28. Sheshshayee, M. S., Krishnaprasad, B. T., Nataraj, K. N., Prasad, T. G., Shankar, A. G. and Udayakumar, M., *Curr. Sci.*, 1996, **70**, 672–675.
29. Krishna Prasad, B. T., Sheshshayee, M. S., Nataraj, K. N., Shankar, A. G., Udayakumar, M and Prasad, T. G., *Curr. Sci.*, 1996, **70**, 675–680.
30. Hubick, K. T., Shorter, R. and Farquhar, G. D., *Aust. J. Plant Physiol.*, 1988, **15**, 799–813.
31. Farquhar, G. D., Lloyd, J., Taylor, J. A., Flanagan, L. V., Syvertsen, J. P., Hubick, K. T., Wong, S. C. and Ehleringer, J. R., *Nature*, 1993, **363**, 439–443.
32. Ehleringer, J. R., in *Stable Isotopes and Plant Carbon/Water Relations* (eds Ehleringer, J. R., Hall, A. E. and Farquhar, G. D.), Academic Press, New York, 1993, pp. 155–172.
33. Flanagan, L. B., Phillips, S. L., Ehleringer, J. R., Lloyd, J. and Farquhar, G. D., *Aust. J. Plant Physiol.*, 1994, **21**, 221–234.
34. Flanagan, L. B., in *Stable Isotopes and Plant Carbon/Water Relations* (eds Ehleringer, J. R., Hall, A. E. and Farquhar, G. D.), Academic Press, New York, 1993, pp. 71–90.
35. Flanagan, L. B. and Ehleringer, J. R., *Plant Physiol.*, 1991, **97**, 298–505.
36. Francey, R. J. and Tans, P. P., *Nature*, 1987, **327**, 495–497.
37. Wang, X-F. and Yakir, D., *Plant Cell Environ.*, 1995, **18**, 1377–1385.
38. Wright, G. C., Hubick, K. T. and Farquhar, G. D., *Aust. J. Plant Physiol.*, 1988, **15**, 815–825.
39. Condon, A. G., Richards, R. A. and Farquhar, G. D., *Crop Sci.*, **27**, 996–1001.
40. Martin, B. and Thorstenson, Y. R., *Plant Physiol.*, 1988, **88**, 213–217.
41. Hubick, K. T., Farquhar, G. D. and Shorter, R., *Aust. J. Plant Physiol.*, 1986, **13**, 803–816.
42. Hall, A. E., Ismail, A. M. and Menendez, C. M., in *Stable Isotopes and Plant Carbon/Water Relations* (eds Ehleringer, J. R., Hall, A. E. and Farquhar, G. D.), Academic Press, New York, 1993, pp. 349–369.
43. Acevedo, E., in *Stable Isotopes and Plant Carbon/Water Relations* (eds Ehleringer, J. R., Hall, A. E. and Farquhar, G. D.), Academic Press, New York, 1993, pp. 399–417
44. Ehdaie, B., Barnhart, B., Waines, J. R., in *Stable Isotopes and Plant Carbon/Water Relations* (eds Ehleringer, J. R., Hall, A. E. and Farquhar, G. D.), Academic Press, New York, 1993, pp. 419–434.
45. Johnson, R. C. and Bessett, L. M., *Crop Sci.*, 1991, **31**, 157–162.
46. Richards, R. A. and Condon, A. G., in *Stable Isotopes and Plant Carbon/Water Relations* (eds Ehleringer, J. R., Hall, A. E. and Farquhar, G. D.), Academic Press, New York, 1993, pp. 451–462.
47. Meinzer, F. C., Goldstein, G. and Grantz, D. A., *Plant Physiol.*, 1990, **92**, 130–135.
48. Porter, H. and Farquhar, G. D., *Aust. J. Plant Physiol.*, 1994, **21**, 507–516.
49. White, J. W., in *Stable Isotopes and Plant Carbon/Water Relations* (eds Ehleringer, J. R., Hall, A. E. and Farquhar, G. D.), Academic Press, New York, 1993, pp. 387–397.

ACKNOWLEDGEMENTS. We thank UAS, Bangalore for providing the facilities and the Australian Council for International Agricultural Research (ACIAR) for financial assistance. We are grateful to Dr Greame Wright, Kingeroy, Australia and Dr R. C. Nageshwara Rao, ICRISAT, India. Special thanks are due to Dr Anura V. Kurpad, Head, Nutrition Research Laboratory, St. John's Medical College, Bangalore for the analysis of ^{18}O in leaf water samples.

