude that size ratios are useful descriptors of animal communities and it is a useful measure of species diversity, which can be used for monitoring purposes. Imbalances in weight ratios provide a measure of identifying perturbations due to species loss or arrival of new species within a natural ecosystem.

Key words: body size, co-existence, weight ratio

Résumé

Nous avons employé le rapport du poids corporel pour déterminer le degré de “ richesse spécifiqueg” (*species-packing*) des herbivores du delta de l'Okavango (22.000 km^2) et nous l'avons comparé à celui de quatre aires de conservation de taille similaire mais qui varient par la diversité de leurs types d'habitats. C'étaient le Parc National d'Etosha (23.175 km^2) en Namibie, le Parc National de Hwange (14.621 km^2) au Zimbabwe, le Parc National de Kafue (24.000 km^2) en Zambie et le Parc National Kruger (19.633 km^2) en Afrique du Sud. Nous avons envisagé des raisons écologiques possibles pour expliquer les manques dans les assemblages. Le rapport de poids (mesure du degré de *species-packing)* des herbivores du delta de l'Okavango était de 1,25, avec un total de 27 espèces, ce qui est beaucoup moins que la valeur théorique attendue de 2,0. L'analyse à une voie de la covariance (ANCOVA) montrait qu'il y avait des différences significatives du degré de *species-packing* entre le delta de l'Okavango et les autres aires de conservation de taille semblable en Afrique du Sud ($F_{1,5} = 166$; $P < 0,001$). En faisant la régression de l'hétérogénéité de l'habitat (exprimée comme le nombre de types d'habitats différents) sur le *species-packing* des cinq aires de conservation, on a obtenu une relation linéaire positive avec $R^2 = 0,76$, ce qui implique que 76% de la variation du degré de *species-packing* dans les cinq aires de conservation s'expliquent par la variation de l'hétérogénéité des habitats. Nous concluons que les rapports de taille sont des indicateurs utiles des communautés animales et que c'est une mesure utile de la diversité des espèces qui peut servir à des fins de monitoring. Des déséquilibres de rapports de poids fournissent une mesure pour identifier les perturbations dues à la perte ou à l'arrivée de nouvelles espèces dans un écosystème naturel.

Introduction

Factors allowing co-existence among ecologically similar species are long-standing and fundamental issues in community ecology. Central to the debates in community ecology is the extent to which co-existence among related species is attributable to differences in morphology purported to reflect their food niches (Case, 1981; Carothers, 1986). Early community ecologists (e.g. Hutchinson, 1959; MacArthur & Levins, 1967) proposed that competition prevents co-existence of species that are morphologically too similar. Hutchinson (1959) observed that character displacement among sympatric species, in both vertebrates and invertebrates leads to sequences in which each species is roughly twice the mass of the next.

Since Hutchinson's (1959) weight ratio theory, it has been widely proposed that body size plays a significant role in predicting animal abundance and patterns of assemble (Damuth, 1981; Schmidt-Nielsen, 1984; Fa & Purvis, 1997). 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) demonstrated that the ratio of sizes of adjacent species in a size-ordered assemblage tends towards constancy or that all ratios exceed some minimum similarity.

Based on the Hutchinson's weight ratio theory, Prins & Olff (1998) hypothesized that in a functional group, 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 & Olff (1998) further hypothesized that when species are too similar in body mass, they might not profit sufficiently from facilitation interactions, and competition will occur. They further argue that when species are too different in body mass, the larger herbivore will keep the grass at an equilibrium at which the vegetation quality is too low for small herbivores. In this case facilitation will not occur. May (1973) hypothesized that complex or highly heterogeneous systems are expected to support a higher diversity (high degree of species-packing), while simple or homogeneous systems are likely to support low species diversity (low degree of species-packing) suggesting that habitat diversity might be the decisive factor in allowing co-existence and grazer community structure.

