

Intraspecific variation in group size in the blackbuck antelope: the roles of habitat structure and forage at different spatial scales

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Abstract The main ecological factors that are hypothesized to explain the striking variation in the size of social groups among large herbivores are habitat structure, predation, and forage abundance and distribution; however, their relative roles in wild populations are not well understood. I combined analyses of ecological correlates of spatial variation in group size with analyses of individual behaviour in groups of different sizes to investigate factors maintaining variation in group size in an Indian antelope, the blackbuck *Antilope cervicapra*. I measured group size, habitat structure, forage, and the occurrence of predators in ten blackbuck populations, and, at a smaller spatial scale, within an intensively studied population. To examine the processes by which these ecological factors influence group size, I used behavioural observations and an experiment to estimate the shape of the relationship between group size and potential costs and benefits to individuals. Group size varied extensively both among and within populations. Analyses of spatial variation in group size suggested that both forage and habitat structure influence group size: large-scale, among-population variation in group size was

primarily related to habitat structure, while small-scale, within-population variation was most closely related to forage abundance. Analyses of individual behaviour suggested that larger groups incur greater travel costs while foraging. However, individuals in larger groups appeared to experience greater benefits, namely the earlier detection of a “predator”, a reduction in vigilance, and an increase in the time spent feeding. Overall, these findings suggest that individuals in groups experience a trade-off between predation-related benefits and costs arising from feeding competition. Habitat structure and forage likely influence the nature of this trade-off; thus, variation in these ecological factors may maintain variation in group size. The role of predation pressure and other factors in explaining the remaining variation needs further exploration.

Keywords *Antilope cervicapra* · Intraspecific variation · Group living · Habitat structure · Forage

Introduction

The size of social groups varies widely among animals, from populations in which individuals are primarily solitary to those in which most individuals are found in aggregations of many hundreds (Lott 1991). How can we test hypotheses for this wide variation? Many ungulates show extensive intraspecific variation in grouping (e.g., fallow deer *Dama dama*, Thirgood et al. 1999; oribi *Ourebia ourebi*, Brashares and Arceese 2002), and offer the opportunity to investigate the processes underlying such behavioural variation. I studied the relative importance of factors influencing group-size variation among and within populations of an Indian antelope, the blackbuck *Antilope cervicapra*.

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The distribution of group sizes in a population can be viewed as the outcome of decisions made by multiple individuals evaluating the benefits and costs of being in groups of different sizes (Alexander 1974; Pulliam and Caraco 1984). Possible benefits to group living include reduced predation risk, maintenance of forage quality, increased hunting success, better access to information about resources, better defence of resources, and reduced risk of infanticide. Proposed costs of grouping include increased feeding competition, risk of acquiring diseases, and conspecific aggression (reviews in Pulliam and Caraco 1984; Krause and Ruxton 2002). Of all these, minimizing predation risk is arguably the most general and important benefit to grouping, especially in large herbivores such as macropods, bovids, and cervids (Jarman 1974; Kaufmann 1974; Hirth 1977; Brashares and Arcese 2002). Grouping may reduce per capita predation risk through earlier detection of predators, dilution and confusion effects, and/or cooperative defence (Pulliam and Caraco 1984; Krause and Ruxton 2002). Individuals in groups may also experience benefits related to reduced predation, such as spending less time being vigilant and more time feeding compared with solitary animals (Underwood 1982; Blumstein and Daniel 2002). The main cost of grouping in large herbivores is generally considered to be feeding competition (Terborgh and Janson 1986). Animals in groups may have to forage over larger areas and/or spend more time searching for food than solitary animals (Wrangham et al. 1993). Given these costs and benefits of group formation, ecological factors that influence the shape and magnitude of the relationship between group size and any cost or benefit are likely to affect optimum group size.

The main ecological factors thought to affect the payoffs to group formation in large herbivores are predation pressure, habitat structure, and resource abundance and distribution (Lott 1991; Brashares and Arcese 2002). Predation pressure influences the magnitude of anti-predation benefits that individuals gain by joining larger groups. An increase in predation pressure is predicted to favour an increase in group size (Brashares and Arcese 2002). The second factor, habitat structure, is thought to affect group size by modifying the anti-predation benefits associated with grouping, and group size is expected to increase with habitat openness (Jarman 1974). The third factor, resources, is proposed to affect grouping primarily by modifying feeding competition, a cost to grouping (e.g., Chapman et al. 1995). When resources are relatively scarce and/or distributed in small, distant patches, large group sizes are not economical because the cost of competing for food outweighs any benefits. Thus, group sizes should increase with forage abundance and distribution.

