

Habitat separation among ungulates in dry tropical forests of Ranthambhore national park Rajasthan

S. BAGCHI, S.P. GOYAL* & K. SANKAR

Wildlife Institute of India, P.O. Box No. 18, Dehradun – 248 001, Uttarakhand, India

Abstract: According to niche theory, differential use of shared resources facilitates the co-existence of species in a community. Niche relationships have been studied for a wide variety of taxa, but such understanding from tropical ungulate assemblages in south-east Asia is lacking. We investigated habitat relationships in an assembly of four wild ungulates viz., chital (*Axis axis*), sambar (*Cervus unicolor*), nilgai (*Boselaphus tragocamelus*) and chinkara (*Gazella bennetti*) from western India, using Discriminant Analysis. Ecological similarity between the four species was analysed in terms of 20 variables and the two cervids were found to use similar habitat features and the two bovids formed an analogous group. These two groups or “guilds” differentiated from each other in terms of vegetation structure as the cervids selected for *Anogeissus-Grewia* forest community while the bovids occupied *Acacia-Butea* scrub community. Habitat-use overlap between the two bovids appeared unstable in the light of theoretical aspects of population dynamics of interacting species. However, there is scope to achieve stable coexistence by differentiating over alternate resource axes like food.

Resumen: De acuerdo a la teoría del nicho, el uso diferencial de recursos compartidos facilita la coexistencia de las especies en una comunidad. Las relaciones de nicho han sido estudiadas para una gran variedad de taxa, pero todavía no se tiene un entendimiento de ellas para ensamblajes de ungulados tropicales en el sureste de Asia. Nosotros investigamos las relaciones de hábitat en un ensamble de cuatro ungulados silvestres, que son: chital (*Axis axis*), sambar (*Cervus unicolor*), nilgai (*Boselaphus tragocamelus*) y chinkara (*Gazella bennetti*) del occidente de la India, por medio de un Análisis de Discriminantes. La similitud ecológica entre las cuatro especies fue analizada en términos de 20 variables, y se encontró que los dos cérvidos usan características de hábitat similares y que los dos bóvidos forman un grupo análogo. Estos dos grupos o “gremios” se diferenciaron entre sí en términos de la estructura de la vegetación, ya que los cérvidos seleccionaron la comunidad de bosque de *Anogeissus-Grewia*, mientras que los bóvidos ocuparon la comunidad arbustiva de *Acacia-Butea*. El solapamiento en el uso del hábitat entre los dos bóvidos parece ser inestable de acuerdo con aspectos teóricos de las dinámicas poblacionales de especies interactuantes. Sin embargo, hay cierta posibilidad de alcanzar una coexistencia estable mediada por la diferenciación sobre ejes de recursos alternativos, como los de alimento.

Resumo: De acordo com a teoria de nicho, o uso diferencial dos recursos partilhados facilita a coexistência das espécies numa comunidade. As relações de nicho têm sido estudadas numa variedade alargada de taxa, mas tal compreensão falta para um conjunto de ungulados tropicais no sudeste asiático. As relações de habitat foram investigadas para um conjunto de quatro ungulados selvagens viz., “chital” (*Axis axis*), “sambar” (*Cervus unicolor*), “nilgai” (*Boselaphus tragocamelus*) e “chincara” (*Gazella bennetti*) da Índia Ocidental, com recurso a análise discriminante. A semelhança ecológica entre as quatro espécies, foi analisada fazendo uso de 20 variáveis. Encontrou-se que os dois Cervídeos usavam o mesmo tipo de habitat e os dois bóvidos formavam um outro grupo análogo. Estes dois grupos, ou “associações”, diferenciam-se

*Corresponding Author: Tel.: 91 135 2640111-5, Fax: 91 135 264117. e-mail: goyalssp@wii.gov.in

entre si em termos da estrutura da vegetação, já que os cervídeos seleccionam a comunidade florestal dominada pela *Anogeissus-Grewia* enquanto os bóvidos ocupam a comunidade arbustiva de *Acacia-Butea*. A sobreposição quanto ao uso do habitat entre os dois bóvidos parece instável face aos aspectos teóricos da dinâmica de populações de espécies inter-actantes. Contudo, há espaço para conseguir uma coexistência estável diferenciando eixos alternativos de recursos como seja a alimentação.

