

Scale and selection of habitat and resources: Tibetan argali (*Ovis ammon hodgsoni*) in high-altitude rangelands

N.J. Singh, N.G. Yoccoz, N. Lecomte, S.D. Côté, and J.L. Fox

Abstract: Processes of habitat selection occur at multiple spatiotemporal scales, where large-scale selection is often determined by predation risk and landscape features, and finer scale selection by resource abundance and quality. To determine whether this hierarchy exists in relatively homogenous systems, we investigated patterns of habitat (landscape topography) and resource (feeding patch and plant group) selection by a medium-sized ungulate, the Tibetan argali (*Ovis ammon hodgsoni* Blyth, 1840), in the high-altitude rangelands of the Indian Trans-Himalaya. We ran ecological niche factor analyses to explore habitat selection, bias-reduced logistic regression to analyze the selection of feeding patches, fuzzy correspondence analysis for vegetation categories, and microhistological analyses for the selection of plant groups. For springs and summers of 2005–2007, argali preferred an intermediate range of altitude, slope, and forage abundance. Selection of feeding patch was mainly determined by forage quality, not biomass, selecting graminoids and forbs, in particular. The avoidance of habitat with high forage abundance could indicate a trade-off between forage quality and quantity; a pattern consistent at the feeding-patch scale. Our results provide evidence that the hierarchical pattern of habitat selection probably also occurs in relatively homogeneous systems.

Résumé : Les processus de sélection de l'habitat agissent à plusieurs échelles spatiotemporelles : la sélection à grande échelle est souvent déterminée par le risque de prédation et les caractéristiques du paysage, alors que la sélection à une échelle plus fine l'est par l'abondance et la qualité des ressources. Afin de déterminer si une telle hiérarchie s'établit dans les systèmes relativement homogènes, nous avons étudié les patrons de sélection de l'habitat (topographie du paysage) et des ressources (taches d'alimentation et groupes de plantes) chez un ongulé de taille moyenne, le mouflon du Tibet (*Ovis ammon hodgsoni* Blyth, 1840) dans des pâturages de haute altitude du Trans-Himalaya indien. Nous avons procédé à une analyse factorielle de la niche écologique pour étudier la sélection d'habitat, une régression logistique avec réduction du biais pour analyser la sélection des taches d'alimentation, une analyse de correspondance floue pour les catégories de végétation et des analyses micro-histologiques pour la sélection des groupes de plantes. Durant les printemps et étés 2005–2007, les mouflons ont préféré des gammes intermédiaires d'altitudes, de pentes et d'abondance de fourrage. La sélection des taches d'alimentation est déterminée principalement par la qualité et non la biomasse du fourrage, avec une sélection particulière des graminoides et des plantes herbacées non graminéennes. L'évitement des habitats à forte abondance de fourrage pourrait indiquer un compromis entre la qualité et la quantité du fourrage, un patron qui est compatible à l'échelle de la tache d'alimentation. Nos résultats apportent des confirmations que le patron hiérarchique de sélection des habitats existe probablement aussi dans les systèmes relativement homogènes.

[Traduit par la Rédaction]

Introduction

Habitat and resource selection by animals occurs at different spatiotemporal scales (Johnson 1980; Manly et al. 1993; Boyce 2006). Animals generally make hierarchical decisions on where to establish a home range first and then on how to use the different parts of their home range (Myysterud et al. 1999; Johnson et al. 2001; Anderson et al. 2005). We here

describe habitat scale as the landscape's topographic characteristics, which contain a mosaic of different resources that are exploited in well-defined seasonal and daily cycles (Green and Bear 1990; Begon et al. 2006). In ungulates, the processes of habitat and resource selection may be influenced by the need to maximize net-energy intake, minimize predation risk and thermal stress, or maintain social contacts with conspecifics (e.g., Fryxell and Lundberg 1997; Fortin et

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al. 2003). The strength of trade-offs resulting through these constraints usually varies among seasons.

Heterogeneous ecosystems have been widely studied at multiple spatial and temporal scales in the context of selection of habitats and resources by animals. Often such studies have focused on forage biomass, predator space use, forest cover, and snow conditions (e.g., Schaefer and Messier 1995; Mårell and Edenius 2006). Habitat and resource selection by ungulates in these systems is often explained as a trade-off between predation risk and forage quality or quantity (e.g., Rettie and Messier 2000; Grignolio et al. 2007; Hamel and Côté 2007). In general, broad-scale selection is determined by factors such as topography, predation, snow, and distance to water, whereas finer patch scale and plant species selections are better explained by forage characteristics, nutrient requirements, and interspecific as well as intraspecific interactions. Despite such a general pattern, the importance of these biotic and abiotic factors can be system- and species-specific, thereby limiting our understanding of poorly known ecosystems, such as extreme arid and (or) cold environments (Caughley et al. 1988; Bangs et al. 2005).

Rangeland ecosystems at high altitude that support several ungulate species are relatively simple, resource-limited, and homogeneous in terms of landscape and habitat structure (Schaller and Gu 1994; Fox 2004). They host several and rare ungulate species that have been relatively little studied in the context of habitat and resource selection. Altitude (>3500 m), a major characteristic of these rangelands, defines a particular set of extreme temperature, precipitation, moisture, and vegetation characteristics (Schaller 1998; Körner 1999; Rawat and Adhikari 2005). Similar to the heterogeneous systems, herbivores in these systems are also constrained by predation risk and extreme weather events at broader scales, and forage availability and quality at finer scales (Harris and Miller 1995; Schaller 1998; Renaudeau d'Arc et al. 2000; Namgail et al. 2004). At the seasonal scale, the period of plant growth is short, and thus ungulates in these rangelands adopt an opportunistic mixed feeding strategy so as to satisfy their energy needs while maintaining nutrient balance (Schaller and Gu 1994; Shrestha et al. 2005). Plants contain maximum nutrient content during the short growth period and their digestibility rapidly decreases towards the end of the growing season (Long et al. 1999).