Received 13 November 1997, revised accepted 1 April 1998

Analysis of habitat-use using ordination: The Nilgiri tahr in southern India

M. D. Madhusudan*[†] and A. J. T. Johnsingh

Wildlife Institute of India, P.O. Box 18, Dehra Dun 248 001, India
[†]Present address: Centre for Ecological Research and Conservation, 3076/5, IV Cross, Gokulam Park, Mysore 570 002, India

Most conventional analyses relating to habitat use by large vertebrates are built on a univariate framework. Although they afford the major advantage of being simple to perform and interpret, they fail to take into account the interacting effects of multiple habitat variables on animal habitat use. Using data on the Nilgiri tahr (*Hemitragus hylocrius*), an endangered mountain goat of the Western Ghats, this paper presents a simple ordination technique, Principal Components Analysis, to analyse habitat use. We demonstrate that the distribution of all-male herds correlate with better foraging opportunities, and the distribution of female herds correlate with better security from predation. We also present an index to assess the relative importance of different variables in determining habitat use in the tahr. Finally, we encourage a wider application of such simple multivariate analyses in large animal ecology.

KNOWLEDGE of how an animal selects and uses its habitat is essential to many ecological studies, particularly in planning conservation strategies for rare and endangered species. Biologists studying large vertebrates have traditionally described animal habitat-use by considering individual resources in an animal's habitat such as food, water, and cover as variables. Then, using various measures of resource selection, they examine degrees of selection of these variables, or their proportionate use relative to availability in the animal's habitat[1–6]. Resource selection indices and availability-use analyses adequately describe whether an animal selects or avoids individual features of its habitat. These analytical techniques, however, suffer from certain drawbacks in describing animal habitat-use.

First, they assume an *a priori* knowledge of what constitutes significant habitat variables for an animal – a precondition that is seldom satisfied for many species. Second, knowledge of an animal's apparent preference or avoidance of a particular habitat variable yields no indication of its importance relative to another habitat variable that is similarly preferred or avoided. Finally, in describing habitat-use, these analytical techniques consider individual variables as disparate features of an animal's habitat. Animal habitat-use, however, is a multi-dimensional concept involving several *interacting* variables in the organism's physical and behavioural

*For correspondence. (e-mail: mdm@arbornet.org)

environment. There is, therefore, a need to adopt techniques of analyzing animal habitat-use which overcome these drawbacks.

Ordination, illustrated here using Principal Components Analysis (PCA) (ref. 7), represents one way of circumventing problems associated with traditional habitat-use analysis. Using ordination, a multi-dimensional data set can be rendered in fewer dimensions (ideally two) to allow examination of intrinsic patterns in the original data set. Further, it allows the construction of 'principal components' that are a weighted sum of all the variables, the weights being assigned such that the first component captures as much of the variation in the variables as possible. Successive components similarly extract maximum residual variation, and are orthogonal (uncorrelated) to the preceding components. Only those components which explain more variation than is contained in any single variable (a threshold specified usually by an Eigen value > 1) are considered significant in further analyses. PCA reveals, by means of the weight (or factor score coefficient) the relative importance of each variable in constructing the factor. Further computational details of the procedure are available elsewhere[7].

We illustrate the application of PCA to analyse habitat use in the Nilgiri tahr *Hemitragus hylocrius* (Mammalia: Bovidae), and attempt to identify variables that best describe the habitat used by the tahr. Further, we also show how two social units in the tahr – bachelor herds and female herds – cue in to different variables in their use of habitat. The Nilgiri tahr is a primitive goat endemic to the southern Western Ghat hill ranges of Peninsular India. Tahr are sexually dimorphic: males are up to 70% larger than females. They are grazers occupying grasslands (usually at elevations over 1000 m above sea level) near steep, precipitous terrain, which they negotiate adeptly to escape from predators. Uncontrolled poaching and large-scale loss and fragmentation of its habitat due to the advent of commercial plantations (e.g. tea, wattle, eucalyptus, and pine) have resulted in decline in tahr populations all over its range. This has necessitated its inclusion as an endangered species under Schedule I of the Indian Wildlife (Protection) Act 1972, and the 'vulnerable' category of the IUCN's Red list for mammals[8].

