NICHE RELATIONSHIPS OF AN UNGULATE ASSEMBLAGE IN A DRY TROPICAL FOREST

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Niches of 2 cervids (chital, *Axis axis* and sambar, *Cervus unicolor*) and 2 bovids (nilgai, *Boselaphus tragocamelus* and chinkara, *Gazella bennetti*) from semiarid forests in western India were studied for habitat use and food habits. Habitat use was analyzed by discriminant analysis using 20 variables, and food habits investigated by analyzing undigested plant remains in pellets. Cervids and bovids differentiated primarily according to vegetation and terrain features, and the 2 deer species showed separation in diet. The 2 cervids selected forested areas, whereas the 2 bovids selected scrubland and were more tolerant of disturbances like livestock grazing and also showed a high similarity in food habits. Habitat use and food habits were analyzed with nonmetric multidimensional scaling to assess their combined effects. A greater degree of similarity in resource use between the 2 bovids suggests that they may be competitive, at least during periods of forage scarcity.

Key words: *Axis axis*, *Boselaphus tragocamelus*, *Cervus unicolor*, discriminant analysis, *Gazella bennetti*, niche theory, nonmetric multidimensional scaling

The "niche" (Hutchinson 1957) is recognized as the region in n-dimensional space where the fitness of an individual of a species is positive (Green 1971). Although neutralists have questioned such an approach, describing patterns of coexistence of species traditionally assumes that each species is adapted to exploit a unique niche—shady or sunny, wet or dry, etc., thus allowing coexistence (Whitfield 2002). The use of multiple resources allows for partitioning, resulting in niche differentiation and coexistence (Schoener 1974). In a community (or guild), niche differentiation occurs along several dimensions to facilitate coexistence, and the number of dimensions increases with species richness (Schoener 1974, 1983). Under the Hutchinsonian premise of n-dimensional hypervolume, niche differentiation (and resource-use overlap) is generally complementary; when species are similar on 1 dimension, they differ on another. Habitat is the most common dimension partitioned, followed by food resources (Schoener 1974, 1983; Toft 1985). Temporal partitioning becomes important in environments where resources are renewed rapidly (Kotler et al. 1993; Ziv et al. 1993). Besides invertebrates, amphibians, reptiles, birds, and small mammals (Cody 1978; Dueser and Shugart 1978; Green 1971; Jones and Barmuta 2000; Marnell 1998; Reinert 1984), temperate and Afro-tropical assemblages of large mammals also have been studied (Gordon and Illius 1989; Jarman and Sinclair 1979; Jenkins and Wright 1988; Johnson et al. 2000; Putman 1986; Voeten and Prins 1999). However, these issues remain largely unstudied for ungulates of the Oriental region, and very few reports are available (Green 1987; Johnsingh and Sankar 1991; Martin 1982).

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To examine the principle of complementary resource-use overlap, we studied niche relationships in an assemblage of wild ungulates from dry tropical forests of western India. Habitat separation among 2 cervids (chital, *Axis axis* and sambar, *Cervus unicolor*) and 2 bovids (nilgai, *Boselaphus tragocamelus* and chinkara, *Gazella bennetti*) was studied. Simultaneously, an investigation of food habits was conducted for assessing ecological separation along these 2 dimensions. We predicted that if a species pair was similar on any 1 of these dimensions, they would be segregated from the other. Specifically, if they showed similarity in habitat use, they would differentiate in their diet.