The Okavango Delta is a complex and highly productive natural ecosystem with a high diversity of habitat types, and as such should support higher species diversity than less complex systems in the southern Africa. In this paper, we use body WRs to determine the degree of species-packing (Prins & Olff, 1998) of the Okavango Delta grazers. Grazers here refer to species, which use substantial amount of grasses as forage, including mixed feeders such as impala and elephant. We further compared the degree of species-packing of the Okavango Delta to that of four major conservation areas in southern Africa of similar sizes but varying in the diversity of habitat types (Table 1). They are Etosha National Park (23,175 km^2) in Namibia, Hwange National Park (14,621 km^2) in Zimbabwe, Kafue National Park (24,000 km^2) in Zambia and Kruger National Park (19,633 km^2) in South Africa. We expect no significant differences in the degree of species-packing between the Okavango Delta and Kafue National Park because both are wetlands ecosystems with similar habitat types, while we expect significant difference between the Okavango Delta and Hwange, Etosha and Kruger. Hwange and Etosha have lower spatial heterogeneity than the Okavango Delta, while Kruger has a higher spatial heterogeneity and higher number of habitat types than the Okavango Delta (Table 1).

Table 1 Sizes of conservation areas, number of species and degree of species-packing

Conservation area	Area (km^2)	Number of habitats	Number of grazer species	Slope	Weight ratio (WR)
Okavango	22,000	11	27	0.214	1.25
Etosha NP	23,175	7	24	0.308	1.36
Hwange NP	14,621	9	27	0.250	1.28
Kafue NP	24,000	11	30	0.226	1.25
Kruger NP	19,633	16	37	0.191	1.21

Materials and methods

Study area

The Okavango Delta is located between 19° and 20°S and 22° and 24°E. Two main river systems, the Cubango and the Cuito, drain southwards from Angola into the Okavango River, which spreads out into a deltaic shallow water body which covers approximately 22,000 km^2. The Okavango Delta wetlands are divided into three physiographic regions: (i) The Panhandle area which has perennial surface water up to 4 m deep; it is characterized by meandering channels flanked by permanent swamps. (ii) Low lying seasonally inundated areas, the extent of which varies to a large degree depending on the magnitude of annual floods from Angola and the amount of local rainfall. (iii) Higher, dry land masses, of which there are three major examples: Moremi Game Reserve, Chief's Islands and Western sand-veld tongue (Paterson, 1976; McCarthy, Stainstreet & Caincross, 1991; McCarthy, Ellery & Ellery, 1993). Within these three broad divisions is an interlocking mosaic of habitat types that provides suitable habitat for large wild animals.

Table 2 List of grazers and intermediate feeders larger than 2 kg known to occur permanently in the Okavango Delta (OD), Kafue Flats (KF), Kruger National Park (KNP), Etosha National Park (ENP) and Hwange National Park (HNP)

Species	Scientific name	BW	ln BW	OD	KF	KNP	ENP	HNP
Whyte's hare*	*Lepus victoriae*	2.0	0.693		1	1		
Cape hare*	*Lepus capensis*	2.2	0.788	1		2	1	1
Egyptian goose*	*Alopochen aegyptiacus*	2.3	0.833	2	2	3	2	2
Red rock hare	*Pronolagus randensis*	2.4	0.875			4		
Scrub hare	*Lepus saxatilis*	2.5	0.916	3			3	3
Natal red rock hare	*Pronolagus crassicaudatus*	2.7	0.993			5		
Southern tree hyrax	*Dendrohyrax arboreous*	2.9	1.064		3			
Springhare*	*Pedetes capensis*	3.2	1.163	4	4	6	4	4
Rock hyrax	*Procavia capensis*	3.6	1.281	5		7	5	
Savanna cane rat	*Thrynomys swinderianus*	4.8	1.569		5			
Spurwinged goose*	*Plectropterus gambensis*	5.4	1.686	6	6	8	6	5
Greater cane rat	*Thryonomys gregorianus*	6.8	1.917	7	7	9	7	6
Leopard tortoise*	*Gechelone pardalis*	8.0	2.079	8	8	10	8	7
Sharpe's grysbok	*Raphicerus sharpei*	9.3	2.23		9			
Klipspringer	*Oreotragus oreotragus*	11.9	2.477		10	11		8
Oribi	*Ourebia ourebi*	14.1	2.646		11	12		
Yellow baboon	*Papio cynocephalus*	19.5	2.97		12			
Grey rhebok	*Kobus vardoni*	20.0	2.996			13		
Vaal rhebok	*Pelea capreolus*	25.8	3.25			14		
Mountain reedbuck	*Redunca fulvorufula*	29.5	3.384			15		
Chacma baboon*	*Papio ursinus*	29.5	3.384	9		16	9	9
Springbok	*Antidorcas marsupialis*	39	3.664	10				
Impala*	*Aepyceros melampus*	52.5	3.96	11	13	18	10	10
Common reedbuck*	*Redunca arundinum*	58.0	4.06	12	14	19	11	11
Bushpig	*Potamochoerus larvatus*	70.0	4.248	13	15	20	12	12
Puku	*Kobus vardoni*	71.5	4.27		16			
Common warthog*	*Phacochoerus africanus*	73.5	4.3	14	17	21	13	13
Sitatunga*	*Tragelaphus spekei*	76.8	4.341	15	18			14
Nyala	*Tragelaphus angasi*	86	4.454			22		
Kafue lechwe	*Kobus leche*	91	4.511					
Red lechwe*	*Kobus leche (kafuensis)*	91	5.511	16	18			15
Tsessebe*	*Damaliscus lulatus*	119	4.779	17		23		16
Ostrich*	*Struthio camelus*	120	4.787	18	19	24	14	17
Hartebeest	*Alcelaphus buselaphus*	171.7	5.146	19	20			
Waterbuck*	*Kobus ellipsiprymnus*	211	5.352	20	21	25	15	18
Oryx	*Oryx gazella*	225	5.416	21				19
Blue wildebeest*	*Connochaetes taurinus*	226	5.421	22	22	26	16	20
Sable	*Hippotragus niger*	227	5.427	23	23	27	17	21
Common zebra*	*Equus quagga*	235.0	5.46	24	24	28	18	22
Roan	*Hippotragus equinus*	270.0	5.598	25	25	29	19	23
Eland	*Taurotragus oryx*	471	6.155	26	26	30	20	
Buffalo*	*Syncerus caffer*	631	6.447	28	27	31		24
White rhino	*Ceratotherium simum*	1875	7.536			32		
Hippopotamus*	*Hippopotamus amphibius*	1900	7.55	29	28	33	21	25
African elephant*	*Loxondota africana*	3550	8.175	30	29	34	22	26