We collected data for this analysis between November 1994 and April 1995 at Eravikulam National Park, Kerala[9]. All information to habitat-use was collected at weekly intervals by walking two ridge-top trails (total length = 16 km) which ensured complete visual coverage of the study area. All tahr groups sighted on these trails were assigned to one of three social units: bachelor groups (males > 4 years), female groups (adult females, yearlings, kids, and sub-adult males), and mixed groups (female groups with ≥ one adult male). The time of the study corresponded to the post-rut and birth season in the tahr. We used information from earlier studies on mountain ungulates[10] to short-list a set of six habitat variables relating to topography, terrain, and forage abundance, and examined their role in the tahr's use of habitat. Variables associated with the location of each tahr group, viz. altitude, slope, rockiness, volume of graminoid forage, and distances to cliffs and *shola* (stunted evergreen forest patches), respectively, were measured from the trails described earlier. It was possible to obtain exact measurements for certain variables (e.g. altitude slope), but only estimates could be made for variables relating to distance (i.e distance to cliffs, and *shola*) and rockiness. Therefore, for the purpose of analysis, we ranked the values taken by these variables, and used the rank scores instead of field-estimates.

PCA was performed on the SPSS/PC + software[11] with the default options of Pearson's correlation coefficient matrix as the input, and a Varimax rotation of factors. The PCA extracted two components, which summarized 74.8% of the variation in the system (Table 1). PC1 accounted for 55.0% of the variation and significant positive correlations with graminoid forage volume and distance to cliffs and negative correlations with rockiness

Table 1. Summary statistics of the Principal Components Analysis

		PC1		PC2	
Habitat variable	Communality	*r*	*C*	*r*	*C*
Altitude	0.59	0.30	0.02	0.71*	0.54
Distance to cliffs	0.63	0.79*	0.25	0.07	–0.03
Distance to *shola*	0.74	–0.11	–0.13	0.85*	0.71
Graminoid forage volume	0.86	0.91*	0.28	0.19	0.05
Rockiness	0.91	–0.95*	–0.30	–0.12	0.01
Slope	0.77	–0.88*	–0.29	0.02	0.12
		Eigenvalue = 3.30 % variation explained = 55.0		Eigenvalue = 1.19 % variation explained = 19.8	

r = Pearson's correlation coefficient, *C* = Factor score coefficient;
*Correlation significant at $P = 0.05$.

and slope. PC2, on the other hand, accounted for 19.8% of the variation in the system and was positively correlated with altitude and distance from *shola*.

To facilitate visual interpretation of overall habitat-use patterns in the tahr, all sightings on trails were plotted by social unit on a scatter-plot of their principal component scores. The ordination of tahr social units on the two-factor axes (Figure 1) revealed interesting differences in their use of habitat. Although overlap occurred, bachelor and female herds occupied distinct regions in factor space, separating along PC1 and PC2. In the habitat continuum available to the tahr, bachelor herds ($n = 47$) occupied areas at higher altitudes that were less steep and rocky, farther from cliffs, and contained higher volumes of graminoid forage relative to the areas used by female herds ($n = 140$). Female herds contained defenceless young and used secure areas near cliffs more than did bachelor herds. Bachelor herds, on the other hand, seemed to be trading security from predation for access to better foraging opportunities by using gentler terrain. Since habitat-use patterns of mixed groups ($n = 15$) were obscured by their small sample size, we only present them on the scatter plot (Figure 1), but omit them from subsequent analysis and discussion. Further analyses of segregation patterns between the social units in the tahr are available elsewhere[9].

We used nonparametric Wilcoxon–Mann–Whitney test[12] on the PC1 and PC2 scores to illustrate how results from the above exploratory analysis can be extended to make statistical inferences about observed patterns. The test statistically validated the above differences in habitat use between bachelor and female herds, along both PC axes ($U = 1005$, $z = 7.1$, $P \ll 0.05$ for PC1, and $U = 1442$, $z = -5.8$, $P \ll 0.05$ for PC2).

However, several strong and significant relationships between the habitat variables considered in the analysis (Table 2) made it difficult to tease apart the influence exerted by individual variables in producing overall patterns of habitat use by tahr. Therefore, we constructed a composite index using the results of the PCA to isolate and measure the relative importance of different habitat variables in the tahr's use of habitat. The index was computed as follows:

$$I_v = E_1(r_{v1} \times C_{v1}) + E_2(r_{v2} \times C_{v2}),$$

where, I_v = Index of relative importance of variable V; E_1 and E_2 are Eigen values of principal components (PC) 1 and 2, r_{v1} and r_{v1} are Pearson's correlation coefficients (or weights) of variable V in constructing PC1 and PC2, respectively. This index indicated that, among the six habitat variables, rockiness exerted the greatest influence on the tahr's use of habitat (I = 0.94), followed by slope (I = 0.85), available graminoid forage volume (I = 0.85), distances from *shola* (I = 0.77) and cliffs (I = 0.65). Altitude (I = 0.48), *per se*, was the least important to the distribution of female or bachelor herds.