We assessed at different spatiotemporal scales the habitat and resource selection of Tibetan argali (*Ovis ammon hodgsoni* Blyth, 1840), a near-threatened species (IUCN 2009) for which little is known about resource use. Argali is a medium-sized ungulate inhabiting the gentle and undulating rangelands of the Tibetan Plateau (Fox et al. 1991). In such a terrain, argali relies on speed for escaping predators and may select slopes to visually scan for predators, as do other ungulates of similar size (e.g., Harris and Miller 1995; Hunter and Skinner 1998; Hamel and Côté 2007). Specifically, we explored whether factors linked to landscape topography and forage characteristics determined spring and summer selection at the habitat (~620 km²), resource (feeding patch, 25 m radius circle or 1925 m²), and plant-group scales.

We tested the following hypotheses for habitat and resource selection:

Habitat scale — (i) if predation risk determines habitat

selection, argali will select topographic characteristics that provide escape from predation; (ii) if forage characteristics determine habitat selection, argali will select the habitat with highest vegetation biomass (here tested using the normalized difference vegetation index (NDVI); for description see the Materials and methods).

Resource scale (feeding patch and plant groups) — (i) if forage abundance determines selection of the feeding patch, argali will select feeding patches with higher plant biomass; (ii) if forage quality determines selection of the feeding patch, argali will select feeding patches with a higher percentage of green tissue (here considered an index of forage quality). Additionally, argali will select plant groups of highest quality among graminoids, forbs, and shrubs.

Temporal scale (spring and summer seasons) — we predict that (i) habitat selection in spring will be determined by the availability of snow-free areas because forage availability in spring is low. On the other hand, because of increased forage availability (biomass and quality) in summer, we predict that (ii) habitat selection in summer will be determined by predation risk (because of lambing) and forage characteristics. Also, with the disappearance of snow and vegetation in the early stages of growth, along with the need to re-build lost energy reserves, (iii) forage quality should determine selection of the feeding patches during both spring and summer.

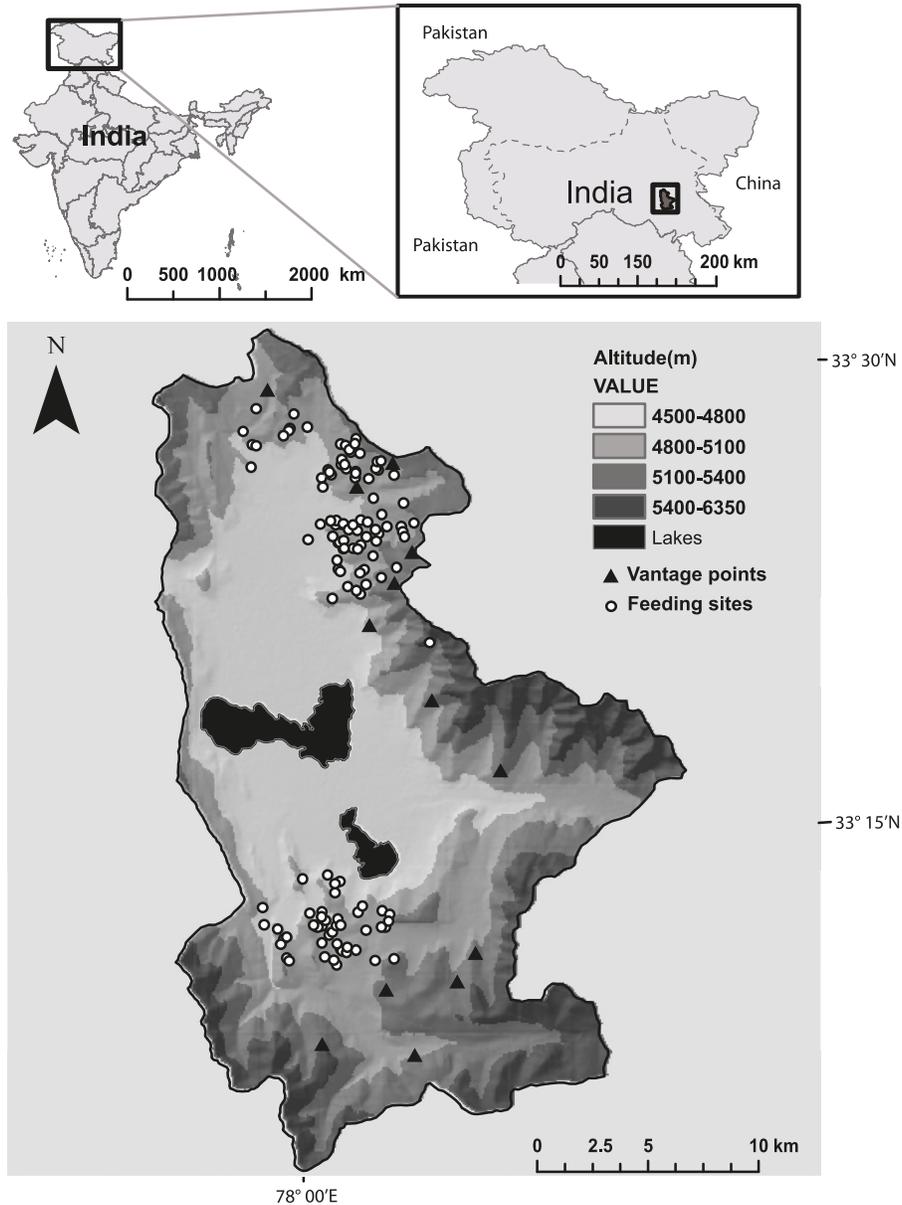
Materials and methods

Study area

The study was conducted in during the springs and summers of 2005–2007 in the Trans-Himalayan rangelands of eastern Ladakh, India (32°15'N, 78°00'E) (Fig. 1). The spring season spans from May to mid-June (mid-June is generally the period when the winter snow disappears at 4500 m of altitude), and summer spans from mid-June to August (end of August is the end of the peak growing season).

