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European Journal of Zoological Research, 2013, 2 (2):1-9
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ISSN: 2278–7356

Habitat selection and niche segregation between chital and nilgai in Keoladeo National Park, India

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ABSTRACT

Winter habitat selection by two sympatric species chital and nilgai was studied in the semi-arid environment from January 2006 for four months. Pellet group count was used to study the degree of habitat segregation at spatial scale. A total of 2042 pellet groups of chital and 255 pellet groups of nilgai were recorded at 100 sampling points laid randomly across five different habitat types. Chi squared analysis and resource selection indices revealed that both species utilized different habitat categories differentially thereby giving a pattern of selectivity amongst resource states. Chital utilized, more than its availability, woodland habitat with high shrub density and diversity and sparsely available grass and herb cover which formed under storey during winter. Nilgai, on the other hand, showed utilization, more than availability in dense to discontinuous thickets with high tree density and shrub cover to browse. Chital showed a wider niche breadth (0.911) in comparison to nilgai (0.766) with an overall niche overlap of 0.762. The segregation between the two species during winter was hypothesized to be low with high overlap at the spatial scale. It was found that there is high potential for competition between the two species, and the presence of one species may negatively influence the distributional pattern of the other.

Key words: Chital, habitat segregation, niche overlap, nilgai, resource selection.

INTRODUCTION

The term habitat refers to an area that meets an animal's basic life requisites such as food, water, cover and space [1]. A number of interdependent variables play a vital role in the formation of a particular habitat. According to Norman *et al*. [2], an animal occupies or utilizes a habitat based on the spatio-temporal variation of such interdependent habitat variables. Most of the wildlife habitats are shared by more than one species of wild ungulates. Wild ungulates, coexisting in the same habitat, use it differentially with reference to resource, space and time as a result of resource competition or overlap [3, 4, 5]. The abundance of animals and distribution of their populations vary in space and time, often with availability of the environmental components necessary for the life [6]. Even among two species using the same habitat, there is a certain degree of temporal or dietary separation. Temporal and spatial separation in the habitat utilization has been reported for most wild ungulates species in India [7, 8, 9, 10, 11, 12] and elsewhere [3, 13, 14, 15, 16]. Habitat utilization and selection and thus, partitioning of resource(s) or utilization pattern, has often been described as a complex multi-dimensional, multi-scaled process [17, 18] which is rarely a random phenomenon [19, 20]. Although, competition is generally believed to be a central biotic factor structuring herbivore communities [21, 22] other factors may also influence the use of habitat by herbivores: weather conditions and predators [19] and the food supply [23, 24].

At the study site natural predation is negligible as there is no large carnivore but occasionally Golden jackal (*Canis aureus*) and feral dogs do predate on chital [25]. We focused on the role of interspecific competition in habitat selection by chital and nilgai particularly in winter when available resources further shrink to scarcity. We then

assessed the niches of the two species and the overlap there in different habitat states. We hypothesized that both species utilize the different habitat patches uniformly.

MATERIALS AND METHODS

The World Heritage as well as Ramsar site Keoladeo National Park (hereafter KNP) (27°7.6′–27°12.2′N and 77°29.5′–77°33.2′E) was created over 250 years ago and was initially a natural depression. It is a 29 km^2 walled preserve, divided into 15 management blocks and surrounded by about 14 villages. Thick alluvium dominates the park and scattered saline patches are also present especially in the drier areas. The temperature varies from 0.5 °C to 50 °C, the minimum being in January and the maximum in May–June. Rainfall occurs through the south-west monsoon, mainly during July–August with an average rainfall in the area for the past 100 years being 655 mm. The KNP is rich in its fauna and flora. It has more than 350 species of birds, 27 mammals, 13 reptiles, 7 amphibians, 40 fish 16–18 and 375 species of angiosperms, of which 90 are wetland species [26]. The vegetation of the area is a mixture of xeric and semi-xeric species explicitly described by Prasad *et al*. [27]. The ungulate fauna comprise sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelus*), chital (*Cervus axis*) and wild pig (*Sus scrofa*). Although, the National Park consists these four species of ungulates but data for sambar and wild boar was not found enough for analysis.

