



Animal - Habitat relationships in high altitude rangelands



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On the wild bleak uplands of Tibet, where for hundreds of miles not a tree is to be met with; where in every direction, as far as the eye can reach, there is nothing but a vast expanse of barren soil, rock and snow; where there is no shelter from the glare of cloudless noon, nor from the freezing winds that sweep the naked hills with relentless force towards the close of the day; here, in the midst of solitude and desolation, where animal life has apparently to struggle for existence under every disadvantage, is the home of the great wild sheep.

Alexander Kinloch (1892)

*to
my family
for all their love & care*

Advisors

Prof. Nigel G. Yoccoz, University of Tromsø

Dr. Joseph L. Fox, University of Tromsø

Dr. Yash Veer Bhatnagar, Nature Conservation Foundation

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Abstract

Singh N.J. 2008. Animal-Habitat relationships in high altitude rangelands. PhD Thesis. University of Tromsø, Norway.

This study conducted in the high altitude rangelands of Indian Transhimalaya, deals with basic questions regarding the ecology of an endangered species, the wildsheep Tibetan argali (*Ovis ammon hodgsoni*) and applied issues related to its conservation and potential conflict with the local nomadic pastoralists. The basic questions on ecology are aimed at delineating the habitat and resource selection processes, identifying factors causing sexual segregation and efficient surveying and sampling. The applied aspect focuses on the changing face of pastoralism and the potential impacts of modernising livestock husbandry on argali.

Overall, the study provides a general framework towards the understanding of argali-habitat relationships at different spatio-temporal scales. The spatial determinant associated with altitude in the area, predicts argali habitat and resource selection in this relatively homogenous landscape. These determine the range of other topographic variables and forage characteristics selected by argali. The selection of feeding patches in the selected range of altitude and topography is mainly characterised by their greenness and the quality of plant groups. Adjusting to changing forage quality, argali display an opportunistic feeding strategy, selecting grasses in early spring and switching to forbs later in summer. Nevertheless, the habitat selection process did not appear to differ among the sexes to drive sexual segregation. There was, however, strong segregation among the sexes as well as between lactating and non lactating females. The reasons for segregation appeared to be predominantly social, but driven ultimately by predation and concomitantly by resources. The habitat selection information was used to design a stratified random sampling strategy that led to i) a significant reduction in survey effort in sampling these sparsely distributed species and ii) reduction in sampling bias.

The applied aspect of the study outlines and evaluates the dramatic changes in the nomadic pastoralism that have occurred in the past five decades in the study area. These have led to a loss of pastures (-25 to -33%) of the nomads, consequent readjustment in traditional patterns of pasture use, intensified grazing pressures (25 to 70%) and rangeland degradation in the area. Such changes may have serious consequences on the survival of local wildlife, as tested with a study of the effects on argali of livestock presence and resource exploitation. Hence, a successful conservation and recovery strategy should focus on: minimising the impacts of livestock on argali, identifying the factors affecting the persistence of the current populations, increasing local sub populations of this species to prevent extinction due to stochastic events, prevent loss of genetic diversity and excessive fragmentation and thus ensuring gene flow.

Ecological Niche Factor Analyses (ENFA), bias-reduced logistic regression and Fuzzy correspondence analyses (FCA) were used to answer habitat and resource selection questions. A sexual segregation and aggregation statistic (SSAS) was used to estimate the components of sexual segregation and test segregation. SSAS combined with canonical correspondence analyses (CCA) allowed the estimation of segregation based on habitat variables. Logistic regression models were formulated to estimate models on which the stratified random sampling strategy was based. The

overall study also included surveys, interviews and literature reviews to understand the nomads' movement and pasture use patterns of their livestock. Kernel density estimations (KDE) were used to estimate extent of range overlaps between livestock and argali.

Keywords: high altitude, homogeneous, argali, habitat selection, resource selection function, ENFA, stratified random sampling, sexual segregation, SSAS, livestock, predation, resources.

Introduction

The high altitude Tibetan plateau rangelands are unique ecosystems in terms of landscape, climate, biodiversity and nomadic pastoralism. These systems are characterised by harsh and unpredictable climate and typically relatively homogeneous plains to rolling hills landscape which support a wide variety of wildlife and since c. 3000 years ago, livestock grazing. However, the systems and most of the wildlife supported have been relatively little studied in the context of their distribution, ecology, population dynamics, and social behaviour. Existing information about them comes from surveys conducted using convenience sampling, which is generally based on accessibility of the areas (e.g. remoteness, harsh and unfavourable conditions), limited funds and logistics. Hence most of the surveys have been constrained due to such limitations. It is challenging to undertake research in these systems because most of the species are rare and protected and sampling and monitoring processes are effort intensive. Most of the large herbivore species surviving in this extreme ecosystem have been hunted extensively in the past for trophy and meat, resulting in decimation to critical levels. Despite a hunting ban in the recent decades, threats other than hunting are apparently intensifying, especially competition with grazing livestock.