Key words: Habitat, niche, Rajasthan, semi-arid, ungulates.

Introduction

The “niche” concept was introduced by Grinnell (1917) and Elton (1927), but reformulated by Hutchinson (1957) as the region in n -dimensional space where the fitness of an individual of a species is positive (Green 1971). Analysis of niche differences reflects the evolutionary adjustments in a community, designed to facilitate coexistence of ecologically similar species (Dueser & Shugart 1979; Reinert 1984). Often such analyses concern the limits of ecological similarity that necessitate the partitioning of resources for coexistence in a Gaussian framework (May 1973). However, there has been considerable debate over the number of dimensions to be used for applying field data to the Hutchinsonian model (Green 1971; Hutchinson 1968). It is believed that coexisting species segregate primarily by habitats and subsequently by dietary and temporal specialisations (Schoener 1974, 1983; Toft 1985). Multivariate statistical methods like Discriminant Analysis are a popular tool for representing niche geometry and studying natural communities (Green 1971; Dueser & Shugart 1978; Reinert 1984; Edge *et al.* 1987; Marnell 1998; Wei *et al.* 2000). Alongside other taxa like invertebrates, amphibians, reptiles, birds and small mammals (Green 1971; Schoener 1977; Cody 1978; Dueser & Shugart 1978; Reinert 1984; Marnell 1998; Jones & Barmuta 2000), temperate and Afrotropical large mammal assemblages have received some research inputs in this regard (Putman 1986; Jarman & Sinclair 1979; Jenkins & Wright 1988; Gordon & Illius 1989; Voeten & Prins 1999; Johnson *et al.* 2000) but these issues remain largely unattended for ungulates of the Oriental region.

We studied the niche relationships in an assembly of wild ungulates from the dry tropical forests of western India. Habitat use patterns of chital (*Axis axis* Erxleben, Cervidae) sambar (*Cervus unicolor* Kerr, Cervidae), nilgai (*Boselaphus tragocamelus* Pallas, Bovidae) and chinkara (*Gazella bennetti* Sykes, Bovidae) were studied using Discriminant Analysis as the analytical tool.

Materials and methods

Study area

Data were collected between November 2000 – April 2001 in the semi arid dry deciduous forests of Ranthambhore National Park (392 km²) which is a part of Ranthambhore Tiger Reserve (1334 km²; 25° 54' N – 26° 12' N and 76° 22' E – 76° 39' E), Rajasthan, western India. The vegetation of this region is tropical dry deciduous forest and tropical thorn forest (Champion & Seth 1968). *Anogeissus pendula* Edgew, *Acacia leucophloea* (Roxb.) Willd. and *Butea monosperma* (Lamk.) Taub. are the dominant trees, *Grewia flavescens* Juss. and *Copparis sepiaria* L. are the common shrubs (Bagchi 2001). Terrain is hilly, undulating with wide valleys and plateaus. The common wild ungulates are chital, sambar, nilgai and chinkara while wild pig (*Sus scrofa* L., Suidae) and blackbuck (*Antilope cervicapra* L., Bovidae) also occur in some areas and the major carnivores are tiger (*Panthera tigris* L.) and leopard (*Panthera pardus* L.).

Sampling

Animal distribution was sampled for two seasons (winter: November 2000 – February 2001 and summer: March – April 2001) in an intensive

study area (34 km²) using eight line transects (ranging from 1.5 to 2.8 km) totaling 19.5 km. A transect was divided into 200 m segments, each being represented by a sampling station of a 10 m radius plot having a nested 5 m radius plot where several habitat variables were measured. Each sampling station (n = 99) represented its corresponding transect segment and animals sighted in a particular segment were considered to be using the properties reflected by the sampling station.

In each season, data on 19 habitat variables (Table 1) were collected from every sampling station and in addition, the evidence for human disturbances like livestock grazing was also recorded.