MATERIALS AND METHODS

Study area.—Data were collected between November 2000 and April 2001 in the semiarid dry deciduous forests of Ranthambhore National Park (392 km^2), which is part of Ranthambhore Tiger Reserve (1,334 km^2; 26°N, 76°E), Rajasthan, western India. The region is characterized by a tropical dry climate with 4 distinct seasons. March to June is summer, followed by monsoon (July to August), a short postmonsoon (September to October), and winter (November to February). Average annual rainfall is about 800 mm (mostly during July and August), and droughts are frequent. During the study, 24 mm of precipitation was received. The vegetation of this region is tropical dry deciduous forest and tropical thorn forest (Champion and Seth 1968). *Anogeissus pendula*, *Acacia leucophloea*, and *Butea monosperma* are the dominant trees, and *Grewia flavescens* and *Capparis sepiaria* are the common shrubs (Bagchi 2001). Leaf fall sets in by October, eventually leading to a period of forage scarcity during summer until there is fresh sprouting during monsoon followed by dry winters. The terrain is hilly and undulating, with valleys of *Acacia–Butea* scrub and slopes dominated by *Anogeissus* forest. In addition to the 4 ungulates studied, wild pig (*Sus scrofa*) and blackbuck (*Antilope cervicapra*) also occur in some areas. Major carnivores are tiger (*Panthera tigris*) and leopard (*Panthera pardus*).

Sampling.—Distribution of animals was sampled for 2 seasons (winter: November 2000 to February 2001; summer: March 2001 to April 2001) in a 34-km^2 study area using 8 line transects. Transects were laid in a stratified random manner (according to broad topographic classes like slopes, valleys, and plateaus) and ranged from 1.5 to 2.8 km, for a total of 19.5 km. Each transect was divided into 200-m segments, each segment represented by a sampling station located at the midpoint, where a 10-m radius plot contained a nested 5-m radius plot in which habitat variables were measured. A solitary animal or group of animals sighted in a particular segment of a transect was considered to be selecting the habitat properties represented by the sampling station ($n = 99$) within the segment.

In each season, data on 19 habitat variables (Table 1) were collected from every sampling station. In addition, evidence of human disturbances like livestock grazing (dung of domesticated species, such as cattle, *Bos taurus* and buffalo, *Bubalus bubalis*) within each sampling station was also recorded. Variables were related to vegetation structure and composition of the tree layer (10-m plot) and shrub layer (5-m plot), phenology, ground cover (determined using line intercept method on 10-m plot and arcsine-transformed for analysis), weight of palatable litter (mainly fallen *Anogeissus* leaves) after removing inedible material (using four 25 by 25-cm quadrats placed randomly inside the sampling station), and distance to nearest water source. Leaf stage of trees and shrubs was scored on a 5-point scale based on proportion of young leaves (0) to mature (4) leaves. Greenness was scored on a similar 5-point scale from fully green (4) to fully dry (0). Distance to water from a sampling station was estimated with 500-m precision from a map (1:50,000 scale, Survey of India topographic maps). Each transect was walked 7 times in a season (by the 1st author and an assistant) to record distribution of animals, resulting in a total of 273 km. Successive walks on the same transect were separated by a period of 6–7 days. Sightings of each species recorded in a transect segment were related to the corresponding habitat measurements.

Fresh fecal samples of the 4 species were collected opportunistically and dried for analysis of undigested plant fragments. Twenty pellet groups of each species were collected for each season, and 2 pellets from each pellet group were selected randomly to make 2 composite samples. Following Holechek (1982), each com-

TABLE 1.—Habitat variables collected from sampling stations ($n = 99$) in Ranthambhore National Park, India, during November 2000 to April 2001. Tree and ground cover, slope, and distance to water were measured in 10-m radius plots. Shrub variables were measured in 5-m radius plots, and litter weight within 4 quadrats (25 by 25 cm) inside the 10-m radius plots. Girth at breast height (GBH) of trees was measured to the nearest centimeter.

Variable	Winter		Summer	
	$\bar{X}$	SD	$\bar{X}$	SD
Tree variables				
No. of trees per 10-m plot	12.56	9.79		
GBH of trees in a plot (cm)	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[a]	0.97	0.17	1.03	0.30
Greenness of trees[b]	1.04	1.21	0.47	0.90
Canopy cover (%)	45.1	38.1		
Shrub variables				
No. of shrubs per 5-m plot	8.47	7.30		
Shrub height (cm)	87.40	82.17		
Leaf stage of shrubs[a]	0.89	0.40	1.06	0.64
Greenness of shrubs[b]	1.35	1.34	0.83	1.28
No. of shrub species per plot	1.88	1.31		
Ground cover				
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 (g)	5.32	4.20	4.42	3.81
Slope (°)	5.78	6.80		
Distance to water (m)	1,085	445	1,150	400

[a] Scale of leaf stage on a 5-point scale, from 0 (young) to 4 (mature).