While studies from a range of taxa provide support for each of these factors individually (e.g., Hirth 1977;

Chapman et al. 1995), their relative importance in wild populations is rarely assessed simultaneously (but see Brashares and Arcese 2002) and is, therefore, still not well understood. In this paper, I evaluate the relative importance of habitat structure, forage abundance and distribution, and predator occurrence towards maintaining variation in group size in blackbuck. I first use data from ten blackbuck populations to evaluate the relative abilities of these ecological factors to explain large-scale variation in group size. I also examine group-size variation at a smaller scale, within a single population in a heterogeneous habitat. Finally, to explore the processes by which these ecological factors might influence the payoffs to group size, I use detailed observations of the behaviour of individuals together with an experiment to quantify the shape of the relationship between group size and hypothesized costs and benefits. I measured two main predation-related benefits: the probability of detecting a predator (expected to increase with group size), and the time spent foraging versus being vigilant (expected to be greater in larger groups). The other main predation-related benefits, dilution and confusion effects, are difficult to measure since predation is difficult to observe in the wild. The main cost I measured was feeding competition. In large herbivores, this cost is thought to be mainly reflected in the distances that groups cover while foraging (expected to increase with group size).

Methods

Study species

The blackbuck is an endangered antelope native to the Indian subcontinent. It is a group-living grazer found in a wide range of habitats, from semi-arid grasslands to open woodland (Ranjitsinh 1989; Isvaran 2005). Throughout its range, its diet is dominated by grasses; forbs and browse typically form a relatively small and seasonally varying proportion of its annual diet (Mungall 1978; Ranjitsinh 1989; Jhala 1997). The main social groups found in blackbuck are (1) all-male groups (males of all age classes), (2) female groups (females of all age classes and immature males), and (3) mixed-sex groups (males and females of all age classes). Group sizes vary widely both among and within populations (Ranjitsinh 1989). Groups occupy overlapping home ranges and are typically unstable, changing in size several times in a day (Mungall 1978). Blackbuck are thought to have been hunted mainly by cheetah (*Acinonyx jubatus*) until the cheetah's recent extinction in India (Ranjitsinh 1989). Wolves (*Canis lupus*) are currently the main predators of adult blackbuck. Blackbuck flee when approached by predators and are

thought to rely on early detection and flight to escape predation (Mungall 1978; Ranjitsinh 1989).

Study sites

I studied among-population variation in group sizes at nine populations in India during August–November 1998 and August–November 1999, and one in the USA in May 1999. For the Indian sites, these months correspond to mid- to post-monsoon (when forage is most abundant), the fall mating season of blackbuck. The Indian sites were spread throughout the range of blackbuck in India (details of sites in Isvaran 2005), and lay in semi-arid regions with habitats ranging from open grasslands to thorny shrublands and woodland. I also studied a free-ranging blackbuck population at Kyle ranch in Texas, USA. Blackbuck were introduced into Texas about 80 years ago and have multiplied rapidly (Mungall 1998). Blackbuck in Texas allow one to examine whether determinants of social organisation identified for the Indian populations hold in a new environment.

I studied within-population variation in group size and individual behaviour at Velavadar, Gujarat, in 2000 and 2001. This site, 34 km² in area, is a mosaic of grasslands, shrublands and mudflats. The population, one of the largest in India, has fluctuated around 1,850 animals since 1969 (Jhala 1993). Here, wolves, the main predators of adults, are reported to kill 35–39 blackbuck/wolf/year (Jhala 1993).

Among-population variation in group size and its potential correlates

A group was defined as all individuals ≤ 50 m of another individual (Clutton-Brock et al. 1982). Groups could typically be identified unambiguously because distances between neighbours within a group (e.g., Velavadar: mean = 4 m, range = 1–30; $n = 60$) were usually considerably less than those between groups (e.g., Velavadar: mean = 280 m, range = 110–1,150; $n = 45$). Group sizes in each population were measured through one of two methods: either total counts or transects (Sutherland 1996). Total or direct counts are a recommended census technique for species like blackbuck that aggregate and inhabit relatively open areas (Sutherland 1996; Jethva and Jhala 2004). At seven of the ten study sites, 3–5 total counts were conducted during morning or evening hours, when animals were most active. During each count, the whole study area was systematically covered and the number and sex of individuals in each group encountered was recorded. At three sites (Guindy, Point Calimere, and Kyle ranch), the

vegetation (woodland with grassy openings) was too dense for total counts. Instead, at these sites I walked six or seven 1-km strip transects 100 m wide (laid similarly to those described below for habitat variables) and recorded the number and sex of individuals in all encountered groups. Additionally, to assess whether group sizes simply vary with population density (as might be expected under a null model), I used these census data to estimate population density, calculated as the total number of individuals sighted divided by the area sampled (the study area for total counts and the area of the strip transect for transects; additional details in Isvaran 2005).