Table 1. Description of the habitat variables collected in Ranthambhore National Park during November 2000- April 2001. (Bagchi *et al.* 2003).

Variables	Winter	Summer
	Mean ± SD	Mean ± SD
Tree variables ¹		
No. of trees	12.56 ± 9.79	–
GBH of trees in a plot	57.71 ± 25.59	–
Sum of all GBH per plot (cm)	645.08 ± 406.32	–
Height of canopy (m)	7.21 ± 2.33	–
Leaf stage of trees	0.97 ± 0.17	1.03 ± 0.30
Greenness of trees	1.04 ± 1.21	0.47 ± 0.90
Canopy cover (%)	45.1 ± 38.1	–
Shrub variables ²		
No. of shrubs	8.47 ± 7.30	–
Shrub height (cm)	87.40 ± 82.17	–
Leaf stage of shrubs	0.89 ± 0.40	1.06 ± 0.64
Greenness of shrubs	1.35 ± 1.34	0.83 ± 1.28
No. of shrub species	1.88 ± 1.31	–
Ground cover ^{1*}		
% Grass cover	7.30 ± 10.07	–
% Litter cover	20.45 ± 13.22	–
% Rock	9.24 ± 6.60	–
% Bare soil	12.64 ± 10.63	–
Others		
Litter weight ³ (gm)	5.32 ± 4.20	4.42 ± 3.81
Slope ¹ (degrees)	5.78 ± 6.80	–
Distance to water ¹ (m)	1085 ± 445	1150 ± 400

¹ from 10 m radius plot, ²from 5 m radius plot, ³by 25 cm x 25 cm quadrats

* data on ground cover needed arc sine transformation.

Variables were related to vegetation structure and composition, phenology, ground cover (using point intercept method), weight of palatable litter (using 25 cm x 25 cm quadrats) and distance to nearest water source (Table 1). Phenological data like leaf stage of trees and shrubs was scored on a 5-point scale (0 to 4) of proportion young to mature leaves, greenness was scored on a 5-point scale (0 to 4) from fully green to fully dry. Distance to water from a sampling station was estimated from a map (1:50,000 scale Survey of India toposheets) and put into 500 m intervals. Each transect was walked seven times in a season to record animal distribution, resulting in 273 km of walk. Sightings of each species recorded in a segment of a transect were related to the corresponding habitat measurements.

Statistical analysis

Habitat-separation between four species was analysed in terms of the differences between the properties of the segments in which they were sighted. First step in Discriminant Analysis was a multivariate analysis of variance (MANOVA) for testing the hypothesis of equality of the four group centroids (Reinert 1984; Schneier 1993) using Pillai's trace as the test statistic (Venables & Ripley 1994). Subsequently, a pair-wise multiple comparison was done using Hotelling's T-square test. Based on the results of MANOVA, the second step was Discriminant Function Analysis (DFA) to examine separation between groups that were identified as distinct (Green 1971; Dueser & Shugart 1978; Reinert 1984; Edge *et al.* 1987; Marnell 1998; Wei *et al.* 2000). Stepwise procedure was adopted with maximisation of distance between group-centroids (Mahalanobis distance) set as the criterion (Edge *et al.* 1957). Discriminant Function Scores from a secondary DFA model with all four species were used to assess the degree of habitat-overlap following May & MacArthur (1972) and May (1973, 1975). Box's modification of Bartlett's test was used to evaluate homogeneity of covariance matrices; but we could not test for multivariate normality of our data. Analyses were carried out with data from two seasons using SPSS (Norussis 1994) and S-PLUS (Mathsoft Inc.; Venables & Ripley 1994) softwares.

Results

Results are based on 258 sightings of chital, 198 for sambar, 196 for nilgai and 52 sightings of chinkara.