The Tso Kar area hosts high-altitude rangelands (4500–6300 m). The main features of the site are open rolling hills, broad valleys, alluvial plains, and two lakes (a freshwater lake (4 km²) and a salt-water lake (16 km²) bounded by mountain massifs). Vegetation patches are characterized by a mosaic of alpine steppe, desert, and meadows. These rangelands are dominated by graminoids such as needlegrass (genus *Stipa* L.), bog sedge (genus *Kobresia* Willd.), bluegrass (genus *Poa* L.), wildrye (genus *Elymus* L.), and sedge (genus *Carex* L.), representing about 77% of the total plant biomass (Rawat and Adhikari 2005). Other plant communities include forbs (e.g., sagebrush (*Artemisia* L.), crazyweed (*Oxytropis* DC), and cinquefoil (genus *Potentilla* L.)) and shrubs (e.g., pea shrub (*Caragana versicolor* Benth.) and me (genus *Eurotia ceratoides* (L.) C.A. Mey.)). The climate is typical of high altitude cold desert ecosystems, with temperatures ranging from –40 °C (minimum winter) to 25 °C (maximum summer), and mean annual precipitation of about 200 mm (Rawat and Adhikari 2005). About 130–150 argalis inhabit the basin region (~620 km²; Singh et al. 2010). The other wild ungulates found in the region include a population of over 300 kiangs (*Equus kiang* Moorcroft, 1841) and about 50 blue sheep (*Pseudois nayaur* (Hodgson, 1833)) (Fox 2004). The main predator in the area is the Tibetan

Fig. 1. Study area showing the range of altitudes available to Tibetan argali (*Ovis ammon hodgsoni*) along with the main water bodies in eastern Ladakh, India. All locations of argali groups and vantage points are also indicated.



wolf (*Canis lupus chanco* Gray, 1863), which was occasionally observed in the study area. The Samad nomadic community occupies the area in seasonal camps only in winter, where they herd approximately 18 000 livestock of sheep, goats, and yaks (Hagalia 2004; Singh 2008). Domestic horses are also present but in small numbers. The nomadic camps are moved into the area during winter and moved out before spring (Hagalia 2004).

Selection at different scales

Habitat scale

During three field seasons in the spring (May–June) and summer (July–August) of 2005–2007, habitat use by argali was determined through repeated scans every 15 min ($n =$

360 scans; Altmann 1974), using 15×45 spotting scopes. All surveys were conducted from 13 vantage points every 4 days. These vantage points were determined during previous reconnaissance surveys of this open rolling terrain to allow for a complete overview of the study area. The total sampling effort was 1.9 ± 0.3 h per group observation (mean \pm SE) (Singh et al. 2009).

To maintain independence among observations (Machlis et al. 1985), the same group of argalis were not observed on successive days. The new groups were identified based on their location and group composition. As the group composition changes frequently, we kept track of the groups seen and sampled areas far from where earlier groups were observed. The observations covered the entire daylight period, i.e., between the hours of 0600 and 1900, and lasted,

Table 1. Summary of environmental variables estimated to assess habitat selection of Tibetan argali (*Ovis ammon hodgsoni*) in eastern Ladakh, India, from 2005 to 2007.

Variable	Estimate	Range	Spring (<i>n</i> = 22)		Summer (<i>n</i> = 108)	
			Mean	SE	Mean	SE
Altitude (m)	Field validation and DEM	4633 to 5573	4798	18	4933	14
distTslp (m)	Classification of DEM slope raster into slope >10° and <10°, and calculation of nearest distance to a group	0 to 988	315	48	318	20
NDVI	MODIS (250 m) images with $NDVI = (IR_{band\ 4} - R_{band\ 3}) / (IR_{band\ 4} + R_{band\ 3})$, where IR is the infrared band and R is the red band	0.07 to 0.2	0.1	0.01	0.2	0.00
Northness	Aspect transformed into northness as $\cos(\text{aspect})$	-1 to +1	-0.03	0.13	-0.08	0.07
SARI	$(SD \text{ of slope} \times \text{variety of aspect}) / (SD \text{ of slope} + \text{variety of aspect})$	1.04 to 4.7	3.04	0.16	3.05	0.06
Slope (°)	Field validation and DEM	0.8 to 29.7	13.3	1.46	13	0.5

Note: DEM, digital elevation model; distTslp, distance to slope; NDVI, normalized difference vegetation index; SARI, slope–aspect ruggedness index. MODIS images available from NASA at <http://modis.gsfc.nasa.gov> [accessed 24 July 2007]. SARI is described in detail by Nelleman and Fry (1995).

on average, 1.5 h each. All individuals were unmarked and could not be consistently identified, so analyses and conclusions are at the group scale (group size = 5.6 ± 4.2 ; mean \pm SD). Locations of feeding groups (*n* = 120; spring = 22, summer = 108) were recorded using a GPS (with position accuracy of 3 ± 1 m; mean \pm SD) and plotted on a map. Once a feeding site was identified and the observation ended, one observer visited during the same day the estimated centre of the feeding site, while another observer ensured that the right location was identified using radio-contact. Altitude and slope were determined on site.

For each recorded feeding site located with GPS, we estimated altitude, slope, aspect, ruggedness, and distance to the nearest 10° (or more) slope. In addition, we used NDVI as a proxy of forage abundance (see below for details on the definition of habitat variables). NDVI is a satellite-based vegetation estimator correlated with vegetation productivity and crude protein (quality) in different ecosystems (Kawamura et al. 2005; Pettorelli et al. 2005; Hamel et al. 2009), and with total biomass in arid continental grasslands in particular (Kawamura et al. 2003, 2005).

Definitions of habitat variables

Spatial variables were prepared in ArcGIS version 9 (Environmental Systems Research Institute (ESRI) Inc., Redlands, California, USA). A digital elevation model (DEM) was obtained from Surface Radar Topography Mission (90 m resolution) for the Ladakh region. Terrain variables extracted from DEM included altitude, slope, aspect (0°–360°) transformed into “northness” ($\cos(\text{aspect})$) and a slope–aspect ruggedness index (SARI) (Nelleman and Fry 1995; Jepsen et al. 2005). SARI (see formula in Table 1) is an index that combines the attributes of slope and terrain heterogeneity (variety and variability) and provides high index values where the terrain is simultaneously rugged and steep, intermediate values in rugged and level areas, and lowest values in flat terrain and very steep (but not rugged) slopes. Distance to slope (distTslp) was estimated as the minimum distance between the estimated centre of an argali group and the nearest slope <10°.

We used NDVI (see formula in Table 1) as an index of forage abundance, estimated from three MODIS scenes (250 m resolution) of the Tso Kar region or springs and

summers of 2005–2007. Higher resolution Landsat images (30 m) generated negative values for NDVI, irrespective of the presence of vegetation (validated through field observations; *n* = 120 random points) in many areas inhabited by argalis, and were hence not used for analyses. July is the period during which vegetation biomass is at its peak in the high-altitude rangelands and is also the end of the growing season (Karnieli et al. 2006; Singh et al. 2009).