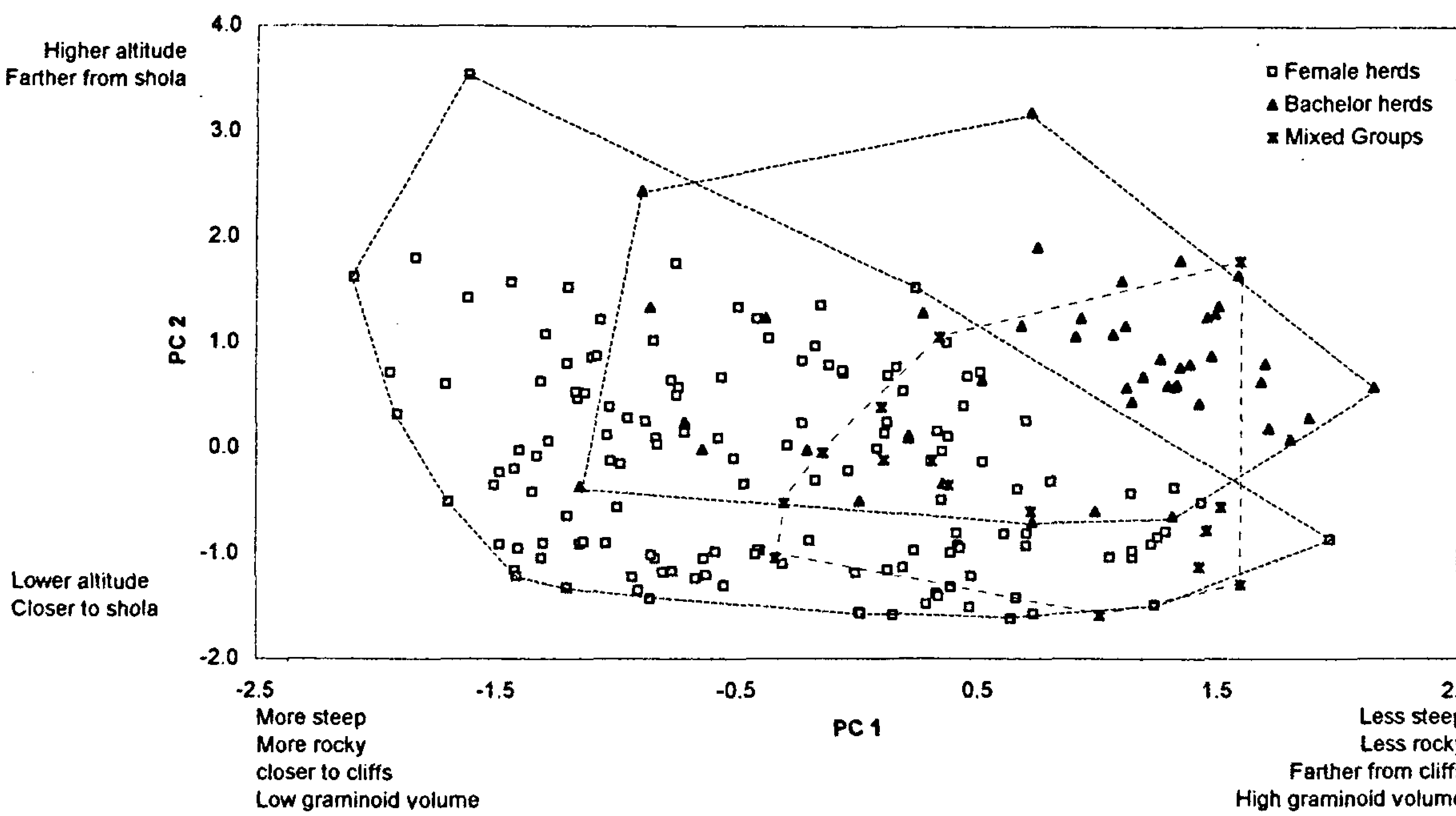

Figure 1. Location of female, bachelor and mixed herds in factor space.

Table 2. Relationships between variables: Pearson's correlation coefficient matrix

	Altitude	Distance to cliffs	Distance to *shola*	Graminoid forage volume	Rockiness	Slope
Altitude	1.0000	0.2752*	0.2472*	0.3653*	–0.3055*	–0.1898*
Distance to cliffs		1.0000	–0.0113	0.6115*	–0.6624*	–0.5803*
Distance to *shola*			1.0000	0.0698	–0.0365	0.0310
Graminoid forage volume				1.0000	–0.9146*	–0.7207*
Rockiness					1.0000	0.7945*
Slope						1.0000

*Relationship significant at $P < 0.05$.

