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Social organisation and population structure of ungulates in a dry tropical forest in western India (Mammalia, Artiodactyla)

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Abstract

Grouping characteristics and population structure of chital (*Axis axis* Erxleben), sambar (*Cervus unicolor* Kerr), nilgai (*Boselaphus tragocamelus* Pallas) and chinkara (*Gazella bennetti* Sykes) were studied in dry tropical forests of Ranthambhore Tiger Reserve in semi-arid western India during November 2000 to April 2001. Mean and typical group sizes were highest for chital (winter: 4.7 and 9.2, respectively; summer: 4.5, 7.9), followed by sambar (winter: 3.4, 4.2; summer: 4.2, 6.8), nilgai (winter: 2.9, 4.5; summer: 2.5, 4.9) and chinkara (winter: 2.6, 3.3; summer: 2.5, 3.2). Population structure was biased towards females in chital (86.4 males: 100 females) and sambar (83.2:100), while it was biased towards males in nilgai (116.8:100) and chinkara (119.8:100). Ratio of young to adult females was highest for sambar (38.2 young: 100 females), followed by chinkara (35.2:100), chital (28.0:100) and nilgai (23.9:100). Variations in grouping patterns according to habitat and season have been investigated. The importance of constant monitoring of ungulate population structure is emphasised for this drought prone region.

Keywords: group composition; group size; population structure; social organization; tropical ungulates.

Introduction

Understanding behavioural and demographic aspects of wild animals facilitates population monitoring and effective conservation planning (Caughley 1977, Khan et al. 1995). While estimation of density and biomass of ungulates in the Indian sub-continent has received some research attention (e.g., Schaller 1967, Eisenberg and Seidensticker 1976, Dinerstein 1980, Karanth and Sunquist 1992, Khan et al. 1996, Biswas and Sankar 2002, Bagchi et al. 2004), studies on their social organisation and population structure are few (Rahmani 1990, Barrette 1991, Khan et al. 1995, Pendharkar and Goyal 1995, Raman 1997).

We studied the social organisation and population structure of four wild ungulates (namely, chital, *Axis axis* Erxleben; sambar, *Cervus unicolor* Kerr; nilgai, *Boselaphus tragocamelus* Pallas and chinkara, *Gazella bennetti* Sykes) in a dry tropical forest of western India. Inter-related aspects, such as body size, metabolic requirements, food habits, home range, mating system, quality and abundance of forage and predation pressures, influence the social organisation in animals (Jarman 1974, Geraldeau 1988, Fritz and de Garine-Wichatitsky 1996). These relationships form a web of interdependent features and any attempt to subdivide the continuum poses problems in interpreting cause-effect relationships (Leuthold 1977). Considering food habits, browse tends to be of higher nutritive quality than grasses, but is scattered among widely dispersed individual plants. Therefore, in order to optimise the net returns for members of a foraging party (Geraldeau 1988), browse is most economically exploited by single animals or by very small groups (Leuthold 1977, Fritz and de Garine-Wichatitsky 1996). The small-bodied chinkara with high metabolic requirements is known to be a browser (Rodgers 1988) inhabiting open scrubland (Prater 1971) and we expect it to be occurring in small groups. Sambar, a large-bodied browser (Johnsingh and Sankar 1991) inhabits forested areas where forage is patchily distributed, so we also expect them to occur in small-sized groups. The medium-sized chital is a mixed-feeder (Johnsingh and Sankar 1991) and inhabits both forested as well as open areas. Forest edges are known to facilitate herd formation in this species (Barrette 1991) and we expect them to occur in larger groups than chinkara and sambar. Generalisations are difficult for nilgai as the grouping patterns keeps changing according to the mating season and its ability to adapt to human disturbance (Bagchi et al. 2003a). Following the "structuralist" viewpoint of Barrette (1991), we expect all species to form larger groups in open areas than in closed forests. The effect of habitat in determining grouping patterns can be masked by seasons and we expect interaction effects of this type to influence the social organisation of the four ungulates. Population structure in ungulates is usually skewed towards females and is attributed to sexual selection (Clutton-Brock et al. 1982). We expect the population structure of ungulates in a dry deciduous environment to conform to such generalisations. Among the deer (chital and sambar), males carry antlers which are periodically shed, nilgai shows a great degree of sexual dimorphism with males being considerably larger than females, while chinkara males have larger and more elaborate horns than the females.