In this context of limited knowledge and risk of local extinction, conservation of such rare species remains a challenge. More basic ecological information about a species' habitat and resource use should aid in understanding their survival requirements and to provide a basis for further management policies. Hence, we initiated one of the first efforts to undertake detailed habitat selection studies on a rare wild sheep species, the Tibetan argali (*Ovis ammon hodgsoni*) inhabiting these rangelands with the following goals:

- I.** to understand the multiscale habitat selection process and unveil the primary factors determining the distribution of the population,
- II.** to identify and understand the causes of sexual segregation,
- III.** to predict and identify areas for sampling based on habitat use data, so as to improve the process of sampling and monitoring and reducing the sampling effort,
- IV.** to document and understand the pasture use patterns by nomads and their livestock,
- V.** to assess the impact of livestock herding on the habitat use of argali,
- VI.** to update the current status of argali population in India and identify conservation threats.

The thesis is based on the following papers:

1.

Singh, N.J., Yoccoz, N.G., Lecomte, N., Côté, S.D., Fox, J.L. Scales and selection of habitat and resources: Tibetan argali in high altitude rangelands
(Submitted to *Journal of Zoology*)

2.

Singh, N.J., Bonenfant, C., Yoccoz, N.G., Côté, S.D. Proximate and ultimate causes of sexual segregation in the Eurasian wild sheep Tibetan argali
(Submitted to *Behavioural Ecology and Sociobiology*)

3.

Singh, N.J., Yoccoz, N.G., Bhatnagar, Y.V., Fox, J.L. Using resource selection functions to sample rare species in high altitude ecosystems: a case study with Tibetan argali
(Submitted to *Biodiversity and Conservation*)

4.

Singh, N.J., Fox, J.L., Bhatnagar, Y.V., Lecomte, N., Yoccoz, N.G. Changing nomadic pastoralism in Transhimalayan rangelands of India: Causes and consequences
(Submitted to *Global Environmental Change*)

5.

Singh, N.J., Bhatnagar, Y.V., Yoccoz, N.G., Fox, J.L. Assessing wildlife - livestock interactions in the Indian Transhimalaya: Tibetan argali as a case study
(*Manuscript*)

6.

Singh, N.J., Fox, J.L., Bhatnagar, Y.V. Tibetan argali in India, Nepal and western Tibet Autonomous Region, China- status and conservation
(*Book Chapter– Argali Biology and Conservation, Denver Zoological Foundation (In press)*)

Background

Animal habitat relationships

Habitat is an area with a combination of resources (e.g. food, cover, water), and environmental conditions (e.g. temperature, precipitation, presence or absence of predators, and competitors) that promotes occupancy by a given species (or population) and allows those individuals to survive and reproduce (Rosenzweig 1981, Arthur et al. 1996). Assessing animal habitat relationships is central to animal ecology and essential for conservation and management (Johnson 1980). Animals use habitats in a way to maximize net energy intake for growth and reproduction, minimize predation risk and thermal stress, and maintain social contacts (Fryxell and Lundberg 1994, Kie 1999). Such decisions follow a hierarchical fashion and vary over multiple spatial and temporal scales (Senft et al. 1987, Kie et al. 2002, Boyce et al. 2003). The extent to which this spatio-temporal heterogeneity modulates habitat selection and species interactions has been widely studied in ecology (Kotliar and Wiens 1990, Kie et al. 2002, Fryxell et al. 2005). High altitude rangeland ecosystems which support several ungulate species are relatively simple and homogeneous in terms of landscape and habitat structure. These systems have been little studied in the context of how processes such as multiscale resource selection by herbivores operate in the absence of large habitat heterogeneity.

High altitude rangeland ecosystems

The high altitude rangelands of the Tibetan plateau are some of the world's most remarkable grazing ecosystems with 85% of the landmass lying above 3000m (Schaller 1998, Miller 1999). Much of this relatively homogeneous landscape is comprised of lake basins varying in size, with no outlets and is fringed by rolling mountains and hilly plains. The climate is extreme and windy with intense solar radiation and rapid changes in daily average temperature (max 25°C to -40°C). The primary vegetation formations comprise alpine meadows, alpine steppe and desert steppe. The growing season for vegetation lasts about three months maximum in summer, depending on the altitude (Schaller 1998, Rawat and Adhikari 2005).