[b] Scale of greenness on a 5-point scale, from 4 (fully green) to 0 (fully dry).

posite sample was ground with a grinding mill (Cyclotec-1093 sample mill, Tecator, Hoganen, Sweden) to 1-μm size, treated with Hertwig solution, and mounted with Hoyer solution on glass slides. Three slides from each sample were examined under a compound microscope to identify undigested plant fragments as ''grass'' or ''browse'' (Stewart 1967). Fifty fragments were identified in each slide to determine the proportion of grass in the diets of the 4 species, which placed them along a grazer–browser continuum. This approach is relatively crude and is often influenced by differential digestibility of plants (Stewart 1967).

Statistical analysis.—Habitat segregation among the 4 species was determined from differences in variables of the transect segments in which animals were sighted. Discriminant anal-

ysis involved a multivariate analysis of variance (MANOVA) to test the hypothesis of equality of the 4 group centroids (Reinert 1984; Schneier 1993) using Pillai's trace as the test statistic (Venables and Ripley 1994). Subsequently, pairwise multiple comparisons were made using Hotelling's T^2 test. Based on the results of MANOVA, the 2nd step undertaken was discriminant function analysis to examine the means of separation between groups (Dueser and Shugart 1978, 1979; Edge et al. 1987; Green 1971; Marnell 1998; Reinert 1984; Wei et al. 2000). A stepwise procedure was adopted with maximization of distance between group centroids (Mahalanobis distance) as the criterion (Edge et al. 1987). Discriminant functions were created 1st to differentiate between the cervids and bovids and subsequently to differentiate among all 4

species, with discriminant function scores considered as the ''resource utilization functions'' (May 1973; May and MacArthur 1972). Differences of mean discriminant function scores of the 4 species were used to obtain their relative separation as a dissimilarity matrix. A corresponding dissimilarity matrix was constructed to represent the relative separation of the 4 species in terms of food habits along the grazer–browser continuum.

The information in these 2 dissimilarity matrices was combined using nonmetric multidimensional scaling to assess the joint relationship and the nature of ecological separation. Nonmetric multidimensional scaling attempts to find structure in sets of distance measures by assigning observations to specific locations in a conceptual space (2-dimensional for our data), such that (dis)similarities between points in this space match the given (dis)similarities as closely as possible (Norussis 1997). Because this enables representation of the 4 niches, as in Venn diagrams, we considered nonmetric multidimensional scaling an appropriate way of analyzing niche geometries. Number of iterations was decided on the basis of Young's S-stress formula and was stopped when S-stress was less than 0.005 (Norussis 1997; Spence 1978).

Analyses were carried out with data from each season using SPSS (Norussis 1994, 1997) and S-PLUS software (S-PLUS 1998; Venables and Ripley 1994), with significance judged at α = 0.05 level. The assumption of equal dispersion of matrices was not met by the data, suggesting that the 4 species exhibited 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). Also, because more than 1 species can occur in the same segment, this can inflate likelihood of type II errors in the discriminant function analysis model. Hence, the true differences between the 4 niches are likely to be slightly greater than that suggested by our analysis. Data are given as mean ± SD.

RESULTS

Results are based on 258 sightings of chital (1,196 individuals) on 45 transect segments in winter and 46 in summer. Similarly there were 198 sightings of sambar

(739 individuals) spread over 40 segments in winter and 37 in summer; 196 sightings of nilgai (542 individuals) from 44 segments in winter and 41 in summer; and 52 sightings of chinkara (134 individuals) from 22 segments in winter and 23 in summer. Sighting distance for all species considered together was 47.5 ± 28.5 m from the transect line. Sixty of the 708 sightings were at distances over 100 m, with a maximum of 167 m from the transect.