In this paper, we test field data on grouping patterns and population structure of chital, sambar, nilgai and chinkara against the empirical understanding developed

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by previous studies (Jarman 1974, Leuthold 1977, Clutton-Brock et al. 1982, Underwood 1982, Geraldeau 1988, Fritz and de Garine-Wichatitsky 1996).

Materials and methods

Study area

Data on group size and composition of the four ungulates were collected between November 2000 and April 2001 in the semi arid dry deciduous forests of Ranthambhore Tiger Reserve (1334 km^2, 26°N and 76°E), Rajasthan, western India. The vegetation of this semi-arid region is tropical dry deciduous forest and tropical thorn forest (Champion and Seth 1968). Terrain is hilly, undulating with wide valleys and plateaus. The four common wild ungulates in Ranthambhore are chital, sambar, nilgai and chinkara. Wild pigs (*Sus scrofa* L.) also occur and blackbuck (*Antilope cervicapra* L.) is reported from certain fringe areas. The large predators are tiger (*Panthera tigris* L.) and leopard (*Panthera pardus* L.). The climate is dry subtropical with four distinct seasons: summer (March–June), followed by monsoon (July–August), post-monsoon (September–October) and winter (November–February). An average annual rainfall of approximately 800 mm is received mostly during July–September. Two seasons could be distinguished during our study, winter (November 2000–February 2001) and summer (March–April, 2001).

Methods

An "intensive study area" (ISA) of approximately 34 km^2 of area was chosen, representing all major terrain and vegetation features found in the park. Ungulate populations were sampled systematically using eight line transects (length 1.5–2.8 km) laid in stratified-random manner in the ISA (Bagchi et al. 2003b). The total length of the eight transects was 19.5 km, each of which was walked seven times in each season (winter and summer), resulting in 273 km of walk during the study period. Transects were walked by two observers (first author and an assistant), during early morning and evening hours, when animals were most active in foraging.

On every sighting during transect walks, data on the following aspects were recorded:

i. Species and group size: groups were defined as a single or a cluster of animals within 30 m of each other and showing co-ordinated movements. Later, groups were classified into five categories based on size: solitary (single animal), family unit (2–3 animals), small groups (4–6 animals), medium groups (7–10 animals) and large groups (>10 animals) (adapted from Karanth and Sunquist 1992).
ii. Group composition: the animals were classified as adult males, adult females, yearlings (subadults 1–2 years in age) and fawns (newborn to 1 year in age). No attempt was made to classify yearlings and fawns according to sex. Animals that could not be classified were not included in further analysis.
iii. Location: the habitat type in which the animals were observed was noted. Two habitat categories were recognized: "closed habitats" (forested areas with high canopy cover and high tree density) and "open habitats" (scrub and woodland having lower tree density and low canopy cover; Bagchi et al. 2003a).

The mean group size and the typical group size (Jarman 1974) were estimated for each species. While mean group size represents the number of individuals likely to be encountered in an average group, the typical group size is more animal-centred and represents the number of other members that any individual is likely to find alongside itself (Jarman 1974). Typical group size is often higher than the mean group size and collates several environmental constraints acting on group formation and is possibly a better descriptor of social organisation than mean group size. Several authors have recognised the importance of depicting frequency distribution of individuals along with that for groups (e.g., Barrette 1991, Khan et al. 1995) and we represent both aspects graphically. A two-way analysis of variance (ANOVA) (Sokal and Rohlf 1995) using seasons as block level was used to test for differences in mean group size of each species between the two habitat types. Proportions of age-sex categories were also tested in the same manner, with the data being arc sine ($\text{Asin}\sqrt{p}$) transformed (Sokal and Rohlf 1995).

Results

Most of the animals encountered during transect walks could be classified into appropriate age-sex categories (Table 1). The success of classification was related to body size and relative degree of sexual dimorphism in the four species. Nilgai (99.5%) and sambar (98.5%) were classified more successfully than chital (92.5%) and chinkara (92.5%) (Table 1).

Group size

The mean group size and typical group size of the four species are described for each season in Table 2. Both in terms of mean, as well as typical group sizes, chital formed the largest groups of the four species, while chinkara was the least gregarious (Table 2). This result is consistent with the expected pattern.