In this example, although we use ordination on a small set of variables, and highlight only those influencing habitat use in bachelor and female herds, there is enormous scope for its usage in other situations. Particularly where variables influencing habitat use are not readily apparent, or far too numerous, ordination can be considered either as a valuable data-exploratory tool to choose a smaller, more meaningful set of habitat variables for subsequent univariate analyses, or as a convenient way of reducing dimensionality in the data to facilitate easier interpretation of multivariate data. In keeping with the utility of representing habitat utilization against habitat availability, it is possible to include data on availability of habitat variables in the study area in the ordination so as to allow visual comparisons of usage with availability (both represented on the factor axes as in Figure 1). The index of relative importance introduced here is particularly valuable in assessing the actual importance of various habitat variables to an animal, and in planning management strategies accordingly. Although it is possible that field data often fails to comply with assumptions of a PCA such as multivariate normality, linear interactions between variables and constant variances, we still advocate its use because it is based on a simple correlation matrix of variables, and does not involve distributions or inferential statistics. However, we caution that these assumptions be heeded in situations involving extensions of this approach into inferential statistics (e.g. discriminant function analysis).

Traditionally, ordination techniques have been popular mostly among plant and aquatic ecologists who largely work at the community and ecosystem levels of organization[13]. Working typically with large data sets, they seek to reduce the size and complexity of their data, a facility which ordination allows. However, the use of ordination in large vertebrate ecology has been scant, owing primarily to the fact that ecologists studying large vertebrates seldom work beyond the population and community-subset levels of organization where data is relatively neither vast nor complex. Moreover, obvious behaviours of large vertebrates have been used to generate study hypotheses (even without data exploration) that are later examined. However, it is necessary to complement such intuitive natural history with analytical tools to perceive subtler patterns of behaviour in large vertebrates. As we illustrate in this instance, ordination procedures can be employed effectively at population-level studies of large vertebrates to validate assumptions about habitat choice, and to extend descriptive natural history into the realms of hypothesis testing.

1. Neu, C. W., Byers, C. R. and Peek, J. M., *J. Wildl. Manage.* 1974, **38**, 541–545.
2. Johnson, D. H., *Ecology*, 1980, **66**, 1744–1748.
3. Byers, C. R., Steinhorst, R. K. and Krausman, P. R., *J. Wildl. Manage.*, 1986, **50**, 157–165.
4. Aldredge, J. R. and Ratti, J. T., *J. Wildl. Manage.*, 1986, **50**, 157–165.
5. Thomas, D. L., Manly, B. F. J. and McDonald, L. L., in *Wildlife 2001: Populations* (eds McCullough, D. R. and Barrett, R. H.), Elsevier Science, Essex, 1992, pp. 56–64.
6. Krausman, P. R., Leopold, B. D., Seegmiller, R. F. and Torres, S. G., *Wildl. Monogr.*, 1989, No. 102.
7. Pielou, E. C. in *Interpretation of Ecological Data: A primer in Classification and Ordination*, John Wiley, New York, 1984.
8. Groombridge, B., (ed.), *1994 IUCN Red List of Threatened Mammals*, IUCN, Gland, Cambridge, 1993.
9. Madhusudan, M. D., M.Sc. dissertation, Wildlife Institute of India, Dehra Dun/Saurashtra University, Rajkot, 1995.
10. Schaller, G. B., in *Mountain Monarchs: Wild Sheep and Goat of the Himalaya*, University of Chicago, Chicago, 1977.
11. Norušis, M. J., SPSS/PC + Statistics 4.0: Advanced Statistics, SPSS Inc., Chicago, 1990.
12. Siegel, S. and Castellan, Jr., N. J., in *Nonparametric Statistics for the Behavioral Sciences*, McGraw-Hill Book Company, 1988, 2nd edn.
13. Simberloff, D., Berthet, P., Boy, V., Cousins, S. H., Fortin, M-J., Goldburg, R., Lefkovitch, L. P., Ripley, B., Scherrer, B. and Tonkyn, D., in *Developments in Numerical Ecology* (eds Legendre, P. and Legendre, L.), Springer Verlag, Berlin, 1987, pp. 559–572.

ACKNOWLEDGEMENTS. This work was facilitated via a fellowship to the first author by the Ministry of Environment and Forests, Government of India, via the Wildlife Institute of India (WII). Permission from the Kerala Forest Department enabled us to conduct the study. We acknowledge academic and logistical support to this study from the director, faculty and researchers of WII. We thank A. Edgaonkar, Q. Qureshi, T. R. S. Raman, A. C. Williams, Drs N. V. Joshi, P. R. Krausman and two anonymous referees for their comments on the manuscript.

Received 16 August 1997; revised accepted 18 March 1998