MANOVA showed that the four species utilised significantly different habitat features (Winter: Pillai's trace = 0.35, $F_{(20, 357)} = 1.99$, $P < 0.01$; Summer: Pillai's trace = 0.35, $F_{(20, 357)} = 3.55$, $P < 0.01$). Results from Hotelling's T-square test revealed that there were just two distinct groups. The cervids (chital-sambar) used similar habitat features in each season (Winter: $F_{(20, 128)} = 1.59$, Pr. = 0.06; Summer: $F_{(20, 118)} = 1.58$, Pr. = 0.07) and so did the bovids (nilgai-chinkara) (Winter: $F_{(20, 128)} = 0.53$, Pr. = 0.93; Summer: $F_{(20, 118)} = 0.93$, Pr. = 0.54). However, there were statistically significant differences between all cervid-and-bovid species-pairs (Table 2). The assumption of equal dispersion of matrices was not met by the data (Winter: Box's M = 140.39, $F_{(18, 37168)} = 7.47$, $P < 0.01$; Summer: Box's

M = 97.12, $F_{(18, 20454)} = 5.13$, $P < 0.01$), suggesting that the four species exhibit different patterns of variation with respect to original variables. Nevertheless, such a violation for ecological data does not negate the derivation of biologically meaningful results (Green 1971; Reinert 1984).

Guided by the results from MANOVA, Discriminant Functions were constructed with two groups (cervids and bovids). This DFA identified a single significant Discriminant Function for each season (Winter: eigen value = 0.70, $\chi^2_{df5} = 78.20$, $P < 0.01$; Summer: eigen value = 0.45, $\chi^2_{df3} = 50.69$, $P < 0.01$). The correlations between the original variables and the Discriminant Functions (Table 3) revealed that cervids differentiated from bovids in terms of shrub density, grass cover and tolerance to livestock grazing during winter. Similarly they differentiated in terms of tree greenness, grass cover, slope, proximity to water and toler-

Table 2. Pair-wise comparison by Hotelling's T-square test for equality of group-centroids of four species in Ranthambhore National Park, in terms of habitat-use; across two seasons. (Bagchi *et al.* 2003).

Species pair	F value		Hotelling's T ² Probability	
	Winter (df = 20, 128)	Summer (df = 20, 118)	Winter	Summer
Chital-Sambar	1.59	1.58	0.06	0.07
Chital-Nilgai	2.27	1.97	<0.01	<0.05
Chital-Chinkara	2.96	2.85	<0.01	<0.01
Sambar-Nilgai	5.87	4.56	<0.01	<0.01
Sambar-Chinkara	5.72	3.93	<0.01	<0.01
Nilgai-Chinkara	0.53	0.93	0.93	0.54

Table 3. Summary of significant Discriminant Functions developed by stepwise DFA to differentiate between cervids (chital and sambar) and bovids (nilgai and chinkara) of Ranthambhore National Park, for two seasons. (Bagchi *et al.* 2003).

Seasons	Eigen value	χ^2	Coefficient	Canonical correlation	
				Cervids	Bovids
Winter	0.70	78.20*	Tree greenness	1.45	1.05
			Grass cover	3.90	-0.28
			Slope	5.57	4.19
			Water	3.25	3.83
			Livestock grazing	3.90	5.50
Summer	0.45	50.69*	No. of shrubs	0.23	0.15
			Grass cover	8.94	4.71
			Livestock grazing	1.87	3.98

* denotes $P < 0.01$

ance to livestock grazing in during summer. Over all classification success of the model was between 76 to 78%.

Discussion

Niche partitioning

Since all four species were not using identical habitat features, this led to significant results for the first step of analysis. However, a closer examination revealed that there were in fact just two groups or “guilds”. The cervids were ecologically similar to each other and so were the two bovids (Table 2). Chital and sambar were using areas with higher shrub density, more grass cover, remained closer to water points and were intolerant of livestock grazing (Table 3). The bovids were using areas with greener trees, were more tolerant of livestock grazing and associated degradation causing lower grass cover (Table 3).

The habitat features used by the cervids as per the DFA model, pertain to areas having thick *Grewia* understory in *Anogeissus* dominated forests (Bagchi 2001) and hence they seem to occupy the “forest guild”. Whereas, habitat feature of the two bovids (Table 3) reflect scrub-woodland habitat characterised by *Acacia-Butea* type of vegetation (Bagchi 2001). Hence bovids seem to occupy the analogous “scrub guild”.