Resource scale

Feeding patch

We identified feeding patches of groups as sites where >50% of the argalis from the same group had been seen feeding for more than three consecutive scans (i.e., minimum 30 min). A total of 120 feeding sites were sampled for vegetation parameters after the identification of the feeding site. Parameters of feeding patches were estimated after the animals had left the site by laying six 1 m \times 1 m plots, randomly disposed within a 25 m radius circle around the observed centre of the feeding location. The radius was decided after repeated observations on group size and foraging movements of the groups (radius observed = 25 ± 5 m (mean \pm SE), *n* = 30). For each of the six plots and for every plant group (graminoids, forbs, and shrubs), vegetation height (cm), and percentage of green material were estimated visually. We used four vegetation height categories (0–2, 2–4, 4–6, and 6–8 cm). In each plot, vegetation cover was estimated for each plant group using the point intercept method (Diersing et al. 1992), based on four 0.5 m \times 0.5 m quadrats embedded with 20 metal pins. For each plant group, the percent cover was calculated by dividing the number of touched plants by the pin by the total number of pins in the plot. Mean biomass was then estimated by clipping plants 1 cm above ground in two randomly chosen plots and subsequently extrapolating to the other plots using a regression model, which included plant cover and plant height as predictors. Fresh mass was noted for each plant group sampled using Pesola spring scales (capacities of 10, 30, and 100 g; Pesola AG, Baar, Switzerland). Plant samples were sun-dried in the field before being transferred to laboratory facilities where they were oven-dried at 105 °C for 8 h and dry mass was measured.

To evaluate selection for feeding patches, the sampling design described above was repeated by measuring the same parameters in the same number of plots at a site located 150 m away in a random direction. We determined the distance empirically by observing the feeding behavior of groups ($n = 120$); larger distances (250 and 500 m) generally corresponded to movements among patches (for a similar design see Compton et al. 2002; Hurme et al. 2005; Young et al. 2006).

Plant groups

The selection for forage categories was assessed through composite samples obtained by randomly mixing argali pellets. We collected 10 pellet samples from independent groups each season and each year ($n = 60$). Three slides from each composite sample were prepared with 10 nonoverlapping fragments identified per slide. A total of 350 fragments were observed and collected: 165 for spring and 185 for summer. To prepare reference slides, we sampled plant species eaten by argalis from 20 randomly selected feeding sites (year 2005 = 7 sites; year 2006 = 7 sites; year 2007 = 6 sites). We used the percent relative frequency, i.e., fields with a fragment of a plant group divided by the total number of fields with identifiable plant materials of any species (Gill et al. 1983).

To assess forage quality, 10 g of all dried plant samples collected from the feeding sites ($n = 350$) were used for the biochemical analyses. Crude protein content (CP), neutral detergent fiber (NDF), and acid detergent fiber (ADF) were estimated for grasses, forbs, and shrubs separately for each month (May–August). Crude protein content was analyzed using the macro-Kjeldahl acid digestion technique (Association of Official Analytical Chemists 1984), and NDF and ADF were analyzed with the method of Goering and Van Soest (1970).

Statistical analyses

All statistical analyses were implemented in R version 2.7.2 (R Development Core Team 2008), using in particular the “ade4” and “adehabitat” libraries (Dray and Dufour 1997).

Habitat scale

We mainly used topographical variables and NDVI for the habitat-scale analyses, because the other variables that may affect argali in summer such as water availability were likely not limiting owing to the presence of perennial springs in the area. Also, livestock grazing does not occur in spring and summer in the study area, and was hence not included in the analyses. Because only data on argali presence were available and absence could not be determined without doubt, we performed an ecological niche factor analysis (ENFA; Hirzel et al. 2002; Calenge 2006; Calenge and Basille 2008). ENFA is a presence-based multivariate analysis, which investigates the difference between presence in sites and background or available space in both, the average and the range of variation of the different environmental variables, which are called marginalization and specialization, respectively. We used the Box–Cox transformation family (Hirzel et al. 2002; Venables and Ripley 2002) to transform the distribution of variables into a near symmetric one, an important step before performing ENFA. The slope

and NDVI variables were therefore square-root-transformed. In ENFA, the first axis accounts for the marginality, i.e., the difference between the mean habitat used and the habitat available. Specialization is measured as the ratio of variance of the available habitat to that of habitat used, and this ratio is equal to the eigenvalues for the specialization axes. Part of the variation on the marginality axis is also due to specialization. As with other multivariate methods, eigenvectors are used to interpret the specialization and marginality axes in ENFA (Hirzel et al. 2002). Finally, for a randomly chosen set of data, the random points are expected to have a marginality value of 0 and a specialization value of 1 (Hirzel et al. 2002).

We randomly sampled 240 points to measure availability of habitats using the “random point generator” in the Hawth’s tools extension (<http://spatialecology.com/htools/>; accessed 24 July 2007) for ArcGIS (ESRI Inc.), taking the whole study area as available, excluding the lakes and high summits with snow. No established rule is known to exist to fix a minimum for the sample sizes of the random points, only an assumption toward a greater number of points (Peng et al. 2002).