BW is the body weight in kg while ln BW is the natural logarithm of body weight. Species marked with an asterisk (*) were recorded in the Okavango Delta area between October 2000 and October 2002. Values in the last five columns are ranks. Scientific names are according to Skinner & Smithers (1990).

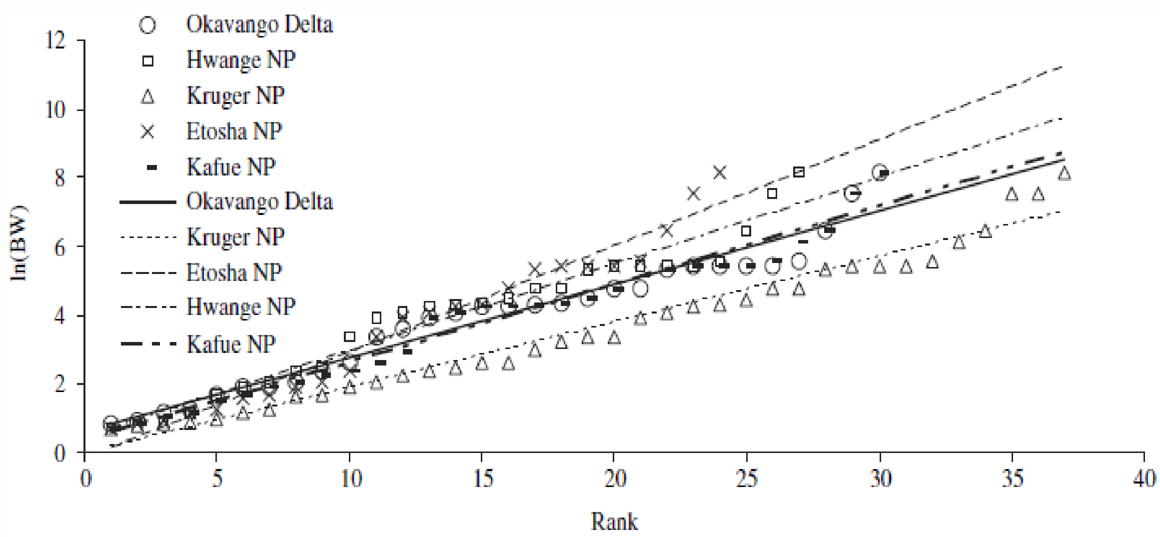

Fig 1 Ranked ln body mass of grazers (W_i) plotted against rank number (R_i) for the Okavano Delta (○, solid thick line, 30 species), Kruger National Park (△, dashed line, 37 species), Hwange National Park (□, dashed line, 27 species), Etosha National Park (×, dashes line, 24 species), and Kafue National Park (-, dashed line, 30 species). The regression lines for each system are as follows: Okavango Delta, $\ln(W_i) = 0.214R_i + 0.614$, $r^2 = 0.95$; Kruger National Park, $\ln(W_i) = 0.191R_i - 0.025$, $r^2 = 0.97$; Etosha National Park, $\ln(W_i) = 0.308R_i + 0.155$, $r^2 = 0.97$; Hwange, $\ln(W_i) = 0.250R_i + 0.474$, $r^2 = 0.95$; and Kafue National Park, $\ln(W_i) = 0.226R_i + 0.375$, $r^2 = 0.97$

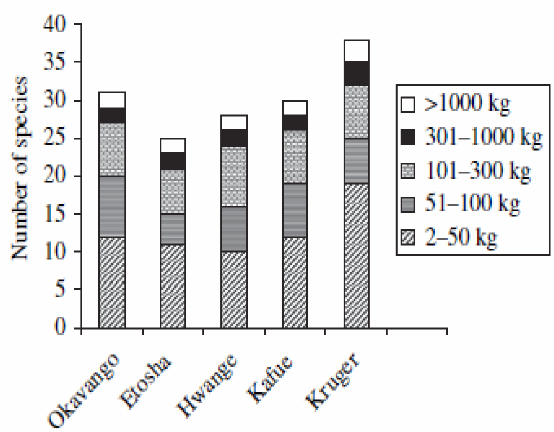

Fig 2 Graphical presentation of weight ranges of large herbivores in different conservation areas

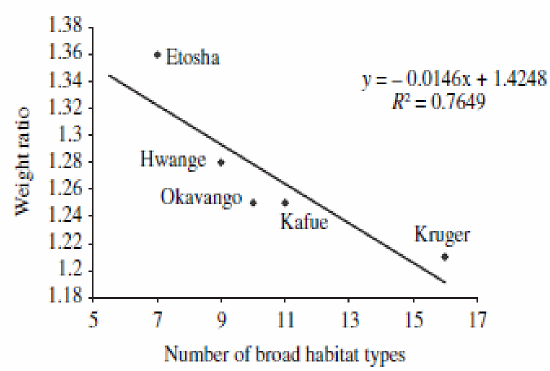

Fig 3 Regression of habitat diversity against the degree of species-packing