Results from MANOVA suggested that the 4 species used significantly different habitat features (winter: Pillai's trace = 0.35, $F = 1.99$, $d.f. = 20, 357$, $P < 0.01$; summer: Pillai's trace = 0.35, $F = 3.55$, $d.f. = 20, 357$, $P < 0.01$). Results from Hotelling's T^2 test revealed 2 distinct groups: the cervids used similar habitat features in each season (winter: $F = 1.59$, $d.f. = 20, 128$, $P = 0.06$; summer: $F = 1.58$, $d.f. = 20, 118$, $P = 0.07$), as did the bovids (winter: $F = 0.53$, $d.f. = 20, 128$, $P = 0.93$; summer: $F = 0.93$, $d.f. = 20, 118$, $P = 0.54$). However, we found statistically significant differences between all cervid and bovid species-pairs (Table 2).

Linear discriminant functions constructed with cervids and bovids (Table 3) revealed that the 2 groups were differentiated primarily in terms of vegetation structure and topography. In general, the deer used areas with higher shrub density and greater grass cover, remained closer to water points, and were intolerant of livestock grazing. Overall classification success of the model was 76–78%. A separate discriminant function analysis (winter: eigenvalue = 0.70, $\chi^2 = 78.20$, $d.f. = 5$, $P < 0.01$; summer: eigenvalue = 0.45, $\chi^2 = 50.69$, $d.f. = 3$, $P < 0.01$) was done with all 4 species to obtain their discriminant function scores as a dissimilarity matrix (difference between mean scores). In general, there was some similarity between the 2 deer and between the 2 bovids, and cervid–bovid pairs showed greater differences.

Percentage contribution of grass to the food habits of the 4 species was as follows:

TABLE 2.—Pairwise comparison by Hotelling's T^2 test for equality of group centroids of 4 species (chital, *Axis axis*; sambar, *Cervus unicolor*; nilgai, *Boselaphus tragocamelus*; chinkara, *Gazella bennetti*) in Ranthambhore National Park, India, in terms of habitat use across 2 seasons.

| | F value | | Hotelling's T^2 probability | |
| | Winter | Summer | | |
Species pair	($d.f.$ = 20, 128)	($d.f.$ = 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

chital—winter 35 ± 6%, summer 29 ± 6%; sambar—winter 62 ± 7%, summer 50 ± 7%; nilgai—winter 39 ± 5%, summer 28 ± 3%; chinkara—winter 48 ± 6%, summer 26 ± 3%. The relative separation of the 4 species was the distance between their mean positions along the grazer–browser continuum, in the form of a dissimilarity matrix. In general, chital and nilgai had similar food habits, as did nilgai and chinkara. Sambar's food habits differed considerably from the other 3 species.

By combining habitat and food dissimilarity matrices through nonmetric multidimensional scaling, 2 independent axes were recognized for each season, representing (dis)similarity among the 4 species (Fig. 1). Differentiation between the deer was greater in food habits than along the habitat di-mension. The bovids attained a lesser degree of separation overall, particularly during summer.

DISCUSSION

Discriminant analysis and nonmetric multidimensional scaling provided an effective description of niche relationships in this assemblage of 4 ungulates. The complementary resource-use overlap principle (Schoener 1974, 1983) could be represented geometrically when habitat and dietary relationships were combined. Cervids and bovids differentiated primarily according to vegetation structure and features of the terrain, and the 2 deer achieved separation in diet. A greater degree of similarity in resource use existed between the 2 bovids, especially during summer.

TABLE 3.—Summary of significant discriminant functions developed by stepwise discriminant function analysis to differentiate between cervids (chital, *Axis axis*, and sambar, *Cervus unicolor*) and bovids (nilgai, *Boselaphus tragocamelus*, and chinkara, *Gazella bennetti*) of Ranthambhore National Park, India, for 2 seasons.