I measured habitat structure and forage abundance and distribution using a combination of transects and sample plots (Krebs 1989; Brashares and Arcese 2002). To ensure that sampling was adequately distributed, I first divided each study site into 4–6 units (depending on the size of the sites). A line transect measuring around 1 km (mean = 850 m, SD = 190, range = 500–1,000) was then laid at random in each unit (using a stopwatch to generate random numbers). Transects ended when the boundary of the study area was reached; hence, transects were occasionally less than 1 km long. Study sites were relatively small (median = 6.1 km², range = 1–34 km²), so this sampling scheme likely provides adequate coverage of each site. Along each transect, I measured the following habitat and forage variables:

1. *Habitat openness*: The aspect of habitat structure thought to most influence grouping is the extent and distribution of open habitat. Therefore, habitats were placed in two categories, open and closed. Open habitats were those without woody shrubs and trees >1 m high (mainly grassland and bare ground), and closed habitats those with woody shrubs and trees >1 m high (mainly shrubland and woodland). At 50-m intervals along each transect, I visually estimated the percentage of area occupied by open and closed habitats in a circular plot of 10-m radius. Habitat openness at each site was then calculated as the mean percentage of open habitat in a plot (first averaged across plots within a transect and then across transects). The total number of plots sampled at each study site varied from 45 to 104 according to the area of the sites (“[Electronic supplementary material](#),” S1).
2. *Habitat patchiness*: The spatial distribution of a particular habitat can vary from a few large patches to many small patches. To obtain an index of the distribution of habitat patches at each study site, I divided each transect into segments of varying lengths, where each segment consisted of successive points with open habitat or successive points with closed habitat as the major habitat type. The lengths of these

segments thus reflect the size of habitat patches through which the transect ran, and the number of segments is an index of the distribution of habitat patches, as heterogeneous habitats yield more segments than homogeneous habitats. Habitat patchiness for a transect was then calculated as the number of habitat segments divided by the maximum possible number of segments (= total number of sampling points on the transect). Thus, a transect with all points falling in open habitat or with all points falling in closed habitat was counted as one segment and received a minimum patchiness score close to zero. At the other extreme, patchiness scores close to one indicate that a transect included many segments of interspersed closed and open habitat patches. The patchiness measure was averaged across transects to obtain a measure of habitat patchiness at each study site.

3. *Forage abundance*: At each sampling point along a transect, I measured grass height with a measuring tape and visually estimated the percentage of area covered by grass in a circular plot 1 m in radius. Grass height \times percent cover was used as an index of forage abundance. As an additional measure of forage abundance, I used annual rainfall, which has been used previously as an indirect measure of primary productivity and food abundance (e.g., Maher 2000; annual rainfall estimates for the different sites are in Isvaran 2005).
4. *Forage patchiness*: Since patchiness of resources has been proposed to influence grouping, the patchiness of the main forage, grass, was broadly estimated in a similar fashion to habitat patchiness. For each transect, I counted the number of segments of successive sampling points at which the circular sampling plots of 1 m radius included $\geq 5\%$ of grass cover (results were not sensitive to the exact value of this cut-off; e.g., cut-offs of 10 and 25% yielded similar results), and those at which grass cover was $< 5\%$. Thus, each transect can be broken down into segments of varying lengths, where each segment consists of successive points with or without grass cover. The number of segments reflects whether forage and non-forage patches are distributed homogeneously or broken up and interspersed. Patchiness for a transect was calculated as the number of segments divided by the maximum possible number of segments.
5. *Predation pressure*: Based on published work from each study site, I placed Indian populations in low (the main predators of adults, i.e., wolves, absent) and high (wolves present) categories of predation pressure (sources of information in “[Electronic supplementary material](#),” S2). At all populations with wolves

reported, I verified their presence during my visits through direct sightings.

Within-population variation in group size and its potential correlates

The ecological correlates of variation in group size within a population were examined at Velavadar, Gujarat, during January–April 2000. The study area was gridded into 14 approximately 1-km² (1.1 \times 1.1 km) sampling units. The approximate grid size was chosen based on the spatial scale over which ecological factors appeared to vary at Velavadar. The exact grid size was dictated by the scale of the map obtained from the Gujarat Forest Department. Data on group sizes in each spatial unit were collected while conducting total counts in the study area. A set of counts was conducted every 2–3 weeks, with each set consisting of 3–5 total counts on consecutive days. Altogether, 19 counts were performed over five time periods (sets). These counts were conducted in morning and evening hours, the whole study area was systematically covered, and the number and sex of all individuals in the encountered groups were recorded.

Habitat structure and forage abundance and distribution were measured in the different spatial units as follows. In each unit, two 500-m transects were laid at random and habitat characteristics and forage were measured as described in the among-population comparison. Furthermore, in each 1-m radius circular plot in which I measured overall grass abundance, I also visually estimated the percentage of area covered by three of the most preferred forage species: *Dichanthium annulatum*, *Chloris virgata*, and *Sporobolus maderaspatanus* (Bor 1960). The first species dominates the diet of blackbuck (30–70% seasonally), and together they form 48% of the annual diet (Jhala 1997). Visual estimates of grass cover were validated with a 1-m² sampling frame.