A rich assemblage of rare and endangered species of flora and fauna is supported by these rangeland ecosystems (Schaller 1977, Shackleton 1997, Schaller 1998). Of special significance in these rangelands are the *Caprinae* (wild sheep and goats). The Himalayan region represents part of the original center of *Caprinae* evolution and as such, encompasses both a high diversity of taxa and wide variety of forms (Shackleton 1997). Most of these species have been little studied in terms of their distribution, population size, dynamics and habitat use (Schaller 1998).

In addition to the biodiversity values, the rangelands also sustain a several thousand year old tradition of nomadic pastoralism (Miller 1999). Since cultivated agriculture is not possible in the high rangelands, grazing by livestock enables pastoralists to convert plant biomass into animal products that are either consumed by pastoralists themselves or sold for income (Miller 1999). The pastoralists track seasonal changes in resources and hence practise seasonal movements in search of better foraging conditions for their livestock.

Tibetan argali

Among the rare and endangered species inhabiting these rangelands, is the Tibetan argali, a subspecies of rare Eurasian wild sheep which has successfully adapted to this harsh resource - limited environment. It is also regarded as the rarest and least studied species of wild sheep (Schaller 1998). It is distributed all across the Tibetan plateau in small and scattered populations (Fox et al. 1991). Within India, argali mostly occur in two main sub populations – eastern Ladakh and north Sikkim (Fox and Johnsingh 1997). Both areas are representative of typical Tibetan plateau ecosystem, which extends into India.



Argali had been hunted extensively, both for trophy and meat in the past; which has led to its present precarious state. It is among the two subspecies of argali which are categorized as endangered by the 'World Conservation Union' (earlier IUCN) and 'The Wildlife Protection Act of India, 1972' (schedule I species - Highest level of protection). The estimated population is around 500 individuals in the Ladakh region and over 200 animals in Sikkim (Singh et al. Paper VI). The estimated suitable area for argali in eastern Ladakh is over 10,000 km² (Chundawat and Qureshi 1999), but today only small herds occur sparsely distributed throughout the region.

Argalis are polygynous, sexually dimorphic in body size, highly gregarious animals, found in small to large single-sex herds all year round, with numbers that may vary up to 100 individuals on the Tibetan plateau (Schaller 1998). During mating season, these herds come together and males compete for access to the receptive females. Females generally give birth to a litter of 1 or rarely 2 lambs. The birthing season is in late May to mid-June (Schaller 1998). With thin, long legs and compact but lithe body, argali are adapted to open terrain, to escape danger through flight (Schaller 1977). They are usually found on high rolling hills and plateaus and on relatively gentle mountain slopes. Adult rams have massive, curled horns with the tips curled outward. Argali have a relatively short life, seldom reaching 10 years (Schaller 1998).

Ecology and conservation

Habitat use and selection

In general, factors such as topography, predation, snow, and distance to water influence ungulate habitat use, whereas forage characteristics, nutrient requirements, and interspecific interactions influence use of habitat and resources (Kie et al. 2002, Anderson et al. 2005). However, these factors vary depending upon the system and species studied (Wallis de Vries and Schippers 1994, Schaefer and Messier 1995, Bangs et al. 2005). Often few data exist on local populations of rare and threatened species and issues of abundance and habitat selection at varying scales are rarely addressed (Roger et al. 2007). Considering the limited large scale habitat heterogeneity, persisting predation risk and variable resource availability and quality, we explored the factors affecting habitat and resource selection by argali at multiple scales.

Distribution and Surveying

The habitat selection information is fundamental for conservation purposes (Manly et al. 1993) and can be vital to identify the areas to focus on survey and sampling. However, this identification process is effort intensive when landscapes are remote, environments are extreme and species are rare. Simple random sampling, often leads to too few observations of rare, patchy species (Edwards et al. 2005). This prevents robust analyses (Green and Young 1993, Edwards et al. 2004) e.g., for use in explanatory or predictive models of suitable habitat or spatial distribution (Hill and Keddy 1992, Wiser et al. 1998). Alternatively, 'convenience sampling' may result into more observations but, because units are selected a priori with unknown selection probability, is likely to lead to biased models. Hence, stratified random sampling based on the strata defined using habitat suitability or ecological niche models can be an efficient sampling approach in cases when rare species have patchy distribution (Edwards et al. 2005, Guisan et al. 2006). Studies on animals rely on estimating resource selection functions based on habitat selection data to predict their distributions (Manly et al. 1993, Schaefer and Messier 1995, Perez-Barberia et al. 2004). Habitat suitability models based on resource selection functions may provide important opportunity to stratify the habitat for survey and sampling of rare species in remote environments.