This pattern of niche differentiation reflects certain phylogenetic aspects of these species. Sambar is oriental in origin and has evolved in forested environments (Schaller 1967; Corbet & Hill 1992). Chital is autochthonous and is adapted to forest edges and ecotones (Schaller 1967; Eisenberg

1981). Nilgai is also an autochthonous species, but has evolved in arid environments, characterised by scrub vegetation (Prater 1971). Chinkara is related to African gazellss and have evolved in open country (Prater 1971; Corbet & Hill 1992). Thus the pattern of niche-differentiation in this assembly as suggested by out data gives useful insight into the evolutionary history of these species. The formation of forest and scrub dwelling guilds can be intuitively appreciated, with Discriminant Analysis providing an elegant description of their niche relationships.

Niche overlap

Following May & MacArthur (1972), a measure of habitat overlap was calculated as the ratio of distance between group centroids (d) to the variance along the resource axis (w). For our data, d was difference between mean Discriminant Scores and w was standard deviation of the scores for each species; derived from the second DFA model created with all four groups. Since species have different habitat-breadths, an asymmetrical habitat-overlap matrix was obtained (Table 4). Magnitude of this ratio increases as overlap decreases and has been theoretically determined to approximate or exceed 1.0 for stable coexistence in a community (May & MacArthur 1972; May 1973). The ratio of d/w is inversely related to the *competition coefficient* used to model multi-species interaction in ecological communities by non-linear differential equations (May 1973). So the habitat overlap matrix (Table 4) is analogous to the community-matrix of Levins (1968) and May (1973, 1975). Thus, low values of d/w would relate to a

Table 4. Asymmetrical habitat-overlap matrix of the four species in Ranthambhore National Park for two seasons.

Seasons	Species	Overlap with			
		Chital	Sambar	Nilgai	Chinkara
Overlap of Winter	Chital	–	1.32	1.41	1.95
	Sambar	0.96	–	1.95	2.33
	Nilgai	1.33	2.56	–	0.50*
	Chinkara	1.22	2.04	0.33*	–
Overlap of Summer	Chital	–	0.21*	1.42	1.54
	Sambar	0.23*	–	1.82	2.35
	Nilgai	2.20	2.53	–	0.19*
	Chinkara	3.03	1.95	0.39*	–

*denotes instances where habitat-overlap appears unstable.

high *competitive coefficient* and consequent effects on population of interacting species. But, when $d \gg w$, there is minimal competitive interaction (May 1973) and subsequent population stability.

Suggestions for instability were found in the overlap between nilgai and chinkara in both seasons (ratio: 0.19 to 0.50) and between chital and sambar during summer (ratio: 0.21, 0.23) (Table 4). This apparent instability between nilgai and chinkara can potentially cause fluctuations in the latter's population because nilgai occurs in much higher densities than chinkara in the region (Bagchi 2001). There is increasing evidence that semi-arid ungulate assemblages are disequilibriumal (Ellis & Swift 1988; Illius & O'Connor 1999) and our data seem to suggest that the extent of ecological similarity might be a determinant of theoretically predictable population fluctuations. But the relationship between chital and sambar is likely due to forage limitations during summer and might not be a permanent feature in the community (as suggested by the values for winter season, Table 4). Such a situation can arise due to seasonal fluctuations in forage quality and quantity in this semi-arid environment.

Conclusions

Discriminant Analysis proved an efficient descriptive tool to elucidate the niche relationships in this assembly of four ungulates. Cervids and bovids were seen to differentiate primarily according to vegetation structure. The overlap in habitat use between the two bovids appears unstable their populations might not be equilibriumal. The overlap between chital and sambar seems to be due to seasonal forage scarcity in this semi-arid environment. However, there is scope for the species to differentiate along alternate resource axes (e.g. food) and attain a stable state of coexistence. Since, our data only suggest a possible relation between niche-overlap and population fluctuations, further studies into population dynamics of these species would help in developing a greater understanding about the functioning of such semi-arid ecosystems.

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