Resource scale

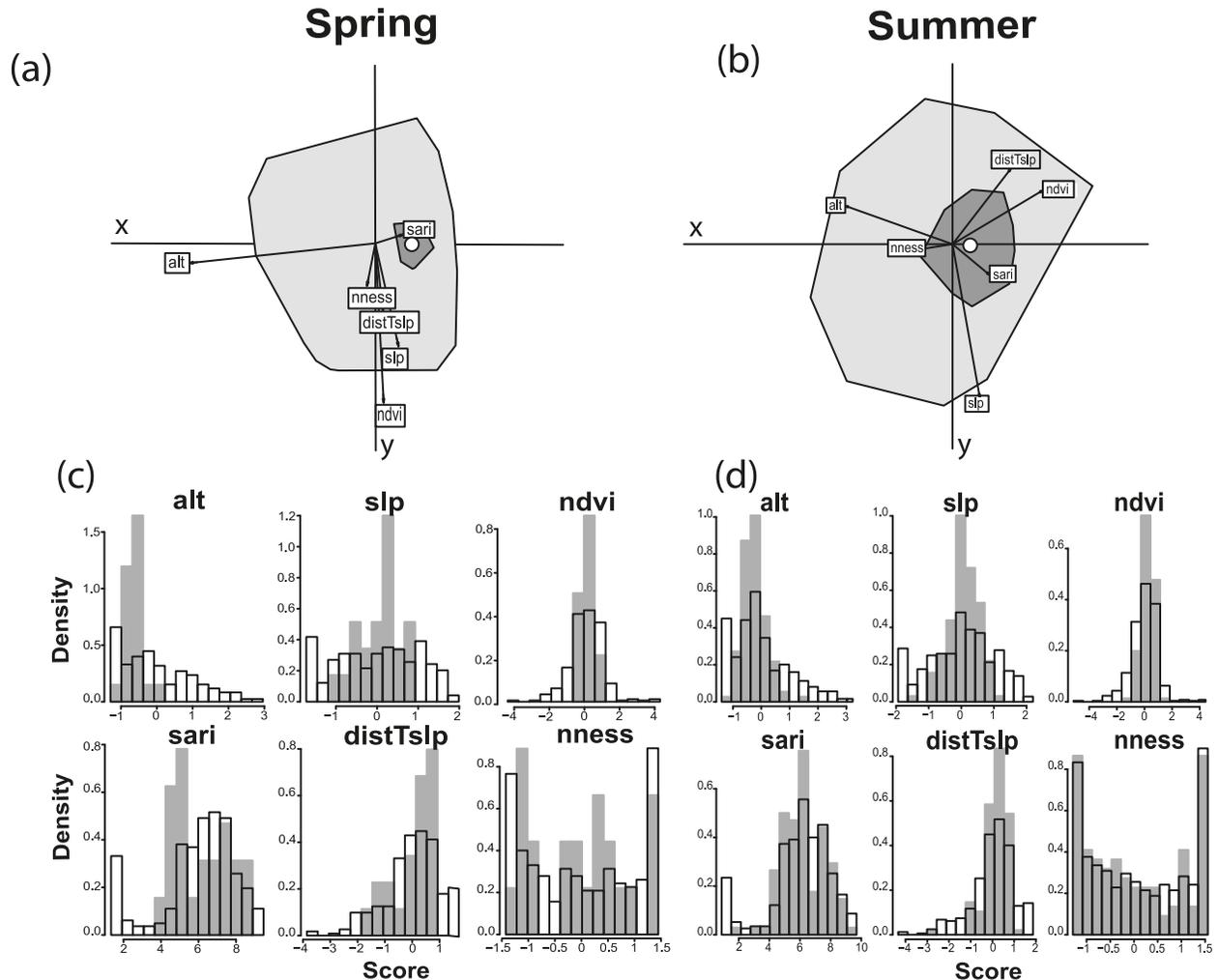
Feeding patch

To test the hypotheses for the resource scale, we developed logistic regression models designed for matched case–control studies (Hosmer and Lemeshow 2000; Compton et al. 2002); also referred to as conditional logistic regression with the following predictor variables: biomass of the plant group, cover, percentage of green tissue, and height. Cover and biomass were both included, as they were weakly correlated (Pearson correlation, $r_p = 0.24$). Because our study design is one feeding site to one control site matched, the conditional maximum likelihood estimates and standard errors (SE) were obtained by the following settings: the sample size is the number of case–control pairs used, covariates are estimated with the differences between the variables (feeding – random), and the value of the response variable is equal to 1 (predictor variables were differences in biomass, cover, height, and percentage of green tissue; Hosmer and Lemeshow 2000). Using such settings, a bias occurs when only positive values are observed for predictor variables, as maximum likelihood estimates are not bounded (Heinze and Schemper 2002). To remove such bias, we used the *brlr* library in R, which implements the penalized likelihood approach (Firth 1993).

Plant groups

To analyze the presence of plant groups in both random and feeding sites, we performed fuzzy correspondence analysis (FCA; Chevenet et al. 1994; Hausner et al. 2003). This method is derived from multiple correspondence analyses (MCA), and allows great flexibility for analyzing affinity of a given variable because it implements not only one variable category as in MCA but multiple variable categories. For both random and feeding sites, the variables were the plant groups (graminoids, forbs, and shrubs); the categories of each variable were green (with fresh green tissue), dry (no fresh green tissue), or absent (a category that was visually estimated).

Fig. 2. Ecological niche factor analysis (ENFA) for selection of spring and summer habitats by Tibetan argali (*Ovis ammon hodgsoni*) in eastern Ladakh, India, from 2005 to 2007. Panels *a* (spring) and *b* (summer) show the marginalization (*x* axes) and specialization (*y* axes) with the scores (lines coming out from the origin for each variable) of the environmental variables plotted with a scale factor of 1. Specialization is shown by the much reduced extent of used habitat (dark gray polygons) compared with available habitats (light gray polygons). The white dots are the centroids of the “used” polygons and the line passing through the centroid of the used polygon and origin (centroid of available polygon) is the marginality axis. The species marginality is the distance between these centroids. Panels *c* (spring) and *d* (summer) display the distribution of used (gray bars) versus available (white bars) environmental variables (for all abbreviations and descriptions see Table 1). The *x* axis represents the scores; they differed between the two analyses (spring and summer). The *y* axis represents the density of points for each used and available site.



Results

Habitat scale

During spring, the first two axes of ENFA (first *x* marginality, second *y* specialization) explained 80.8% of the variation in the data (Fig. 2*a*, Table 2). Alone, the marginality factor accounted for 61.3% of the total variation. Argali preferentially used habitats at lower altitude but more rugged than available (Table 2, Fig. 2*c*). The second axis of ENFA accounted for a high specialization (eigenvalue of 4.7), which is a restricted use for the habitat variables NDVI, slopes, and distance to slopes (Fig. 2*c*). Finally, ruggedness and northness were not related to specialization.