The area available was estimated by grid approximations of the map of the study area and the overall vegetation was categorized into five major habitat types (excluding the wetland ~13.8% of the total park area) *viz.* - dense to discontinuous thorn thickets (DDTT ~13.8%) mainly represented by *Acacia nilotica*, Z*yziphus mauritiana, Prosopis cineraria* and *P. juliflora*, open low grassland (OLGR ~20.7%) represented by *Cynodon dactylon, Sporobolus sp., Dichanthium annulatum, Eragrotis sp*. etc., woodland (WDLN ~10.3%) chiefly comprising climax stage species such as *Mitragyna parvifolia, A. nilotica* and *Z. mauritiana* scattered shrubs such as *Kirgenalia reticulata* and *Capparis separia* are found in the ground vegetation, tall grass savanna (TGRS ~34.5%) representing *Vitiveria zizanoides* and *Desmostachya bipinnata* and scrubland (SCRB ~6.9%) mostly with *P. cineraria, C. separia, K. reticulata* and *Salvadora persica* interspersed by *Mitragyna parvifolia* and *Schyzygium cumini*.

The study was conducted from January through April 2006 during which a total of 100 sampling points were laid randomly away from trails by pacing [28]. Each sampling point consisted of two concentric circular plots of radii 10 m and 5 m. The vegetation variables such as tree numbers were counted in the bigger plot. Percent canopy cover was recorded at four random points in each of the sampling plots using a mirror of 25 cm x 25 cm divided into 100 equal grids. Similarly, shrub species and their numbers were quantified through the smaller plot. The ground cover (grass, herb, litter or bare ground) was estimated by point intercept method [29] by laying a meter stick, graduated at 5 cm intervals, in four cardinal directions in the bigger plot.

Species diversity of shrubs was calculated using Shannon-Weiner species diversity index as:

$$H' = -\sum p_i \times \log_e p_i$$

where p_i = proportion of the *i*th species in the sample. All quantitative data were transformed to ensure that all the habitat variables were distributed normally following Fowler and Cohen [30] and Zar [31].

We counted faecal pellet groups in 5 m radius circular plot sampling unit which was found optimum for the purpose in the study area by Noor *et al*. [32], pellet groups of different species were differentiated on the basis of shape and size only fresh pellets were counted avoiding disintegrated old pellets.

Density of pellet groups was calculated for each sampling point as:

$$\text{Density } (ha^{-1}) = \text{Number of pellet groups} \times 10{,}000/\text{Area of sampling unit } (78.5\ m^2)$$

We determined the habitat preference patterns of the two species by comparing usage and availability. When resources are used disproportionately to their availability, use is said to be selective [33]. The selection of a habitat was determined by estimating selection ratios for different habitat categories. The value of the selection ratio of the habitat unit is proportional to the probability of that unit being utilized by the study animal, given that the selecting animal has unrestricted access to the entire distribution of available units. This index was chosen because it does not fluctuate with inclusion or exclusion of seldom-used resources [34] and is considered more versatile than other selection preferences indices [35]. The index is based on the selection ratio w_i, which is the proportional use divided by the proportional availability of each resource category *i*.

$$w_i = o_i / \pi_i$$

where o_i is the proportion of the observed use of resource in habitat category *i*, π_i is the proportion of the available resource in category *i*. A w_i value larger than 1 indicates a positive selection for the resource and a value less than 1 indicates avoidance of the resource. A value around 1 indicates that the resource was used proportionally to its availability and no resource selection was noticed. Subsequently, the standard error of each selection ratio was calculated as

$$se(w_i) = \sqrt{o_i(1-o_i)/U\pi_i}$$

where U is the total number of observations of use in all categories.