Sexual segregation

Habitat use is influenced by differential energy needs of the sexes of a species. Hence, many sexually dimorphic species' sexes segregate and use different habitats outside the mating season (Main et al. 1996, Bowyer 2004). Information on habitat selection can therefore be vital in identifying the causes of sexual segregation, which has remained a much debated topic over the last few decades. Sexual segregation is a universally occurring phenomenon in many vertebrate species (Main and Coblentz 1996, Main et al. 1996, Ruckstuhl and Neuhaus 2005). It has generally been categorized into *social* (grouping with their own sex), *spatial* and *habitat* (sexual differences in habitat use) segregation (Conradt 1998b, Ruckstuhl 2007). Five popular hypotheses comprising reproductive strategy - predation risk (Main et al. 1996), sexual size dimorphism- forage selection (Main et al. 1996), scramble competition (Geist and Petocz 1977, Bleich et al. 1997), activity budgets (Conradt 1998a, Ruckstuhl 1998) and social preferences (Michelena et al. 2004, Michelena et al. 2005, Perez-Barberia et al. 2005) have been proposed to explain segregation in

polygynous ungulates. Frequently, many of these causes have been observed to act together to explain sexual segregation (Bonenfant et al. 2004, Bowyer 2004, Ruckstuhl 2007). These causes may be categorised into proximate and ultimate causes, which may vary with species and system studied (Bowyer 2004, Ruckstuhl 2007). Animals inhabiting the habitats with little habitat heterogeneity may segregate on factors other than habitat characteristics, leaving social factors to appear prominent in such systems. We explore these hypotheses in argali.

Nomadic pastoralism

IN recent decades, the habitat or pasture use patterns of nomadic pastoralists have been changing rapidly, all across the Tibetan plateau (Schaller 1998, Miller 1999). Especially, the rangelands of the Indian Changthang region of eastern Ladakh have experienced dramatic socio-economic and political changes over the past five decades which has led to several modifications in their traditional pastoral practices (Sabharwal 1996, Namgail et al. 2007a). The main political cause is the influx of Tibetan refugees into Ladakh after the Sino Indian war in 1962. These migrations imposed several transformations in traditional pasture use of local nomads. Impacts of these socio-economic-political changes that followed were assessed in the course of this study. Implications for survival of local wildlife with changing pastoral practices are also discussed.

Argali Livestock interactions

Most of the rare and endangered ungulate species including argali inhabiting the Transhimalayan and Tibetan plateau rangelands occur in small and scattered populations. The primary existing threat to the survival of such small populations is believed to be livestock grazing and associated herding practices. The habitat and pasture use patterns of nomads and their livestock can influence wild herbivores such as argali, either through direct interference or through resource exploitation (Bagchi et al. 2004, Mishra et al. 2004, Bhatnagar et al. 2006b, Namgail et al. 2007b). Under the existing scenarios of changes in patterns of livestock grazing in the Transhimalayas, we studied argali to observe the effects of livestock grazing pattern on their habitat use. We assessed the impact of direct presence and resource exploitation by livestock on argali occurrence in summer and winter.

Status and distribution update

The past surveys on argali in India reported about 200 individuals surviving in small populations in Ladakh (Fox et al. 1991). With the inclusion of more surveyed areas with time, many new argali populations have been reported in new areas (Bhatnagar and Wangchuk 2001, Namgail et al. In press). For effective conservation, there is an urgent need to update the present status of argali population and distribution in India and neighbouring regions. The threats and conservation actions then need to be identified based on the observed distribution and local existing threats. We made extensive surveys in Ladakh, reviewed literature and consulted wildlife department officials during the course of the study to update the current status of argali in India and neighbouring regions. Based on the distribution, we then identified the threats to the existing populations and proposed conservation measures.

Intensive study area

Habitat features

The study area, known as the Tso Kar basin, (c. 650 km²) (Figure 1) is situated in the Changthang region of eastern Ladakh, India (32° 15' N, 78° 00' E). The altitude ranges from 4550 to 6371 m. The main feature of the study area is enclosed basin with two lakes, a smaller freshwater lake called Starsapuk Tso (4 km²) and larger salt water lake called Tso Kar (16 km²). The lakes are surrounded by broad valleys, alluvial plains, and rolling hills.