Habitat use in summer compared with in spring appeared to be less marginalized and specialized (Fig. 2*b*). The first two axes explained 67.3% of the variation. The specializa-

tion of the marginality in summer was more complex than in spring but still represented a high percentage of specialization (41.5%). The complexity was due to increased importance of other landscape variables in addition to altitude and ruggedness. Overall, marginality indicated argali preferences for lower altitude and higher values for NDVI, ruggedness, slope, and distance to slope than available.

The specialization in summer, which explained 26% of the variation, accounted for restricted use of slope, distance to slope, and NDVI (Fig. 2*d*). Compared with spring, argali used habitats at higher altitudes in summer and selected areas with relatively higher NDVI (Figs. 2*c*, 2*d*). Argali also used gentle slopes (i.e., avoided both flat and steep slopes) in spring and summer, though using relatively more rugged areas in summer compared with spring. In terms of

Table 2. Ecological niche factor analysis (ENFA) for selection of spring and summer habitats by Tibetan argali (*Ovis ammon hodgsoni*) in eastern Ladakh, India, from 2005 to 2007.

	Marginality		Specialization 1		Specialization 2	
	Spring	Summer	Spring	Summer	Spring	Summer
Var_Exp %	61.3	41.5	19.5	25.8	10.1	13.6
Altitude	-0.98	-0.66	-0.09	0.20	0.13	-0.67
distTslp	0.04	0.36	-0.33	0.41	0.11	-0.15
NDVI	0.05	0.58	-0.78	0.28	-0.52	-0.68
Northness	-0.04	-0.20	-0.20	-0.03	-0.07	0.02
SARI	0.16	0.23	0.04	-0.16	0.25	-0.25
Slope	0.12	0.17	-0.50	-0.82	0.85	0.21

Note: Factor scores and the variance explained by the factors (Var_Exp%) are presented. Positive ENFA values for marginality indicate that argali preferred locations with higher values of the corresponding variable than the global mean. For specialization, signs have no meaning; only the absolute values matter.

Table 3. Results of bias-reduced logistic regression models at the feeding-patch scale for Tibetan argalis (*Ovis ammon hodgsoni*) observed foraging in eastern Ladakh, India, from 2005 to 2007.

Variable	Spring			Summer		
	Estimate	SE	<i>t</i>	Estimate	SE	<i>t</i>
Biomass	0.30	0.27	1.12	0.09	0.12	0.78
Cover	-0.06	0.20	-0.30	0.02	0.07	0.32
Percentage of green tissue	0.09	0.04	2.64*	0.20	0.05	3.96***
Plant height	0.16	1.21	0.13	0.98	0.60	1.63

Note: *, $p < 0.05$; ***, $p < 0.001$.

distance to slope, argali appeared to venture more in areas away from slopes in summer compared with spring, though showing high specialization for this variable in both seasons.

Resource scale

Feeding patches

For both seasons, only the percentage of green tissue was higher in feeding than in random sites (bias-reduced logistic regression models; spring: $t_{[18]} = 2.6$, $P = 0.002$; summer: $t_{[104]} = 3.9$, $P = 0.0001$) (Table 3). There were no other differences between feeding and random sites for other vegetation variables. For both seasons, FCA showed a clear separation between feeding and random sites, on the first axis in the spring and second axis in summer (Fig. 3). This difference was related to greenness versus dryness in graminoids during spring and summer, but less so for forbs in the spring and shrubs in summer.

Plant groups

Argali diet consisted mainly of graminoids (~70%) during spring (May–June), whereas argalis used much more forbs during summer (July–August) (Fig. 4). Shrubs were marginally used in both seasons. During spring, graminoids contained $16.2\% \pm 2.6\%$ CP (mean \pm SE), $70.6\% \pm 5.3\%$ NDF, and $34.6\% \pm 8.5\%$ ADF, whereas forbs, which were in the early stages of growth, contained $11.4\% \pm 3.6\%$ CP, $43.5\% \pm 9.3\%$ NDF, and $28.7\% \pm 7.1\%$ ADF. The nutrient content changed rapidly with the onset of summer when graminoids contained $7.9\% \pm 3.4\%$ CP, $82.8\% \pm 3.5\%$ NDF, and $40.2\% \pm 3.9\%$ ADF, whereas the CP in forbs increased

to $24.8\% \pm 3.5\%$. The NDF and ADF values for forbs were $33.8\% \pm 3.1\%$ and $28.9\% \pm 4.8\%$, respectively, in summer. The CP content in shrubs also showed a slight increase from $17.5\% \pm 2.4\%$ in spring to $23.2\% \pm 2.6\%$ in summer.