To statistically test for the significant departures of use from availability, the log-likelihood chi-squared test (χ^2_L) was calculated following Krebs [36] and Manly *et al*. [34] as

$$\chi^2_L = 2\sum_{i=1}^{I}[u_i \log_e(u_i / U\pi_i)]$$

Where u_i is the used resource unit in category *i* and I is the total number of categories. If the χ^2_L statistic was significant, the null hypothesis of equitable use of resources was rejected. Subsequently, for each habitat category, simultaneous Bonferroni-adjusted 100(1-α)% confidence intervals for habitat use were constructed as

$$w_i \pm Z_{\alpha/2I}\, se(w_i)$$

Selectivity was considered when confidence limit excluded 1. A habitat was preferred when the lower limit was > 1 and avoided if < 1.

Based on utilization proportions, Levins' [37] niche breadth was calculated as

$$B_i = \frac{1}{I \times \sum_{i=1}^{I} o_i^2}$$

where B_i represents the Levins' measure of niche breadth. B_i is maximum when the pellet-group density is similar in each habitat, and would be minimal if all pellet-groups occur only in one habitat. Overlap in resource use was assessed by Colwell-Futuyma proportional similarity index for niche overlap [38], calculated as

$$C_{cn} = C_{nc} = 1 - \frac{1}{2}\sum_{i=1}^{I}\left|o_{ic} - o_{in}\right|$$

where C_{cn} represents the proportional similarity of niche between (*c*)hital and (*n*)ilgai, O_{ic} and O_{in} are the utilization proportionate of the two species *c* and *n*, respectively, in resource state *i*. Values of C_{cn} range from 0 (no niche overlap) to 1 (complete overlap).