Individual behaviour

To evaluate the shape of the relationship between group size and potential costs and benefits, I used continuous focal animal sampling (Altmann 1974) and followed 60 adult females in groups of different sizes in grassland habitats at Velavadar over 30 days spread over February–April 2000, October 2000, and February–April 2001. I restricted sampling to adult females to minimise heterogeneity in the data arising from age- and sex-related behavioural variation. All individual follows were 10 min long and were performed during morning and evening

hours, times when foraging activity is high (Mungall 1978; Jhala 1997). I focused on foraging periods because some of the main hypothesized costs and benefits of grouping, such as feeding competition and time spent in vigilance versus feeding, are related to foraging. During each follow, I recorded the frequency and duration of all occurrences (Altmann 1974) of these behaviour patterns: (1) alert (head up, ears held forward, still or moving); (2) feeding (head down, ingesting or chewing, still or moving); (3) standing (head up, ears held normal, still); (4) food-searching (head down, moving, without ingesting or chewing); (5) moving (head up, moving, ears held normal). To account for potential effects of habitat structure on vigilance, distance to vegetative cover (shrubs or trees ≥ 1 m high) was recorded. The location of the individual within the group (peripheral, nonperipheral) was also noted. Care was taken to ensure that individuals were not influenced by my presence: observations were made using a 15–45 \times spotting scope, mostly from watchtowers or on foot from a distance of >400 m, and individuals did not appear alert to my presence.

To estimate potential travel costs associated with foraging in larger groups, I followed 26 different groups of varying size for 1 h each during morning or evening hours. Blackbuck show peaks in foraging activity in early morning and evening hours that are about 2 h in duration (Mungall 1978; Ranjitsinh 1989). Thus, 1-h follows are likely representative of behaviour during foraging peaks. During each group follow, I recorded the number of individuals in the group, noted the location of the approximate centre of the group at the beginning and the end of the 1-h follow, and paced out the distance between these two locations. This distance was used as a measure of travel costs during foraging.

Finally, an experiment was conducted to test whether animals in larger groups detected predators earlier, to quantify the shape of this relationship, and to examine whether this relationship was influenced by habitat structure. I approached adult females in groups of different sizes from a fixed distance of about 250 m (range = 245–260 m; measured with a rangefinder, Nikon Laser 400). Individuals were chosen at random from along the periphery or near-periphery of the group. Once the individual appeared to be alert to my approach (defined as alert behaviour with the individual's head oriented in my direction), I halted and used the rangefinder to measure the distance from my location to the individual. This experiment was conducted during foraging periods (morning and evening hours) in two habitats: grassland with ($n = 18$ individuals) and without ($n = 9$) scattered shrubs. Hunting by humans does not occur within Velavadar but has been reported outside the protected area (Ranjitsinh 1989). Because animals do move out of the protected area, and since blackbuck in all

populations showed alert behaviour towards humans, the results from this experiment likely reflect the detection by individuals of an approaching threat.

Analysis

Two measures of group size were used. I calculated mean group size for each population by first averaging group sizes within each total count (or transect) and then across total counts (or transects). Mean group size represents the size of the group that an observer would encounter, on average, in a population. However, it may poorly reflect the size of the group in which an average individual is found. As the focus here is on the costs and benefits to an individual of being in groups of different sizes, I used a recommended individual-centred measure, typical group

size (Jarman 1982), which is calculated as $\frac{\sum_{i=1}^n x_i^2}{N}$ where x_i is the number of individuals in the i th group, n is the number of groups and N is the total number of individuals. A solitary individual was counted as a group of 1. The typical group size represents the group size of the average individual. For each population, this measure was first calculated for each total count or transect and then averaged. For within-population comparisons, estimates for mean group size and typical group size in each spatial unit were first calculated for each total count, then across counts within a time period, and finally across time periods. To assess whether group sizes could be pooled across time periods, I ran a random-effects model with spatial unit and time period as random effects, and with each response data point representing the typical group size from a total count. Likelihood ratio tests were used to test the significance of random effects (Pinheiro and Bates 2000).

Territorial males were not included in the estimation of group sizes since the factors that influence mating-territory location and clustering are thought to differ from those affecting social group sizes. All social group types (described previously) were pooled, but analysing their ecological correlates separately produced similar results.

For both among- and within-population comparisons, I first used parametric (Pearson's) correlation analyses to explore relationships between group size measures and ecological variables. To meet the assumptions of bivariate normality and linearity, group size measures were \log_e -transformed in all analyses, and, if needed, explanatory variables were also suitably transformed: in the among-population comparisons, habitat openness was arcsine square-root transformed, and in the within-population comparisons all explanatory variables were \log_e -transformed. As an additional way of assessing the relative

importance of habitat structure and forage, I ran a multiple regression with group size as the response, and with habitat openness and forage abundance (the main habitat structure and forage variables) as predictors. Predator occurrence was not included in the regression analysis because data were not available for the Texas population. In both among- and within-population comparisons, the results from analysing typical group size and mean group size were very similar. Therefore, here I only present results for typical group size.