Chital In winter, family units were most commonly encountered, while the majority of the individuals occurred in groups of 2–6 animals (Figure 1A). During summer, groups of less than 6 animals were common, while most of the individuals occurred in small-to-medium sized groups (Figure 1A). The results of a two-way

Table 1 Sample size and age-sex classification of four ungulates in Ranthambhore Tiger Reserve during November 2000–April 2001.

	Groups encountered	Individuals encountered	Individuals classified	% Classified
Chital	258	1196	1106	92.5
Sambar	198	739	729	98.5
Nilgai	196	542	539	99.5
Chinkara	52	134	124	92.5

Table 2 Mean and typical group sizes of four ungulate species in Ranthambhore Tiger Reserve during November 2000–April 2001, according to season.

	Mean group size±SE*		Typical group size	
	Winter	Summer	Winter	Summer
Chital	4.7±0.4	4.5±0.4	9.2	7.9
Sambar	3.4±0.3	4.2±0.5	6.0	6.8
Nilgai	2.9±0.2	2.5±0.3	4.5	4.9
Chinkara	2.6±0.3	2.5±0.3	3.3	3.2

*SE is estimated standard error of group size.

ANOVA showed that there were no seasonal, as well as habitat-related, changes in the group size of chital ($p>0.05$ in all cases, Table 3).

Sambar In winter, groups of solitary animals and family groups were common with a majority of animals occurring in groups of 2–6 individuals (Figure 1B). In summer, while solitary animals and family units were again most common, a higher proportion of individuals were found in large groups than in winter (Figure 1B). Sambar occurred in larger groups in open habitats (4.67±0.40 SE) than inside forests (3.23±0.33 SE, Table 3).

Nilgai Groups of more than 6 individuals were not characteristic for nilgai in both seasons. Family units and small groups were the most common. Individuals most frequently occurred in groups with 2–6 animals (Figure 1C). Group size did not vary between habitats across the two seasons ($p>0.05$ in all cases, Table 3).

Chinkara Groups of chinkara never exceeded beyond 6 individuals in either season. Family groups were most common and also contained the highest proportion of individuals (Figure 1D). Larger groups of chinkara were seen to occur in open habitats (2.85±0.19 SE) than in forests (1.60±0.48 SE, Table 3).

Population structure

Sex ratio was skewed towards females in the deer (chital and sambar), while it was skewed towards males in the bovids (nilgai and chinkara) (Table 4). The ratio of number of young animals (fawns) to every 100 adult females was highest for sambar (38.2), followed by chinkara (35.2), chital (28.0) and nilgai (23.9) (Table 4). Group composition did not vary according to habitats and seasons in chital ($p>0.05$). But in sambar, the proportion of females in an average group was higher in forests (0.43±0.02 SE) than in open areas (0.35±0.03) ($F_{1,191}=3.79$, $p=0.05$). In nilgai, the proportion of males in an average group was higher during summer (0.52±0.05 SE) than in winter (0.36±0.04 SE) ($F_{1,192}=4.19$, $p=0.04$). Moreover, the proportion of fawns was higher in an average group during winter (0.11±0.01 SE) than in summer (0.05±0.02 SE) ($F_{1,192}=4.42$, $p=0.03$). There was no difference in group composition between habitats and across seasons in chinkara ($p>0.05$).

Discussion

Group size

Chital has been reported to be gregarious from several regions (Dinerstein 1980, Barrette 1991, Karanth and Sunquist 1992, Khan et al. 1995). But the lack of grassy openings in our ISA might have caused larger groups of chital to be less common (Figure 1A). Both the mean group size and typical group size of chital were found to be lower than that reported from Gir Lion Sanctuary (6.03 and 11.41, respectively, Khan et al. 1995) (Table 2), which has a greater degree of habitat heterogeneity than our ISA.

Sambar is reported to occur in small groups (Karanth and Sunquist 1992, Khan et al. 1995) and we also found solitary animals and families (usually a female with fawn and/or yearling) as the most common social units. But, in summer, the proportions of individuals occurring in larger groups (exceeding 10 animals) increased in comparison to winter (Figure 1B). Stags could have contributed to this by forming bachelor herds after shedding their antlers at the end of winter. This could also have been due to temporary feeding aggregations.