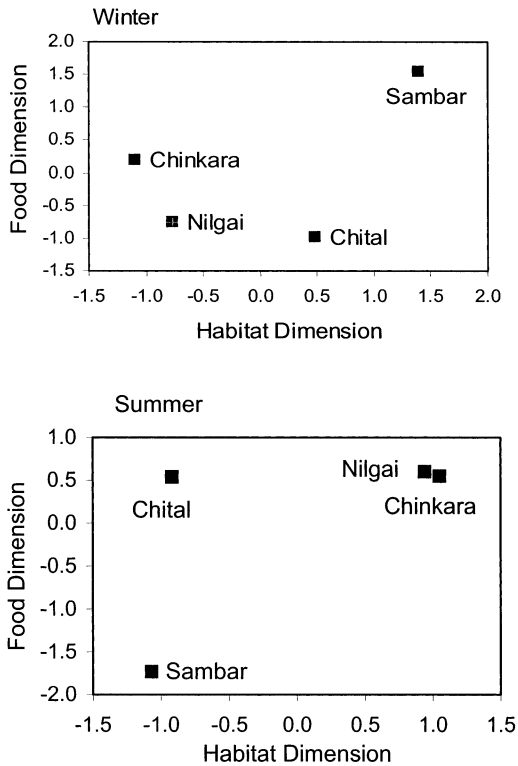| | | | | Fisher's linear discriminant functions | |
Season	Eigen value	χ^2	Variable	Cervids	Bovids
Winter	0.70	78.20	Tree greenness	1.45	1.05
		($d.f.$ = 5, P < 0.01)	Grass cover	3.90	−0.28
			Slope	5.97	4.19
			Distance to water	3.25	3.83
			Livestock grazing	3.90	5.50
Summer	0.45	50.69	No. of shrubs	0.23	0.15
		($d.f.$ = 3, P < 0.01)	Grass cover	8.94	4.71
			Livestock grazing	1.87	3.98

FIG. 1.—Relative positions of 4 species of ungulates (chital, *Axis axis*; sambar, *Cervus unicolor*; nilgai, *Boselaphus tragocamelus*; chinkara, *Gazella bennetti*) along a 2-dimensional (habitat use and diet) resource spectrum for 2 seasons in Ranthambhore National Park, India, as constructed by nonmetric multidimensional scaling.

Sites selected by the deer were characterized by *Grewia* understory in *Anogeissus*-dominated forests (Bagchi 2001), and hence they seem to occupy the "forest guild." The 2 bovids, however, selected scrub–woodland habitat characterized by *Acacia–Butea* type of vegetation (Bagchi 2001) and seem to occupy the "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 (Corbet and Hill 1992; Schaller 1967). Chital and nilgai are autochthonous, but the former is adapted to forest edges and ecotones (Eisenberg 1981; Schaller 1967), and

the latter has evolved in arid environments characterized by scrub vegetation (Prater 1971). Chinkara is related to African gazelles and has evolved in open country (Corbet and Hill 1992; Prater 1971). Thus, the pattern of habitat differentiation in this assemblage, as suggested by our analysis, gives useful insights into the evolutionary history of its constituents.

Unlike the deer, little evidence for complementary overlap was found between nilgai and chinkara, particularly during summer. Finer details regarding food selection do not become apparent in coarse-level analysis such as grass–browse content in diet. The small-sized chinkara is likely to be more selective in foraging than the large-bodied nilgai, but because these semiarid forests support only a few fodder plants, differentiation along this axis is unlikely. It is possible that nilgai and chinkara would compete, at least during periods of forage scarcity such as summer, which can be a regular seasonal feature in such semiarid environments. Low levels of niche-differentiation relate to a higher competitive coefficient and the consequent effects on population dynamics of the interacting species (May 1973; May and MacArthur 1972). Such resource-use overlap can especially affect the population dynamics of chinkara because it occurs at much lower densities than nilgai (Bagchi 2001). Although debatable, semiarid ungulate assemblages can often be nonequilibrial (Ellis and Swift 1988; Illius and O'Connor 1999), and further studies into niche relationships, niche geometry, and population dynamics of these species would contribute to a greater understanding of such semiarid ecosystems.

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