For analysing individual behaviour, from the 10-min follows of individuals, I calculated (1) rate of alert behaviour (number of alert events in 10 min), (2) time spent in alert behaviour (minimum = 0; maximum = duration of follow, 600 s), (3) time spent in feeding behaviour (minimum and maximum as above), and (4) mean duration of feeding bouts (a bout was defined as feeding behaviour lasting at least a second and was judged to be terminated if stopped for at least a second). From the 1-h group follows, the distance covered while foraging was calculated. The relationship between each of these behavioural measures (the response variables) and group size (the main predictor) was estimated in separate multiple regressions while controlling for habitat structure (distance to vegetative cover was included as a second predictor). To meet assumptions of regression analyses, typical group size, both alert-behaviour measures and the duration of feeding bouts were \log_e -transformed. The residuals from these analyses were checked for deviations from model assumptions. All analyses were carried out in the statistical language R, version 2.3.0 (R Development Core Team 2006).

Results

Among-population variation in group size

Mean group size varied among populations from three at Kyle ranch (maximum = 19) to 53 in Velavadar (maximum = 420). Typical group size also ranged widely from six at Guindy and Texas to 223 in Velavadar (S1).

Variation among populations in typical group size was most strongly correlated with habitat openness (Fig. 1; $r = 0.75$, $N = 10$ populations, $P = 0.013$) and habitat patchiness ($r = -0.71$, $N = 10$, $P = 0.023$). Large groups were associated with areas where the main habitat consisted of large stretches of open habitat. Habitat openness and patchiness were correlated ($r = -0.74$, $N = 10$, $P = 0.015$); therefore, their individual effects on typical group size need to be explored further. The Texas population fit well in the pattern shown by the Indian

populations; open habitat was relatively scarce and patchy and group sizes were relatively small (S1).

Typical group size was not significantly correlated with forage abundance ($r = 0.47$, $N = 10$, $P = 0.171$) or forage patchiness ($r = -0.54$, $N = 10$, $P = 0.105$), nor with annual rainfall ($r = -0.49$, $N = 10$, $P = 0.142$), which was used as a secondary measure of forage abundance. In a multiple regression of typical group size (\log_e -transformed), with habitat openness and forage abundance used as predictors, habitat openness explained substantial variation in typical group size (arcsine-transformed: slope(SE) = 2.92(1.16), $t_7 = 2.519$, $P = 0.04$, change in R^2 when dropped from model = 0.37), whereas forage abundance was not significant (slope(SE) = 0.0009(0.001), $t_7 = 0.762$, $P = 0.471$, change in R^2 when dropped = 0.03). Using habitat patchiness instead of habitat openness and grass height or percent greenness as alternative measures of forage abundance also yielded similar results (K. Isvaran, unpublished data).

Typical group size did not differ significantly between populations with low and high predation pressure (low: typical group size = 45, SD = 66; high: typical group size = 87, SD = 94; t -test on \log_e -transformed group sizes: $t_7 = 1.06$, $P = 0.325$); nor was it related to population density ($r = 0.12$, $N = 10$, $P = 0.748$).

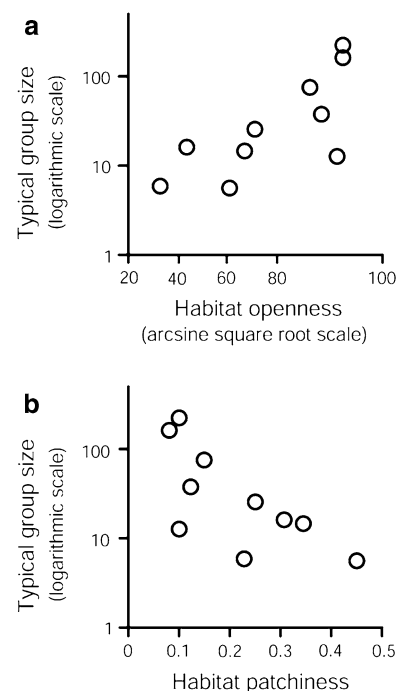


Fig. 1a–b Relationship between among-population variation in typical group size and habitat structure. **a** Habitat openness (mean percent of open habitat); **b** habitat patchiness (see “Methods”). Each data point is a population

Within-population variation in group size

Group sizes at Velavadar varied from solitary individuals to groups of >400 animals. Typical group size varied widely across the 1-km² sampling units but not across time periods (likelihood ratio tests; *time period*: $\chi^2_1 = 0.003$, $N = 266$, $P = 0.957$; *sampling unit*: $\chi^2_1 = 56.9$, $N = 266$, $P < 0.0001$; analysis based on 19 total counts in five time periods; a total of 12,335 individuals in 816 groups summed over all counts was recorded), indicating that typical group size estimates for each sampling unit could be averaged across time periods.