RESULTS

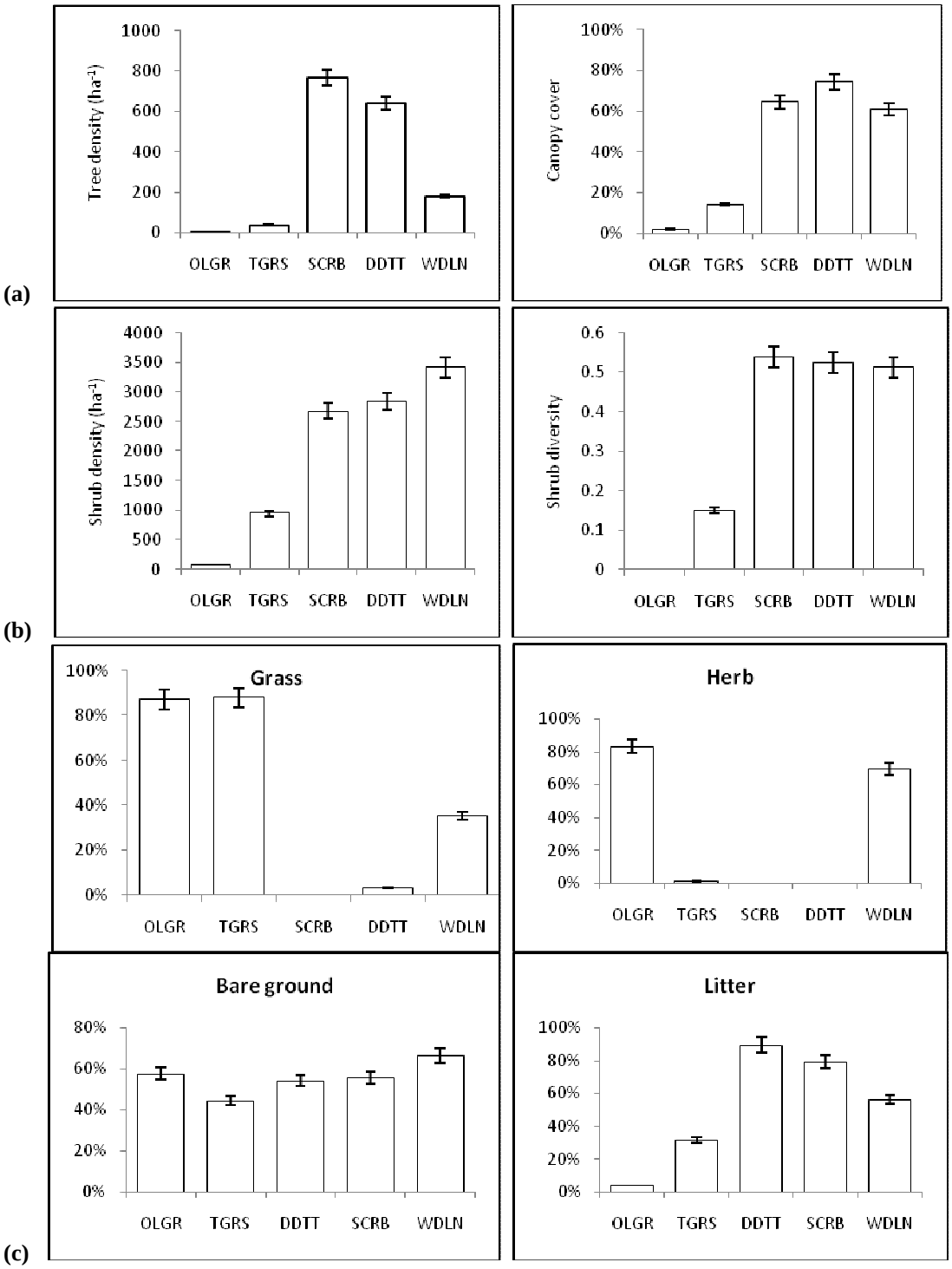

Figure 1: (a) Mean ± SE of forest structure variables in each habitat category, showing tree density (ha^{-1}), and percent canopy cover. (b) Mean ± SE of shrub density (ha^{-1}) and shrub diversity in each habitat type. (c) Mean ± SE of percentage variable cover in each habitat type

Vegetation characteristics

Figure 1 summarises the physical structure and vegetation composition of the habitat types. Tree density declines after the thicket stage due to thinning; scrub vegetation being with highest density because of the species in their early successional stages. Canopy closure occurs highest in the dense to discontinuous thicket stage, but percent canopy cover is then more open in mature forests (Figure 1a). Thus, thermal cover is minimal in open grasslands,

begins to increase in savannah and is greatest in thickets followed by scrub, but declines in mature stands due to reduced tree density and the high broken canopy. Shrub density is minimal in the open grasslands and start getting increased in tall grass savannah and reach to maximum in the mature woodlands with highest canopy opening. The diversity in shrub species decreases slightly from the maximum in the early successional stages of scrub to mature forest stands of woodlands (Figure 1b). The ground cover in woodland is sparse with herbs and grasses patched by bare ground and litter, while scrubs and thickets do not have grass or herb cover mainly due to the saline nature of the soil (Figure 1c).

Habitat selection

A total of 2042 pellet groups of chital and 255 pellet groups of nilgai were observed in the whole study period while assessing for the habitat use and selection pattern. Table 1 presents mean (± SE) pellet group density per hectare in different habitat types of the study area.

Chital utilized habitat categories differentially and was found to show preference for DDTT, WDLN and SCRB habitat categories while utilizing less than their availability the TGRS and OLGR resource states (χ^2_L = 1195.29, P < 0.01) (Table 2). Significant difference was found amongst preferred categories in utilization pattern when compared pair wise: DDTT–WDLN and SCRB–WDLN with χ^2 = 13.121, P < 0.01 and χ^2 = 7.74, P < 0.01, respectively. Thus, habitat category WDLN was the most preferred by chital amongst the three categories.

Nilgai also showed differential use of habitat types preferring DDTT and SCRB while utilizing WDLN in proportion to its availability (χ^2_L = 377.84, P < 0.01). Habitat categories TGRS and OLGR were utilized less in proportion to their availability (Table 2). DDTT was found to be more preferred by nilgai in comparison to SCRB (χ^2 = 8.15, P < 0.01). Both species utilized less, in proportion to their availability, the open habitat resource categories TGRS and OLGR (Table 2).