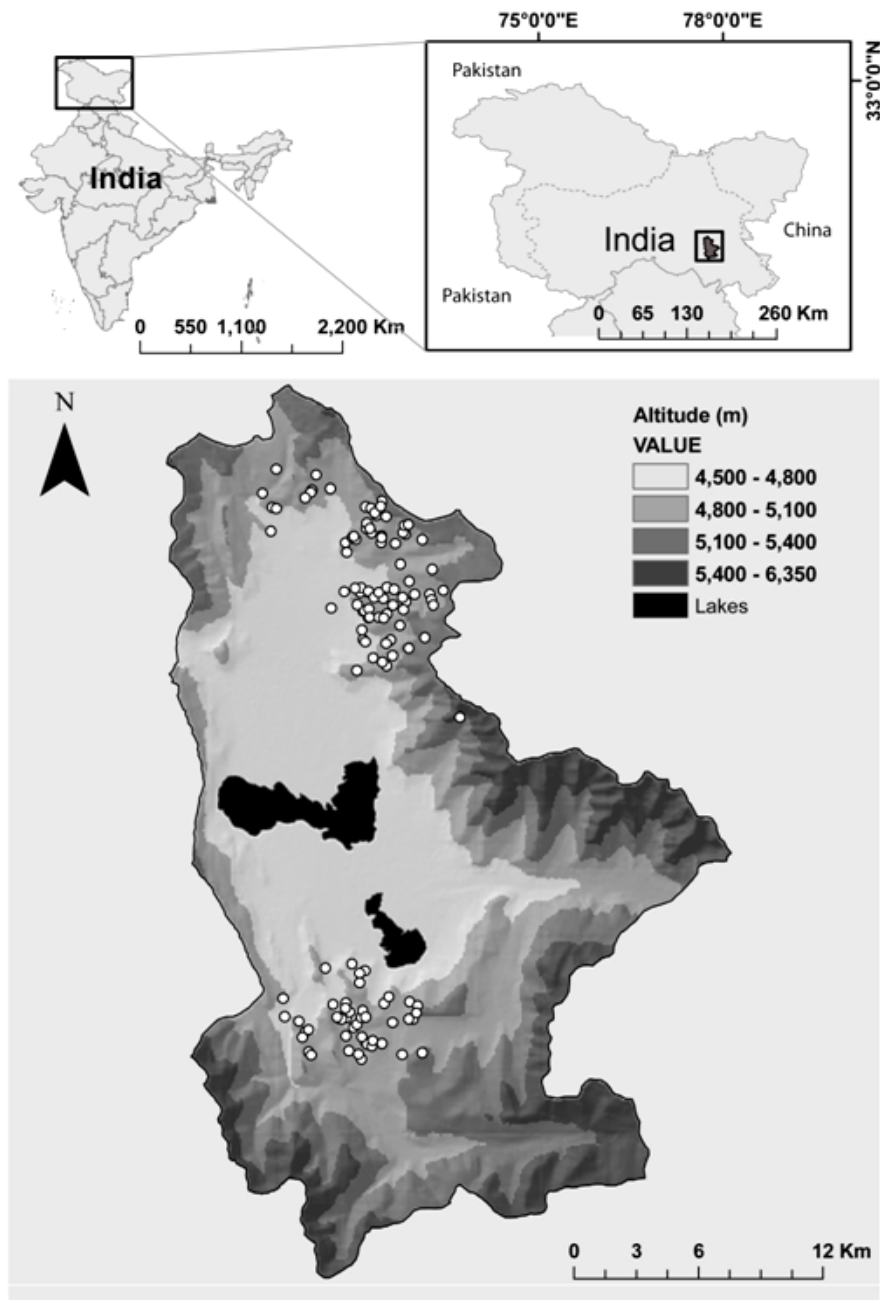


Figure 1. Study area Tso Kar basin, eastern Ladakh, India with the range of altitude and argali locations.



The climate is characteristic of high altitude cold desert ecosystems with temperatures oscillating from -40°C (Min. winter) to 25°C (Max. summer) and a mean annual precipitation of about 200 mm. Most of the precipitation occurs in the form of snow. Strong winds are a general feature of the landscape.

The vegetation can be broadly categorised into scrub formations, desert steppe and marsh meadows. The major plant communities include *Caragana-Eurotia*, *Artemisia-Tanacetum*, *Stipa-Oxytropis-Alyssum*, and *Carex melanantha-Leymus secalinus*. The parts of the study area at very high altitudes (5000 m) have sparse fell-field communities with moss or cushion-like growth forms, e.g. *Thylacospermum caespitosum*, *Arenaria bryophylla*, *Androsace sarmentosa* and a variety of lichens. Stream banks and marsh meadows around both the lakes (except areas of borax and salt deposits) exhibit characteristic sedge-dominated vegetation represented by species of *Carex spp.*, *Kobresia spp.*, *Scirpus spp.*, *Triglochin sp.*, *Pucciniella sp.*, *Ranunculus sp.*, and *Polygonum spp.* (Rawat and Adhikari 2005).



Wildlife and Livestock

About 150 argali inhabit the Tso Kar basin region. Other wild ungulates found in the region include a population of over 300 kiangs (*Equus kiang*) and 50 blue sheep or bharal (*Pseudois nayaur*) (Fox 2004). The key predator for the wildlife and livestock is the Tibetan wolf (*Canis lupus chanco*), which is found in small numbers. Snow leopard (*Uncia uncia*) and lynx (*Lynx lynx*) are also present. About 18,500 livestock comprising sheep, goats, yaks and horses use the area in winter (Sheep Husbandry

Department, Leh 2006). In total about 70 families herd their sheep and goats and yaks inside the basin during winter (Hagalia 2004).