The variation in typical group size among 1-km² sampling units was closely correlated with forage abundance (Fig. 2; $r = 0.74$, $N = 14$ sampling units, $P = 0.003$), but was not correlated with habitat openness ($r = 0.06$, $N = 14$, $P = 0.851$), habitat patchiness ($r = -0.52$, $N = 14$, $P = 0.056$) or forage patchiness ($r = -0.20$, $N = 14$, $P = 0.497$). None of these ecological variables were correlated with each other (Pearson's $r < 0.5$, $P > 0.05$ in all cases). In a multiple regression of typical group size (\log_e -transformed), with habitat openness and forage abundance used as predictors, forage abundance explained substantial variation in typical group size (\log_e -forage abundance: slope(SE) = 0.44(0.12), $t_{11} = 3.651$, $P = 0.004$, change in R^2 when dropped from model = 0.55), whereas habitat openness did not (\log_e -habitat openness: slope(SE) = -0.48(1.36), $t_{11} = -0.35$, $P = 0.733$, change in R^2 when dropped = 0.01). The measure of forage abundance used (the abundance of all grass species) was closely correlated with the combined abundance of the three preferred species ($r = 0.95$, $N = 14$, $P < 0.0001$).

Individual behaviour

Females in larger groups were alert less frequently (slope (SE) = -0.30(0.05), $t_{57} = -6.751$, $P < 0.0001$) and spent

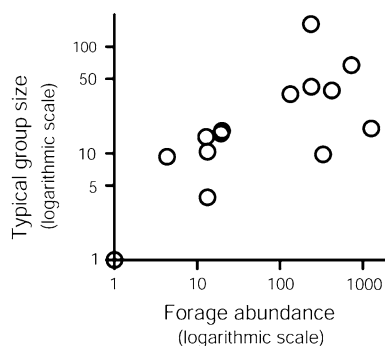


Fig. 2 Relationship between within-population variation in typical group size and forage abundance (mean grass height \times grass cover). Each data point is a 1-km² sampling unit

less time in alert behaviour (slope(SE) = -0.69(0.10), $t_{57} = -7.170$, $P < 0.0001$) than females in smaller groups (Fig. 3, “Electronic supplementary material,” S3). Both vigilance measures showed nonlinear decreases with group size (slope of $\log(Y)$ versus $\log(X)$ was significantly < 1 ; see above, S3, Fig. 3). Also, females farther from vegetative cover tended to be alert less frequently than those closer to cover (slope(SE) = -0.15(0.07), $t_{57} = -2.067$, $P = 0.043$; S3). Peripheral and nonperipheral individuals did not differ significantly in either the rate of alert behaviour ($t_{29} = -0.933$, $P = 0.358$) or the total time spent in alert behaviour ($t_{29} = -1.209$, $P = 0.237$).

Females engaged in longer feeding bouts when in larger groups (slope(SE) = 49.29(8.2), $t_{56} = 6.011$, $P < 0.0001$) and time spent feeding increased rapidly with group size (slope(SE) = 0.33(0.05), $t_{56} = 6.495$, $P < 0.0001$; S3, Fig. 3). The distance travelled by groups while foraging increased with group size (Fig. 3; $distance^{1/2} = 4.01 + 1.95 \times \log_e \text{ group size}$; $R^2 = 0.28$, $N = 26$, $P = 0.005$).

Animals in larger groups detected my approach farther away than those in smaller groups (Fig. 4; analysis of covariance on \log_e -transformed *distance to detection*; intercept: estimate (95% confidence interval CI) = 4.47(4.28–4.66); $\log_e(\text{group size})$: slope(CI) = 0.19(0.13–0.25), $F_{1,24} = 44.057$, $P < 0.0001$; *habitat type*: coefficient-open grassland(CI) = -0.29(-0.45 to -0.12), $F_{1,24} = 12.562$, $P = 0.002$; $\log_e(\text{group size}) \times \text{habitat type}$: $P = 0.43$). The distance to detection increased in a decelerating fashion with group size in both open grasslands and in grasslands with scattered shrubs (slope of $\log(Y)$ versus $\log(X)$ was significantly < 1). Furthermore, individuals in the habitat with greater vegetative cover (grasslands with scattered shrubs) detected my approach at a greater distance than did individuals in open grasslands (Fig. 4).