Table 1: Mean (± S.E) pellet group density (ha^{-1}) in different habitats of the KNP

Habitat	Chital	Nilgai
OLGR	3019.86 ± 514.88	254.77 ± 061.93
TGRS	3133.76 ± 430.17	406.05 ± 068.02
DDTT	2150.32 ± 305.22	779.32 ± 203.44
SCRB	1695.86 ± 348.81	327.57 ± 056.20
WDLN	3539.58 ± 408.81	486.39 ± 136.14

Table 2: Estimated habitat use and selection for chital and nilgai in KNP, India. w_i estimated habitat selection ratio; $se(w_i)$ standard error of selection ratio; w_i (l) and w_i (u) 95% lower and upper confidence limits, respectively; s_i selection level (* used more than expected that is preference), (** used in proportion to availability) and (* used less in proportion to availability or avoidance).**

	Chital					Nilgai				
Habitat	π_i	w_i	$se(w_i)$	w_i (l)	w_i (u)	s_i	w_i		$se(w_i)$	w_i (l)
OLGR	0.24	0.825	0.037	0.730	0.920	*	0.363		0.073	0.174
TGRS	0.40	0.753	0.025	0.688	0.818	*	0.500	0.063	0.339	0.661
DDTT	0.16	1.294	0.056	1.149	1.438	***	2.550		0.192	2.055
SCRB	0.08	1.300	0.084	1.083	1.517	***	1.763	0.272	1.063	2.463
WDLN	0.12	1.583	0.072	1.397	1.769	***	1.375	0.194	0.876	1.874

Niche segregation

Chital showed maximum realized niche in habitat state TGRS and minimum in SCRB while nilgai represented minimum realized niche in OLGR and maximum in DDTT (Figure 2). Chital showed a wider niche width (0.911) in comparison to nilgai (0.766) representing a more generalist behavior than nilgai. The overall niches overlap between chital and nilgai was 0.762. Even though, there seems difference in their respective niche breadths, nilgai seems to share or compete completely with chital as its niche breadth and the overall overlap are similar.

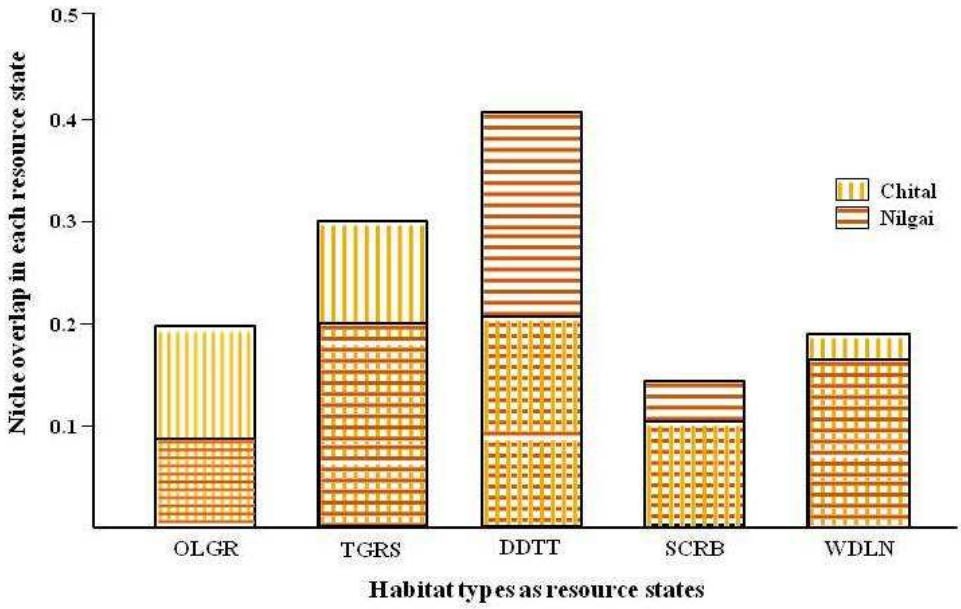

Figure 2: Realised niches of chital and nilgai in different habitat states of the KNP. The cross hatched part of each state is the overlapped portion between chital and nilgai. Note that in DDTT and SCRB chital has lower realised niche than nilgai.

DISCUSSION

The results have shown differential use of habitats proving our hypothesis of selection between habitat types and existence of ecological separation between chital and nilgai. Both chital and nilgai utilized more than one habitat type representing low availability of good quality forage in a particular habitat resource during the winter period.