Areas of lower habitat heterogeneity showed a lower degree of species-packing (higher body WR) while areas with high heterogeneity showed a high degree of species-packing (lower body WR) (see Table 1) and a high species richness. Regressing habitat heterogeneity against species richness yielded a positive linear relationship with $R^2 = 0.98$, with areas of high habitat heterogeneity supporting the highest species richness (Fig. 4).

Discussion

Species-packing

The body WR of grazers of the Okavango Delta (1.25) was less than the theoretical expected ratio of approximately 2.0 suggesting that in theory, they are too closely packed or are too similar in body weight to co-exist according the

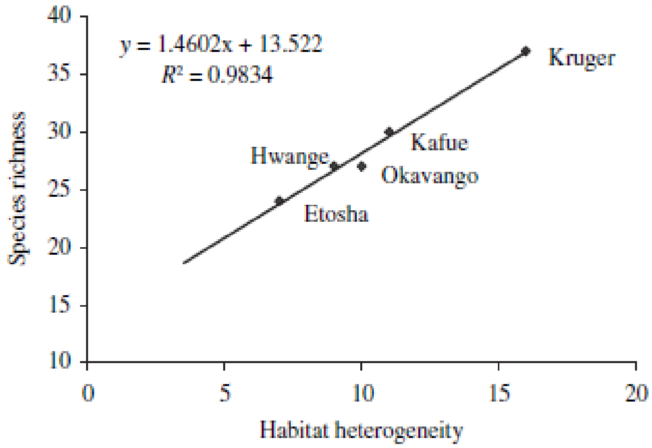

Fig 4 Regression of habitat diversity against the degree of species richness

Hutchinson's Rule. Therefore, our results do not support the Hutchinson's Rule as there are several species with similar body weight co-existing within the grazer assemblage of the Okavango Delta. These include the zebra (*Equus burchelli*) (235 kg), wildebeest (*Connochaetes taurinus*) (226 kg), waterbuck (*Kobus defassa*) (211 kg), sable antelope (*Hippotragus niger*) (228 kg) and roan antelope (*Hippotragus equinus*) (270 kg).