Nilgai is known to occur in small groups (Dinerstein 1980, Khan et al. 1995), with males usually being solitary or in small herds and females forming small herds with fawn and yearlings. We seldom found nilgai to be forming groups of more than 6 individuals, and small-sized groups characterised its social organisation in this region, whereas it forms larger group in more open areas, such as grassy savannah (Bagchi et al. 2003a). The foraging grounds of nilgai were in the scrubland, where food is patchily distributed and group formation would be greatly influenced by the net returns for the group members in a patch (Geraldeau 1988). It is possible that the optimal group size was below 6 and hence prevalent. Mean and typical group sizes of nilgai were found to be very similar to the reports from Gir (2.2 and 3.5, respectively, Khan et al. 1995), where they use similar habitats.

Very little information is available on social organisation in chinkara. Social organisation was observed to be largely asocial and living in small groups. Solitary animals, pairs and family units were most characteristic of this species, as observed by Rahmani (1990).

Effect of season and habitat on group composition

Chital and nilgai did not show any change in group size and composition between habitats across the two seasons. Therefore, seasonal effects on habitat structure do

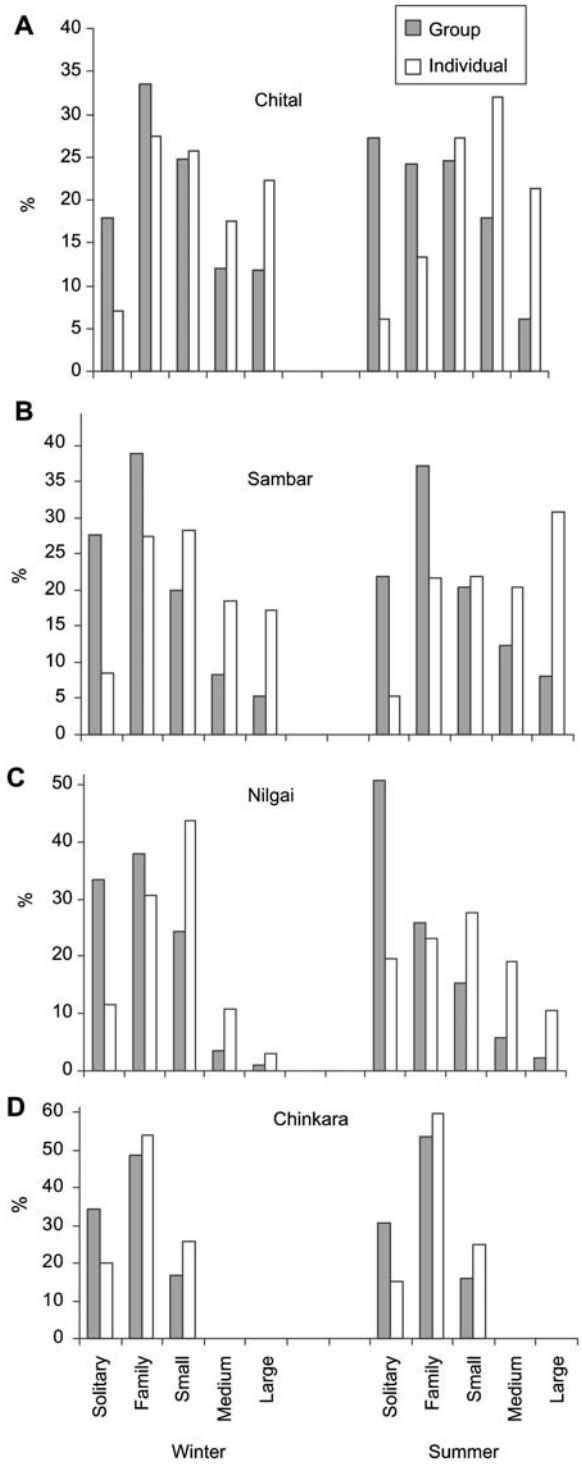

Figure 1 (A–D) Seasonal distribution of groups and individuals among different group size categories in four species in Ranthambhore Tiger Reserve during November 2000–April 2001.

not seem to influence the optimal size of their foraging parties, suggesting that chital and nilgai are generalised in their habitat and dietary requirements, as elaborated by Bagchi et al. (2003a).