Discussion

Among-population variation in group size

Group sizes varied extensively among the ten blackbuck populations, from an average typical group size of six in Guindy to 223 at Velavadar. This large-scale variation in group size was most closely correlated with habitat structure. Group size was positively related to habitat openness and negatively to habitat patchiness, and groups were largest in sites dominated by large stretches of open habitat. Similar increases in group size with habitat openness have been reported from interspecific (e.g., Jarman 1974; Kaufmann 1974) and intraspecific comparisons (e.g., Walther 1972; Hirth 1977), but these studies typically did not include resource variables as potential correlates. Results from blackbuck provide strong support for the

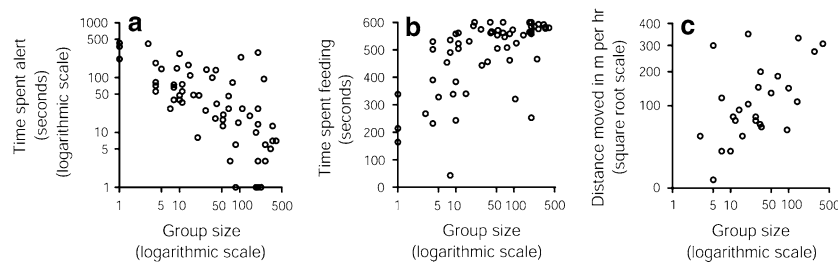


Fig. 3a–c Relationship between group size and **a** time spent in alert behaviour (s), **b** time spent feeding (s). Each data point in **a** and **b** is an adult female blackbuck ($N = 60$). **c** Distance moved while foraging by groups of different sizes during 1 h group follows. Each data point

in **c** is a group. Relationships between group size and the three behavioural variables were decelerating and have been transformed to meet assumptions of statistical analyses (details in S3 and in the text)

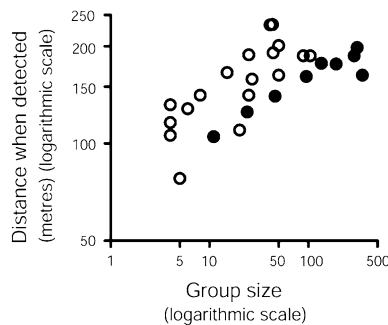


Fig. 4 Relationship between group size and the distance at which the focal animal detects an approaching threat in two different habitats (*open circles*, open grasslands; *filled circles*, grassland with scattered shrubs). The decelerating relationship is displayed on double-logarithmic axes

proposed influence of habitat structure on grouping because this relationship was unaffected by the inclusion of forage abundance in the statistical model.

Habitat structure is thought to affect grouping primarily by interacting with predation pressure and modifying the magnitude of anti-predation benefits that animals gain from joining larger groups. Group formation is proposed to reduce predation risk to a greater degree in open habitats than in closed habitats (Jarman 1974); in open habitats, predation risk is best reduced by grouping to improve detection of predators and to take advantage of dilution and confusion effects. Conversely, in closed habitats, predation risk is best reduced by reducing the probability of being detected by predators, and so individuals should occur in smaller groups (Jarman 1974).

This habitat structure hypothesis relies on predation being an important selective factor and therefore predicts that group sizes should also vary with predation pressure. Interestingly, however, presence of wolves, the main predators of adult blackbuck, was not related to group size variation across populations. Such a relationship may not have been detected by this study for three main reasons. First, it is possible that my measure of predation pressure was not adequate. The two other potential predators of adult

blackbuck, village dogs and humans, were not measured since they are not reported to be significant sources of mortality of adult blackbuck at the study sites I surveyed (Ranjitsinh 1989; Jhala 1993). Second, individuals may be responding to predation levels on a longer time scale than measured by current studies (Byers 1998; Brashares and Arcese 2002). Third, predation may not be the most important factor currently influencing group size (Brashares and Arcese 2002). Perhaps habitat structure modifies payoffs to grouping other than those related to predation risk. The main alternative explanations in the literature for the effect of habitat structure on grouping relate to the processes of group formation and cohesion (e.g., the probability of perceiving and joining other individuals may increase as habitat openness increases, Gerard et al. 2002). Overall, although the relationship between habitat structure and grouping has been reported from numerous large herbivores, our understanding of the underlying mechanisms is still poor.

The third set of ecological variables, forage abundance and patchiness, was not significantly related to among-population variation in group size in blackbuck. An additional analysis showed no relationship between annual rainfall (a crude index of primary productivity) and group size. These results suggest that forage is unlikely to be the primary factor influencing among-population variation in group size in blackbuck. Note that my measure of forage abundance does not incorporate forage-species preferences or forage quality. At the intensive study site, the abundance of three main preferred grasses was strongly correlated with overall grass abundance, suggesting that, at this site, the forage-abundance measure I used was suitable. However, comparable data are not available from the other sites, and it is possible that the suitability of this measure varied among sites. Similarly, perhaps annual rainfall is not a good index of forage for blackbuck.