This observation supports Owen-Smith (1992) and Tokeshi (1999) who 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. Bonyongo (2004) showed that zebra feeding habitats in the Okavango Delta include sites with a high standing crop while wildebeest and tsessebe generally selected sites characterized by shorter swards with high leaf to stem ratio allowing them to co-exist. Similar observations were reported by Bell (1982) and Voeten & Prins (1999).

According to Kingdon (1997), roan select localities with minimal competition irrespective of the herbaceous species composition. In the Okavango Delta, roan and sable antelope occur in low densities in the panhandle area where zebra and wildebeest densities are low (Burns & Griffin, 2000). Waterbuck also occur in low densities, preferring dense riverine woodlands near permanent waters, a habitat type largely avoided by zebra, wildebeest, roan and sable (Biggs, 1979; Kingdon, 1997).

Lechwe (*Kobus leche*) (91 kg), tsessebe (*Damaliscus lulatus*) (119 kg), ostrich (*Struthio camelus*) (120 kg) are among the sets of co-existing grazers with similar body weight. Although both lechwe and tsessebe use floodplain vegetation (Biggs, 1979; Kingdon, 1997), they are ecologically separated as lechwe select wetter areas of the floodplains while tsessebe graze along the margins. During the flooding season, tsessebe retreat to elevated areas while lechwe forage on grasses and sedges emerging from slow floods. Impala (*Aepyceros melampus*) (54 kg) and common reedbuck (*Redunca arundinum*) (58 kg) also co-exist despite similarities in body weight because impala is a mixed feeder while reedbuck is a full time grazer which makes them ecologically separated, hence their ability to co-exist.

Gaps in herbivore assemblages

The absence of smaller animals such as red rock hares (*Pronolagus randensis*), natal red rock hare (*Pronolagus crassicaudatus*), southern tree rock hyrax (*Dendrohyrax arboreous*), Sharpe's grysbok (*Raphicerus sharpei*) and klipspringer (*Oreotragus oreotragus*) in the Okavango Delta is explained by lack of suitable habitats, in particular rock outcrops (Kingdon, 1997). Generally, the Okavango Delta, Etosha, Hwange and Kafue are deficient in species within the 10–30 kg body weight range, whereas Kruger has the high number (8) of species in this range. Most species within this range (e.g. klipspringer, grey rhebok (*Kobus vardoni*), vaal rhebok (*Pelea capreolus*) and mountain reedbuck (*Redunca fulvorufula*) prefer habitats characterized by hills and rock outcrops with short grasses (Kingdon, 1997), a habitat type common in Kruger. Potentially, white rhinocerus (*Ceratotherium simum*) may also be expected to occur in the Okavango Delta, Etosha and Hwange. Accounts from early travelers indicate that the species used to occur in these areas but hunting probably accounts for their current absence.

Beyond 1000 kg, there are apparently too few grazers in all the five areas investigated, and in the African assemblage as a whole. The apparent lack of mega-grazers has been linked to Pleistocene extinctions. Mega-grazers which became extinct during the Pleistocene were Giant Hippo (*Hippopotamus gorgops*), the giant hartebeest (*Megalotragus priscus*) (extinct 12,000 years ago) and the giant buffalo (*Pelorovis antiquus*) that became extinct 4000 years ago (Owen-Smith, 1992; Prins & Olff, 1998). Its therefore likely that the explosion of the African elephant (*Loxodonta africana*) populations whose numbers pose a management problem in many African countries, was the result of a lack of potential competitors.

Conclusions

High habitat diversity allows species of similar sizes to co-exist, hence the high degree of species-packing in the Okavango Delta. Similar conclusions can be drawn for other conservation areas in southern Africa because none of them has a degree of species-packing closer to the theoretically expected value of approximately 2.0. Although size ratio has been sharply criticized for lacking a sound scientific base, it remains a useful descriptor of animal communities. We note that although body size appears to be a useful measure for characterizing herbivore communities, it cannot be used to explain and measure diversity of large herbivores in a community in isolation.

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