Methods, results, data analyses and conclusions

The methods, results and conclusions for the objectives are presented as tables in the following pages. Detailed results are presented in the attached manuscripts referred to by latin numbers (I to VI).

Materials and methods

Objective	Method	Data analysis
I. Multiple scale habitat and resource selection	Repeated instantaneous scan surveys, 13 vantage points, every 4 days at 15 minutes interval, from 0600 to 1900 hrs, using 15X45 scopes during spring and summer months of 2005-2007. GPS locations of the groups.	Ecological Niche Factor Analysis (ENFA), Variables: altitude, slope, aspect, ruggedness distance from flat terrain (distance of the group from nearest 10° slope) and NDVI (Normalized Difference Vegetation Index).
a. Habitat		
b. Resources	Feeding patches - >50% animals feeding from a group during 3 consecutive scans (i.e. min. 30 minutes). 130 feeding patches sampled for vegetation parameters of grasses, forbs and shrubs: Vegetation cover (%), Vegetation height (cm), Vegetation biomass (g), Green tissue (%). 6 X 1-m ² plots randomly disposed within 25-m radius circle around the centre of the patch. Sampling design repeated using 6 plots at random site, 150 m away in a random direction.	Logistic regression for paired design (Conditional logistic regression + bias reduced logistic regression)
Feeding patch		
Plant groups	Plant species observed in feeding vs. random sites as present (green or dry) and absent. Species grouped into graminoids, forbs, and shrubs.	Fuzzy correspondence analysis (FCA)
c. Diet	Micro-histological analyses of feces, % graminoids, forbs and shrubs	
II. Sampling using resource selection functions	Initial data set (2005-2006) - observations I. Effort - No.of obs./vantage point/unit time (Obs/Hr). Estimate-Resource Selection Function (RSF) using initial data - RSF map. RSF stratification into low, med. and high suitability. Random transects in the strata (2007). -Estimate-RSF using initial dataset combined to new observations.	Logistic regression models (LRM) for Use - availability design Model selection using AIC _c Model validation using Boyce's Index
III. Sexual segregation	Observations from I. Groups studied - male, lactating and non-lactating females. Variables - group size, composition, other habitat variables from I. Feeding patch variables for groups - see I. Activity budgets - repeated instantaneous scan surveys, 5 min interval.	Segregation vs. Aggregation - Sexual Segregation and Aggregation Statistic (SSAS) Habitat segregation - SSAS + Correspondence analyses Discriminant analyses (DA)
IV Pasture use patterns of nomads	Interviews - local herders, government departments. GPS locations - Nomad camp sites. Habitat features near camp sites. Literature review.	
V. Impact of livestock on argali space use	GPS locations - Nomad camp sites. Intensity of use - Time spent per campsite per family - 4 seasonal use areas. Argali observations from I	Kernel density estimation (KDE)

Environmental variables estimated to assess habitat selection of Tibetan argali; for each variable the range of values observed at argali feeding sites are provided.

Variable	Methods of estimation	Range
Altitude (m)	Field validation and digital elevation model (DEM)	4633-5573
DistTslp (m)	Classification of DEM slope raster into slope > 10° and calculation of nearest distance to a group	0-988
Ndvi	MODIS (250m) images with $ndvi = \frac{IR(\text{band4}) - R(\text{band3})}{IR(\text{band4}) + R(\text{band3})}$	0.07 - 0.22
Northness	(IR- Infrared band, R-Red band) DEM transformed into northness : cos(aspect)	-1 to + 1
Sari	$\frac{\text{Std.Dev of slope} * \text{variety of aspect}}{\text{Std.Dev of slope} + \text{variety of aspect}}$	1.04 - 4.7
Slope (°)	Field validation and DEM	0.84 - 29.7