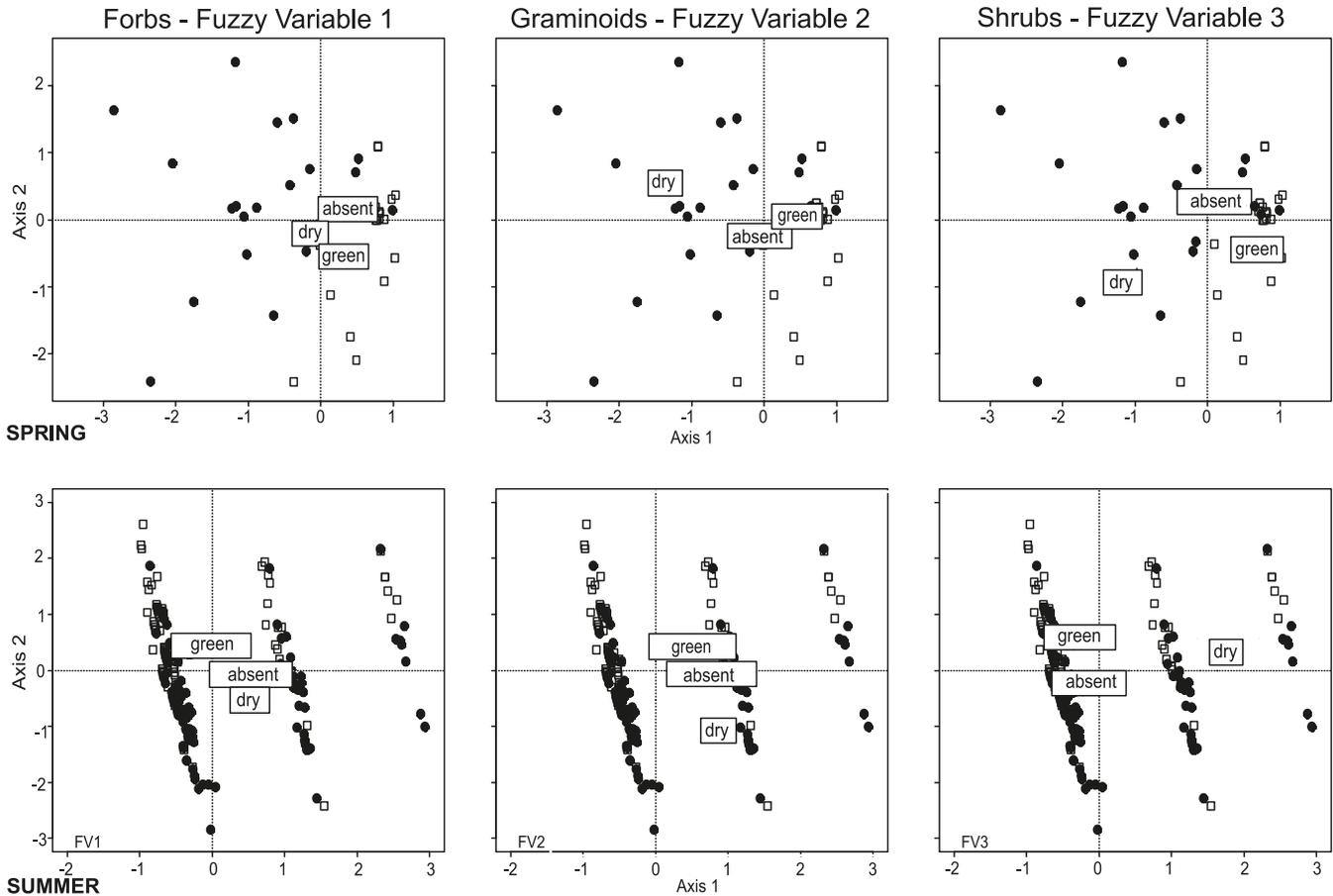
Discussion

At the habitat scale, selection by argali was mainly determined by topographic characteristics and forage abundance, whereas selection at a finer resource scale was mainly determined by forage quality. Such pattern suggests the importance of forage quality at both habitat and resource scales, as NDVI (our proxy of forage abundance) also represents resource quality in grassland steppes (Kawamura et al. 2005). In addition, we showed that selection for forage species depended more on the quality of forage than their quantity, and argalis moved to areas with higher quality forage as the growing season progressed.

Habitat scale

In high-altitude and alpine ecosystems, habitat choice in early spring is usually expected to be limited to areas free of snow or windblown, whereas during summer preferences are expected to widen as more habitat becomes available (Kala and Mathur 2002). Our results showed that habitat selection in spring by argali was characterized by a lower range of altitude, gentle slopes, and intermediate NDVI values and that they always remained close to slopes. The selected mean altitude varied between seasons with selection for relatively higher altitude in summer compared with spring (Table 1). The observation that argali moved from

Fig. 3. Fuzzy correspondence analysis (FCA) of vegetation community categories for selection of feeding patching in spring and summer by Tibetan argali (*Ovis ammon hodgsoni*) in eastern Ladakh, India, from 2005 to 2007. White squares indicate feeding sites and black circles indicate random sites with three categories (green, dry, and absence) for each of the fuzzy variables plant groups (graminoids, forbs, and shrubs). The first two correspondence axes (eigenvalue; spring: axis 1 = 0.14, axis 2 = 0.08; summer: axis 1 = 0.10, axis 2 = 0.08) are presented. The position of boxes (green, dry, and absent) in the direction of clustering of feeding or random sites indicates selection towards these variables.



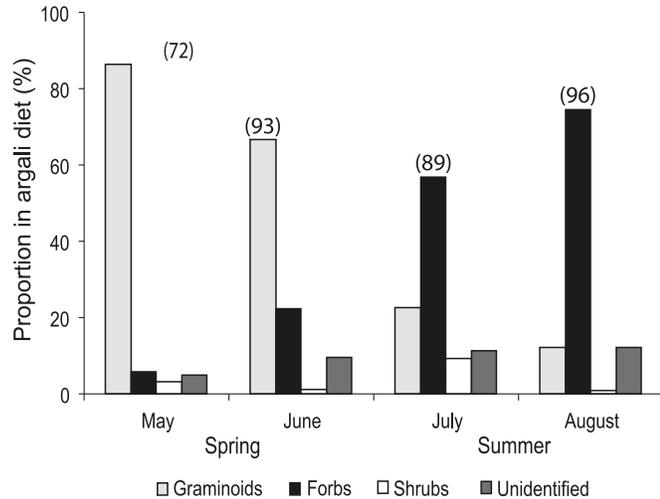
relatively lower areas in spring towards higher altitudes in summer is consistent with the timing of snowmelt in this area, being earlier in the lower range of altitudes. Though measurements of snow accumulation are lacking in our study area, the increased use of higher altitudes in summer could also be linked to the later plant phenology at these sites (Schaller 1998; Kala and Mathur 2002). The increasing use of higher altitude areas in summer could then be the result of argali tracking both snowmelt and plant growth, though the aspect variable, here used as northness, did not play a significant role in the selection of habitat at the landscape scale.

There is a limit to movements to higher elevation and slope values, as very high altitudes (5200–5900 m) are devoid of vegetation (Fox 2004). In addition, the steeper slopes are generally avoided by argali (Namgail et al. 2004), largely because they have a flight escape strategy rather than seeking refuge in cliffs. Gentle slopes in open landscapes such as in the Tibetan Plateau may provide higher grounds allowing a higher visibility to scan for predators, which may explain why argali occurred close to slopes in general and opt for slightly higher slopes in

summer. Also, high ruggedness values observed in open homogeneous landscapes such as in the Tibetan Plateau rangelands are associated with areas of rocky outcrops and scree, which are generally sites providing refuge from snow and cold winds in spring and used as resting places by argali during the hot summer period. Hence, selection of more rugged areas is likely associated with higher daytime temperatures in summer or may provide hiding places for newborn lambs during the lambing period in early summer.