To summarise, habitat structure showed the strongest relationship with among-population variation in group size, but the underlying mechanism is unclear and needs investigation. The potential role of predation in blackbuck grouping also requires further investigation; in particular,

quantitative estimates of wolf densities and the contribution of low sources of mortality (e.g., dogs) to the perception of threat need to be obtained.

Within-population variation in group size

Contrary to the among-population comparison, variation in group size at a smaller spatial scale, within a population, was strongly related to forage abundance and unrelated to habitat structure. Groups were largest in sampling units with large grass patches, suggesting that forage can constrain group size (Terborgh and Janson 1986; Wrangham et al. 1993). Variation in forage abundance among sampling units could lead to variation in feeding competition and so modify the costs of grouping to different degrees. For example, in sampling units with little forage, the costs of feeding competition may exceed the benefits of forming large groups, thereby favouring small group sizes. Conversely, in areas with abundant forage, resources may be sufficient to support large groups.

Interestingly, habitat structure showed a strong relationship with group size among but not within a population. One possible explanation is that the influence of habitat structure on the payoffs to grouping varied much more across populations than within a population. Although the habitat at Velavadar was heterogeneous, the variation in habitat structure within this site (coefficient of variation: habitat openness = 15%, habitat patchiness = 44%) was not as high as that among populations (CV: habitat openness = 32%; habitat patchiness = 58%, S1). Additionally, variation in predation pressure, which needs to be explored further (see above), and its interaction with habitat structure in influencing the anti-predation benefits to grouping may also be greater across than within sites.

Individual behaviour: trade-offs associated with group size

To identify the processes by which ecological factors such as habitat structure affect grouping in blackbuck, a description of the relationship between group size and potential costs and benefits to individuals is first needed. We can then examine how ecological factors affect the shape and magnitude of these trade-offs and so affect grouping. Results from examining the behaviour of individuals in groups of different sizes suggest that grouping in blackbuck involves a balance between predation-related benefits and feeding-competition costs. Individuals in larger groups detected the standardized approach of an observer at a greater distance than those in smaller groups, supporting the idea that group-living yields antipredator benefits. Such early detection provides more

time to respond to a predator, and predators may be less likely to attack if detected from further away (e.g., Lingle and Wilson 2001), especially for species such as blackbuck, which typically flee when attacked and can outrun their predators (Ranjitsinh 1989). The relationship between group size and distance to detection was decelerating, matching predictions from theoretical models that predation-related benefits should show a pattern of diminishing returns with group size (e.g., Dehn 1990).

Interestingly, individuals in a habitat with greater vegetative cover detected my approach sooner than individuals in more open habitats, controlling for group size. The data on vigilance suggest that this is because individuals are more frequently vigilant when they are closer to cover. These results are consistent with the hypothesis that habitat structure modifies the anti-predation benefits to grouping. If grouping is less effective against predation in closed habitats and more time is required to respond effectively (e.g., if shrubs reduce collective-detection benefits and increase interference among fleeing individuals), then individuals are expected to be more vigilant and detect predators at a greater distance.

Another proposed benefit to grouping, time allocation towards feeding versus vigilance, also diminished with group size in blackbuck. The time spent feeding by an individual increased rapidly while the time spent alert decreased sharply with group size. Similar patterns have been reported from a range of gregarious vertebrates (e.g., Lima et al. 1999; Blumstein and Daniel 2002).

Along with greater benefits, individuals in larger groups appeared to also experience greater travel costs while foraging (likely due to increased feeding competition; Chapman et al. 1995). Individuals in larger groups moved over longer distances than those in smaller ones, indicating that, as identified for primates (e.g., Wrangham et al. 1993; Chapman et al. 1995), grouping in ungulates may carry energetic costs, which merit further study. An alternative explanation of these results is that individuals in larger groups may have access to better resources, which may allow them to increase travel and to use their foraging areas differently compared with individuals in smaller groups.

The data on ecological correlates of large- and small-scale variation in group size indicate the generality and overall importance of particular selective factors, while the data on individual behaviour indicate specific mechanisms by which these factors might influence group size. Taken together, these findings suggest that, in blackbuck, individuals in groups experience a trade-off between predation-related benefits and feeding-competition costs; the nature of this trade-off is likely influenced by habitat structure and forage abundance. Variation in these ecological factors may thus maintain variation in group size. Additional factors may explain the variation in group size that is still unaccounted

for. These factors include the risk of acquiring parasites (Mooring and Hart 1992), individual variation in optimal group size, and the specific dynamics of individuals joining and leaving groups (e.g., optimal versus stable group sizes, Pulliam and Caraco 1984). Finally, studies specifically linking processes to large-scale patterns, i.e., how costs and benefits of group-living influence individual fitness and thereby optimum group sizes, and how the shape and magnitude of these trade-offs are modified by small- and large-scale variation in ecological conditions, are required to advance our understanding of the maintenance of group size variation.

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