Objectives, results and conclusion

Objective	Result	Conclusion
I. Multiple scale habitat and resource selection	Argali select an intermediate range of altitude slope, distance to slope and NDVI during spring and summer.	Topographic factors and forage abundance determine broad scale habitat selection.
a. Habitat		
b. Resources	% green tissue main predictor during spring and summer. Green grasses, forbs and shrubs separate the feeding patches from random patches.	% green tissue determines selection of feeding patches by argali.
Feeding patch		
Plant groups		
c. Diet	Grasses dominate argali diet in spring, and forbs dominate during summer.	Grasses in spring and forbs in summer are selected due to their high forage quality.
II. Sexual segregation	Insignificant habitat segregation, spatial component is variable and is likely related to food and predation risk. Social factors predominantly explain sexual segregation.	Predation risk factors and differential use of resources likely drive sexual segregation in argali. Factors related to resources are a proximate cause and predation risk is the ultimate cause of segregation.
III. Sampling using resource selection functions	Model-based stratified random sampling - 16.7% of the total time sampling spent in highest RSF stratum resulted in 50% of the obs. 63.5% of the total survey effort in lowest stratum resulted in 12% obs.	Method has significant implications for reducing survey and sampling effort in the field, especially when dealing with rare species.
IV. Pasture use patterns of nomads	Reduction in pasture area and seasonal movements, increased in households, livestock number and grazing pressure.	Past models of wildlife – livestock coexistence are not valid in the current situation.
V. Impact of livestock on argali space use	Minimum overlap among the core argali areas and livestock camps core zones	Livestock likely affects argali, both through interference and resource exploitation.
VI. Status and distribution update	Argali occur in two main areas in India. The present population is about 680 to 820. About c. 480-620 argali occur in the Ladakh region.	Many new areas with argali identified in Ladakh, since 1991. The current population in Ladakh is as high as 620 compared to 200 earlier.