Sambar showed a tendency to form larger groups in open habitats, while they were often solitary inside forests. This can be viewed as an anti-predatory measure, as smaller groups are less likely to be encountered by an ambush predator, such as tiger in forests; whilst in the open, animals resorted to safety in numbers. Again, females, who were usually associated with fawns and yearlings, occurred preferentially inside forests than in the open, thus adopting a protective measure. Sambar is likely to have a high risk of predation as it forms the bulk of the diet of the tiger in this region (Bagchi et al. 2003b). However, the effect of other constraints, such as forage quality and abundance cannot be completely ruled out.

A higher proportion of fawns during winter in nilgai indicate a calving peak in this species. Our personal observations suggest that nilgai fawns are dropped during early winter, and twinning was common. Moreover, higher proportions of males in an average group during summer suggest the formation of bachelor herds by bulls after the mating season.

Chinkara grouping dynamics were similar to that of sambar. They were usually solitary or as family, possibly because both species are browsers and experience similar dietary constraints.

Table 3 Results of a two-way ANOVA, comparing group size of four ungulates across two seasons (winter and summer) and two habitats (open and closed) in Ranthambhore Tiger Reserve during November 2000–April 2001.

Species	Effect	F	p
Chital	Season	$F_{1,254}=0.51$	0.47
	Habitat	$F_{1,254}=0.85$	0.35
	Interaction	$F_{1,254}=0.93$	0.33
Sambar	Season	$F_{1,194}=2.56$	0.11
	Habitat	$F_{1,194}=7.67$	<0.01
	Interaction	$F_{1,194}=0.01$	0.98
Nilgai	Season	$F_{1,192}=1.07$	0.30
	Habitat	$F_{1,192}=0.01$	0.98
	Interaction	$F_{1,192}=0.21$	0.64
Chinkara	Season	$F_{1,48}=0.13$	0.71
	Habitat	$F_{1,48}=5.72$	0.02
	Interaction	$F_{1,48}=0.01$	0.98

Population structure

Interestingly, the sex ratios of adults in our ISA show different trends among the cervids and the bovids. While in chital and sambar, the sex ratio was skewed towards females, in nilgai and chinkara it was in favour of males. Female bias in deer is common (Khan et al. 1995) and is often interpreted in terms of sexual selection (Clutton-Brock et al. 1982).

Khan et al. (1995) found nilgai in Gir to approximate an even sex ratio at certain times (i.e., 89–97 males per 100 females), but in our ISA, it was slightly biased towards males (Table 3). Unlike Rahmani (1990), the sex ratio in chinkara was also biased towards males (Table 3). Nilgai and chinkara are supposed to be territorial, marking their territories using means, such as dung piles. This increases the likelihood of encountering the same individual (i.e., territorial males) during successive transect walks and this might have influenced our results. But territoriality in these two species is poorly understood in comparison to African bovids (Leuthold 1977). Further, our sample size for chinkara (52 groups, 124 individuals) is low compared

Table 4 Population structure of four ungulate species in Ranthambhore Tiger Reserve during November 2000–April 2001.

	Sample size		Ratios		Young (yearling+fawn)
	Groups	Individuals	Female	Male	
Chital	258	1106	100	86.4	28.0
Sambar	198	729	100	83.2	38.2
Nilgai	196	539	100	116.8	23.9
Chinkara	52	124	100	119.8	35.2

to the other species. Young-to-female ratio was lower in chital and sambar compared to moist forests of southern India (Nagarhole National Park; Karanth and Sunquist 1992).

Environmental stochasticity plays an important role in shaping demographic processes and Ranthambhore is prone to frequent droughts. The ratio of young to adult females is lower for chital and sambar than in moist forests of south India (e.g., Nagarhole National Park; Karanth and Sunquist 1992), possibly due to a drop in reproductive potential following a third consecutive year of low rainfall since 1998.

Conclusions

These results of a two-way ANOVA are in accordance to the expected trends in relation to certain constraints that influence group formation in these species. Ranthambhore thus offers further opportunities to analyse social organisation in terms of other factors, such as predation pressures and ranging patterns. Age-sex structure requires constant monitoring in order to perceive changes in the demography of a population over time. After 3 years of drought, it becomes important to document fecundity and survival of animals in the subsequent years and assess the scope for a revival (e.g., Sankar 1994). It is advisable to monitor the age-sex structure of the animal populations in Ranthambhore so that the long-term trends become evident. The park management can adopt rapid assessment techniques for population monitoring, to obtain this information and facilitate expedient planning.