The intermediate values of NDVI selected at the habitat scale indicate that argali do not select areas with maximum plant biomass. This may be attributed to trade-offs between quality and quantity of plant forage that argali may make, being an intermediate-sized herbivore. The same pattern has been observed in Mongolian gazelle (*Procapra gutturosa* (Pallas, 1777)) (Mueller et al. 2008), which preferred an intermediate range of vegetation productivity, presumably facing quality and quantity trade-offs in areas with low NDVI that limited ingestion rates, and in areas with high NDVI, where the low digestibility of abundant mature forage also limited the intake rate. In addition, higher predation risk and presence of other large herbivores in the lower areas

Fig. 4. Proportion of different plant groups in the spring (May–June) and summer (July–August) diet of Tibetan argali (*Ovis ammon hodgsoni*) in eastern Ladakh, India, from 2005 to 2007. The analysis is based on 350 microhistological fragments found in argali feces (numbers over bars represent the number of fragments analyzed for each month).



may prevent argali from using these sites. Since no predation attempts were observed, we cannot conclude on the effects of predation. On the other hand, areas of high forage biomass that occur near the lakes (Fig. 1) are used throughout winter by thousands of livestock and ~150 kiangs. This high grazing pressure and potential interspecific competition may also lead to a reduction in the quality of the vegetation, even though these areas at low altitude are generally characterized by high plant biomass (Singh et al. 2009). Hence, the preference for intermediate values of the landscape variables altitude, slope, and distance to slope suggests that movements of argali are confined to the narrow belt of vegetation present in the low and high ranges of the mountains. Further approaches testing for the risk of predation versus habitat use could help disentangle such overall patterns of slope use.

Resource scale

Feeding patch

The plant-growing season in alpine environments is rather short, generally ranging from May to July in our study area (N.J. Singh, personal observation). Selection of feeding patch by several ungulates in alpine environments has been explained by individuals tracking new emerging plant growth (Skogland 1984; Mårell and Edenius 2006), which has high available energy and protein, is easy to browse, and contain low amounts of secondary compounds (Albon and Langvatn 1992; Van Soest 1994). Throughout the growing season, the proportion of fiber increases and energy, nutrient levels, and digestibility decrease as the plants age (Hudson and White 1985; Long et al. 1999). In relatively homogeneous high-altitude rangelands, percentage of green tissue can be considered an indicator of forage quality, which initially increases and then decreases as the growing season progresses (Sinclair 1975; Schaller 1998; Shrestha

and Wegge 2008). The selection of intermediate values of NDVI during summer, when biomass is at its peak and for forage quality at level of the feeding patch supports the argument that argali select habitat based on forage quality. Argali in the Trans-Himalayan rangelands of Nepal have also been shown to prefer forage quality over abundance throughout the summer (Shrestha et al. 2005).

Trade-offs between forage quality and quantity may lead herbivores to select diets of intermediate quality to maximize their overall rate of nutrient assimilation (Wilmshurst et al. 1995). However, under circumstances where forage quantity is not a constraint, for instance when animals occur at low densities, herbivores are likely to select forage resources with the maximum nutrient contents, especially when such nutrients mostly limit their growth and (or) reproduction (e.g., Demment and Van Soest 1985). Alternatively, herbivores in environments with low plant biomass but high quality such as in the Arctic may trade off quality for quantity to obtain a more favorable energy return (Van der Wal et al. 2000). Given the low density of argali in the study area and their use of habitats with few competitors and low predation, argali appear to select forage quality over quantity, though such habitats may show low productivity.

Plant groups

Graminoids are dominant in the steppe and rangeland ecosystems (Schaller 1998). With the progression of the short growing season after snowmelt, graminoids undergo rapid growth followed by forbs and dwarf shrubs. However, the nutrient content of graminoids decreases rapidly after spring, whereas forbs retain more nutrients until late summer (Schaller 1998; Wagner and Peek 2006). With this temporal variability, ungulates generally adopt a mixed diet at the large temporal scale, but a selective diet during the short windows of high-quality resources (Schaller 1998; Holdo et al. 2009). With their intermediate body size, argali are expected to have high-energy requirements and should use plants according to their energy content, provided they are readily available. This has been observed in blue sheep in Indian and Nepalese Trans-Himalaya (Mishra et al. 2004; Shrestha et al. 2005). In our case, argali used mainly graminoids in spring and then switched to forbs in summer. These changing foraging strategies add further support for the argali selecting plant quality over quantity, which was already observed at the feeding-patch scale.

During the growing season, crude protein content in graminoids and forbs ranged from 6% to 16% and from 12% to 26%, respectively. The high protein and energy contents in the newly grown vegetation allow herbivores to recover losses in body mass during the short growing season. Comparisons among forages harvested in late summer on the Tibetan Plateau indicated that forbs had the highest crude protein, followed by graminoids and shrubs (Long et al. 1999; this study); hence, forbs may provide the necessary proteins during summer compared with graminoids, which are rather rich in nutrients during spring. Although microhistological analyses of feces did not indicate a common use of shrubs, they do contain green tissue early in the season, which correspond to high-quality resources. Shrubs, however, quickly accumulate secondary compounds (e.g.,

phenols) (Swain 1977), which may prevent their use during summer. Alternatively when forbs of higher quality are readily available, argali may simply use forbs more frequently.

Conclusion

In our study, broad-scale characteristics of the habitat and forage quality determined the selection of resources at large and fine spatial scales, respectively; such pattern is similar to the effects of the hierarchical scale observed in other systems (e.g., Schaefer and Messier 1995; Johnson et al. 2001). We also emphasized the importance of slopes for argali in their habitat selection. Hierarchical effects have been observed, for instance, in high-altitude steppes of Argentina, where broad-scale habitat selection of vicuñas (*Vicugna vicugna* (Molina, 1782)) is determined by the presence of water sources, which also modulate the access to green patches and large diversity of plants at a smaller scale (Renaudeau d'Arc et al. 2000; Arzamendia et al. 2006). We suggest that the avoidance of sites with higher NDVI could be the outcome of quality–quantity trade-offs made by argali, which were further confirmed through selection of greenness at the feeding-patch scale against biomass. With argali selecting resource quality against quantity in the high-altitude rangelands at several spatiotemporal scales, we provide further evidence that the hierarchical pattern of habitat selection also occurs in relatively homogeneous systems.

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