The woodland habitat was found to be utilized more than expected by chital because of palatable and relatively good availability and diversity of shrubs and other ground vegetation. This has also been widely reported that chital prefers flat terrains and valley habitats, frequenting ecotones with high diversity of palatable grass and herb species and early to middle successional stages of vegetation [39, 40, 41, 10] which was not found in the KNP as chital utilized open and tall grasslands less than expected due to non palatability, low diversity of the grass and disturbance due to high visitors' influx during winters owing to its Ramsar Site status. Chital are known to feed on more than 160 species of plants [39, 42]. On the basis of morpho-physiological ruminant feeding types, Hofmann [43] classified chital as an intermediate or mixed feeder while Rodgers [44] had categorized chital as a generalist feeder, with a diet consisting of grasses, forbs, and leaves of woody plants. In Sariska Tiger Reserve, which also has similar semi-xeric and xeric conditions, chital was a grazer as long as green grasses were available (monsoon and post-monsoon seasons), but switched over to broader dietary spectrum comprising fallen leaves, flowers and fruits in winter when food availability became scarce [9]. Since the KNP has peculiar vegetation strata where there is no continuity and all cover patches are discrete, there are fair chances of chital being found all over near edges or between the patches. Small area of the KNP, absence of any predator and relatively high densities [45] precluded chital to confine itself in a specific patch. Chital spend a major portion of their life in foraging, resting, and wandering within their ranges, with the extent of these activities determined by season [39] similar is the trend in the KNP where winters lead chital to wander more in search of food.

On the other hand, nilgai utilized woodland habitat type in accordance to its availability. It preferred the dense to discontinuous thickets and scrubland because of openings in between patches. Nilgai is reported to occur in relatively open areas [46], avoiding very dense forests [47] and preferring scrublands with low tree and shrub densities [8, 9, 10]. Since, there is a slight difference between utilization patterns of both the species, there is a fair

possibility of competition between these two species. They coexist in the same habitat types as far as their spatial requirement is concerned and remain in close proximity to each other in those habitats, which they utilize less than expected, for cover and all. Given the availability of other habitats nilgai did not use them proportionately because of the competition and relatively low densities [45] which precluded it from dispersing in whole of the area. Owing to small area of the park they would tend to share and compete more as they would grow in numbers and cross the threshold of the carrying capacity of the park. There is no natural predation pressure as such but feral dogs do attack males, sub-adults and fawns (pers. observ.). Not only this, there is intense competition from domestic livestock as well but this has been paid no serious attention as it is deemed well in case of vegetation dynamics of the park [25] and some semi-arid areas elsewhere [48, 49].

Habitat selection processes are scale sensitive [33] both on spatial as well as temporal scales [50, 51]. The limitation of the present study was that it was conducted during winter when it is generally contented that large herbivores tend to widen their niche widths in order to avoid competition in the low productive environments. Resource selection in space and time also varies between seasons. According to Boyce [51], different habitats might be selected in different years, and different resource selection factors might apply for different years.

An important caveat here is that habitat selection does not necessarily reflect quality of habitat [52, 53]. It describes the time specific species distribution or the realised niche of the species, which results from competition with sympatric species, livestock, human disturbance, predation and several other biotic and abiotic factors.