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References

Bagchi, S., S.P. Goyal and K. Sankar. 2003a. Niche relationships of an ungulate assemblage in a dry tropical forest. J. Mammal. 84: 981–988.

Bagchi, S., S.P. Goyal and K. Sankar. 2003b. Prey abundance and prey selection by tigers in a semiarid, dry deciduous forest in western India. J. Zool. 260: 285–290.

Bagchi, S., S.P. Goyal and K. Sankar. 2004. Herbivore density and biomass in a semi-arid tropical dry deciduous forest of western India. J. Trop. Ecol. 20: 475–478.

Barrette, C. 1991. The size of *Axis* deer fluid groups in Wilpattu National Park, Sri Lanka. Mammalia 55: 207–220.

Biswas, S. and K. Sankar. 2002. Prey abundance and food habit of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India. J. Zool. 256: 411–420.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York. 234 pp.

Champion, F.W. and S.K. Seth. 1968. A revised survey of the forest types of India. Manager, Government of India Press, Nasik, India. 404 pp.

Clutton-Brock, T.H., F.E. Guinness and S.D. Albon. 1982. Red deer: behaviour and ecology of two sexes. Edinburgh University Press, Edinburgh. 400 pp.

Dinerstein, E. 1980. An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal, part 3: ungulate populations. Biol. Conserv. 18: 5–38.

Eisenberg, J.F. and J. Seidensticker. 1976. Ungulates in southern Asia: a consideration of biomass estimates for selected habitats. Biol. Conserv. 10: 293–308.

Fritz, H. and M. de Garine-Wichatitsky. 1996. Foraging in a social antelope: effects of groups size on foraging and resource perception in impala. J. Anim. Ecol. 65: 736–742.

Geraldeau, L.-A. 1988. The stable group and the determinants of foraging group size. In: (C.N. Slobodchikoff, ed) The ecology of social behavior. Academic Press, San Diego, CA. pp. 33–53.

Jarman, P.J. 1974. The social organisation of antelope in relation to their ecology. Behaviour 48: 215–267.

Johnsingh, A.J.T. and K. Sankar. 1991. Food plants of chital, sambar and cattle on Mundanthurai plateau, Tamil Nadu, South India. Mammalia 55: 57–66.

Karanth, K.U. and M.E. Sunquist. 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarhole, India. J. Trop. Ecol. 8: 21–35.

Khan, J.A., R. Chellam and A.J.T. Johnsingh. 1995. Group size and age-sex composition of three major ungulate species in Gir lion sanctuary, Gujarat, India. J. Bom. Nat. Hist. Soc. 92: 295–302.

Khan, J.A., R. Chellam, W.A. Rodgers and A.J.T. Johnsingh. 1996. Ungulate densities and biomass in the tropical dry deciduous forests of Gir, Gujarat, India. J. Trop. Ecol. 12: 149–162.

Leuthold, W. 1977. African ungulates: a comparative review of their ethology and behavioural ecology. Springer-Verlag, Berlin. 307 pp.

Pendharkar, A.P. and S.P. Goyal. 1995. Group size and composition of the gray goral in Simbalpara sanctuary and Darpur reserved forest, India. J. Mammal. 76: 906–911.

Prater, S.H. 1971. The book of Indian animals. Bombay Natural History Society, Bombay. 332 pp.

Rahmani, A.R. 1990. Distribution, density, group size and conservation of the Indian gazelle or chinkara *Gazella bennetti* (Sykes 1831) in Rajasthan, India. Biol. Conserv. 51: 177–189.

Raman, T.R.S. 1997. Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India. J. Biosci. 22: 203–218.

Rodgers, W.A. 1988. The wild grazing ungulates of India: an ecological review. In: (P. Singh and P.S. Pathak, eds) Rangelands – resource and management. Rangeland Management Society of India, Jhansi. pp. 9–21.

Sankar, K. 1994. The ecology of three large sympatric herbivores with special reference to Reserve management in Sariska tiger reserve, Rajasthan. *Ph.D. Thesis*. Univ. Rajasthan, Jaipur. 190 pp.

Schaller, G.B. 1967. The deer and the tiger: a study of wildlife in India. Chicago University Press, Chicago, IL. 384 pp.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry. W.H. Freeman and Co., New York. 887 pp.

Underwood, R. 1982. Seasonal changes in African ungulate groups. J. Zool. 196: 191–205.

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