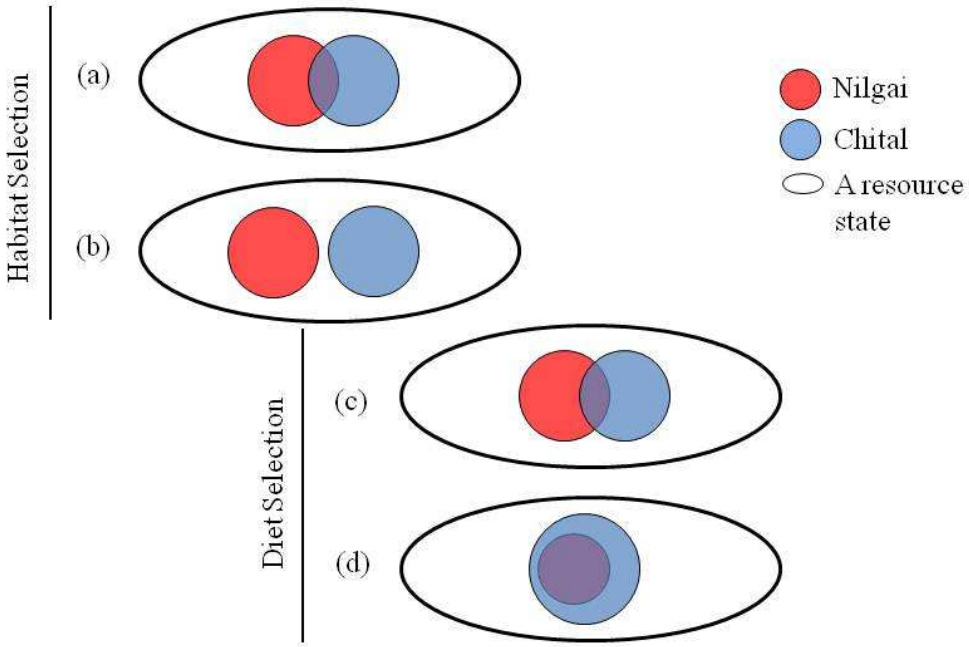

Figure 3: A hypothetical resource utilisation model (in context of the present study) with third and fourth levels of selection (Krausman 1999) comprising two co-existing species, chital and nilgai. Depending on availability of a habitat state, both the species may use the same habitat with no temporal isolation (a) or with temporal segregation (b), as far as spatial requirements are concerned. At the next level of diet selection both species may either utilize totally different sets of resources with no overlap or utilize the same resources with some extent of overlap (c) or the species with lower niche breadth would be forced to have partial share of the resources being utilised by the more generalist species irrespective of the temporal segregation (d).

Niche breadths suggest that both species have generalist habitat associations as far as spatial scale is concerned however, nilgai shows fewer preferences than chital except in case of DDTT and SCRB where nilgai has realised niches more than chital (Figure 2). This overlap in realised niches in each resource category does not represent

competition for the same resources at further fine scale of food material [50, 54] but represents the spatial use and co-existence of both species within each category whereby both are utilizing a given available resource or habitat. Since, we only studied the third order selection [54] of the overall hierarchical selection phenomenon, we can expect few possibilities overlaps in the realized niches at the spatial and temporal scales at the finer level of selection (Figure 3). Temporal segregation may be involved at the habitat selection level only when spatial needs are concerned but at the level of diet selection no segregation is expected as co-existing species would be forced to have competition so as to utilise the resources. The species with narrow niche width would tend to exploit remaining available resources from the generalist species.

Niche separation is actually the process of natural selection, which drives competing species into using different food items, resources or habitats. High niche overlap often results from strong competition or repellence; yet the end result of niche separation can be an observed decrease in competition or avoidance. Some species with high overlap values should interact as competitors or intra-guild predators, while other species with low pair wise overlap values are nonetheless vulnerable to the effects of diffuse competition [55]. In considering the relationship between niche overlap and competition, niche overlap should not be taken as a sufficient condition for competition. Many factors may prevent or diminish competition between populations with similar resource utilization patterns. According to Alley [56], typically opposing forces of intra-specific and inter-specific competition need to be simultaneously considered, for it is the balance between them that in large part determines niche boundaries.

CONCLUSION

The study shows almost uniform utilization amongst all resource states or the habitat types by the two species even though there is statistical difference in utilization patterns. This generalist behaviour and thus niche breadths shown by the two herbivores represent the potential of competition. In the restricted environment during winters the animals are forced to have limited resources thus they utilise almost all habitat types. This becomes more crucial for these two large herbivores as area of the park becomes too small for them to forage.

Acknowledgements
We thank Rajasthan Forest Department for granting permission for the study. We thank Chairman, Department of Wildlife Sciences, for encouragement and support provided during the study. We also thank Director and Dean, Wildlife Institute of India for support. Thanks are due to the field assistant Pajji, who unconditionally helped and assisted in the field.

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