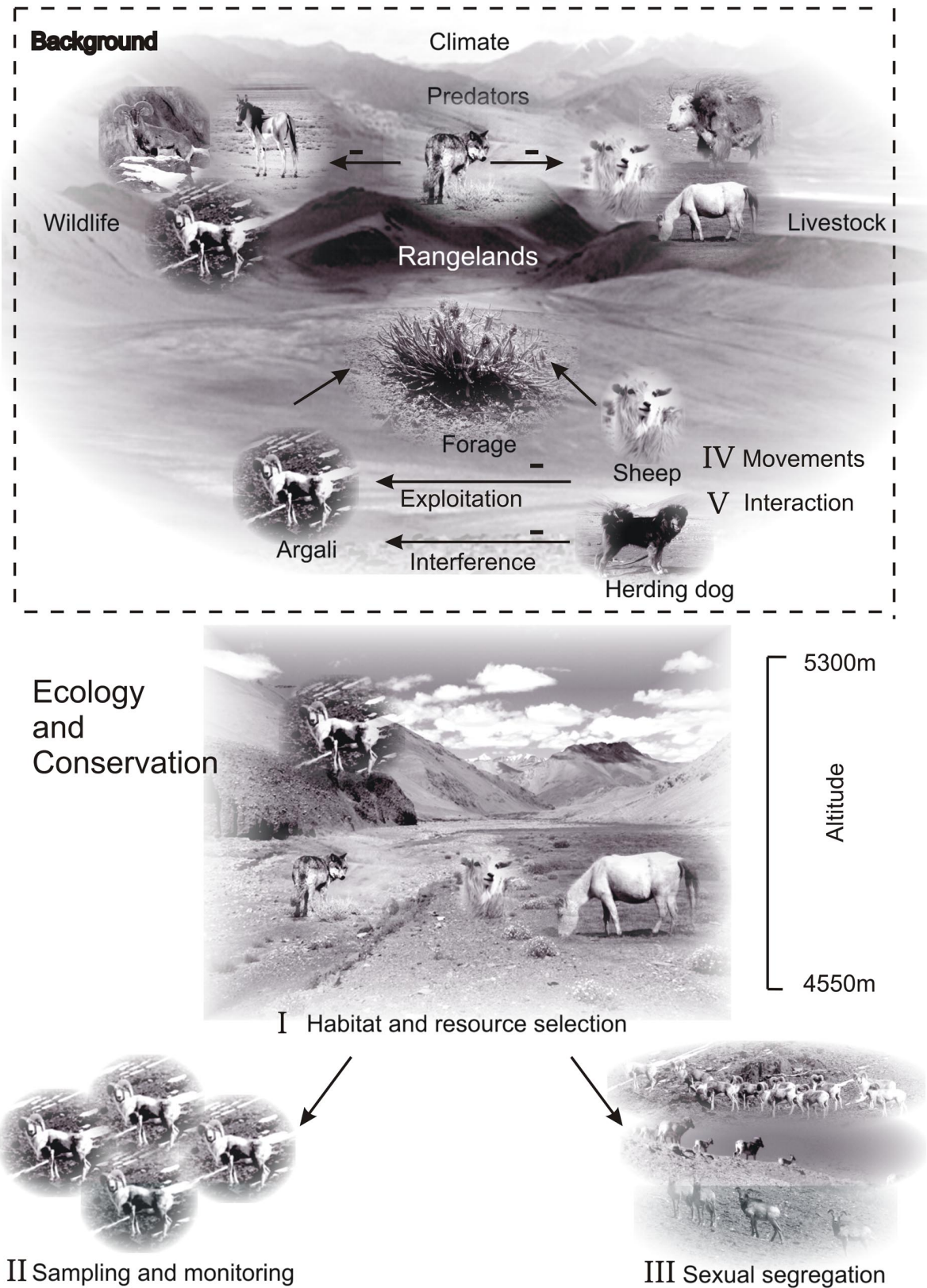


Figure 2. The study framework decomposed into a general background of species interactions and overview of habitat selection of argali in high-altitude rangelands. This ecosystem supports wildlife and livestock which are mainly constrained by climate, predation and forage characteristics. Interference and Exploitation interactions occur between argali and livestock. Each objective is represented by a Roman numeral. Argali select an intermediate range of altitude, slope, and NDVI while livestock mostly use flat areas closer to water with greener pastures (I). Presence of wolves in flat areas is an additional factor, which likely compels argali to use rolling slopes. Habitat selection information can be used to address issues of sampling and sexual segregation.

Discussion

In the ecological context, typical habitat characteristics of the high altitude rangeland ecosystem were studied in relation to their impact on the distribution and habitat use of argali and the seasonal pasture use by nomadic pastoralists. Habitat selection by argali was primarily determined by resources, predation and likely competition with livestock. Resource selection pattern depended on the availability and quality of the resources, predation probably determined selection of topography and competition with livestock directly and indirectly determined use of home range. Nomadic herders followed predetermined seasonal movement patterns, tracking resources and residing in camps at low altitude and in areas near water sources with access to abundant forage.

Distribution and sampling

A restricted range of altitude, slope and NDVI selected by argali determined their distribution in the area, which was likely an effect of predation risk at broad spatial scale or perhaps livestock (refer to limitations section). As more plant biomass becomes available during the short growing season, individuals trade-off security and food to achieve maximum growth and nutrition, and hence selection pattern changes with season. The finer spatial scale selection of feeding patches and plant groups was determined by the presence of green tissue, whose composition determined the quality of patches and plant groups selected by argali. Argalis thus seem to trade-off forage quality for quantity in the high altitude rangelands, as also confirmed by fecal analysis. Information derived from habitat selection models thus provides insights about the distribution of argali over the whole study area. This information may assist in increasing the probability of detection, thereby optimizing surveying and sampling effort. This is particularly needed when sampling rare species and can help in building predictive maps of distribution and prioritising areas for survey.

With intensive survey efforts over time and exploration in new areas have led to discovery of new argali populations in several such areas. These surveys have significantly increased the population estimate of argali in India, indicating that the earlier lower claims were due to absence of surveys in the region rather than actual lower numbers of argali.

Sexual segregation

The factors determining habitat selection when scaled down to sexes, provide insight into phenomena such as sexual segregation, the causes of which have been debated for a long time. Differential physiological and metabolic needs of the sexes during various times of the year as determined by their reproductive cycle, biology and body sizes are met by selecting different habitat characteristics at different times. Considering the habitat characteristics and habitat selected by argali, resource availability acts as a proximate mechanism and reproductive strategy related to predation risk as the ultimate mechanism explaining segregation. The absence of large habitat heterogeneity, the presence of which may provide escape cover from predators is compensated by spending increased time in vigilance by the most vulnerable group (lactating females) and results in differences in activity budgets among the groups. Alternatively, changing resource availability and quality likely

leads to spatial segregation among the groups and separates mothers from other groups due to higher metabolic needs during lactation.

Nomadic pastoralism

Resource variability also determines the seasonal movement patterns of the nomads and the limited low altitude, gentle and snow free places are selected by herders during winter. The Sino-Indian war, internal differences among the nomads and government policies have led to drastic changes in the traditional pasture use patterns of local nomads leading to decreased pasture availability and intensified grazing pressure with additional livestock. These changes have altered the habitat selection patterns of nomads at both spatial and seasonal scale due to the loss of earlier winter pastures. Such changes may have important implications in the future survival of wildlife due to increased competition by livestock, loss of valuable pastures and disturbance.

Argali and livestock

The camp site selection and movement pattern of herders is important in determining the possible impact of livestock use of the area on argali and other wild herbivores. Argali are mainly constrained to a specific range of altitude and hence to resources in that area, which is likely due to the predation escape strategy of argali against wolves. The pastoralists track changes in resource variability, although lower altitude and water accessibility are preferred and limiting conditions. The area influenced by livestock grazing, the grazing period and the amount of resource exploitation may have a possible negative effect on resource availability to argali. With the growing livestock populations and economy, and demand for increased pastures, the pastoralists are becoming intolerant to the local wild herbivores which share the pastures with the livestock and the predators which occasionally kill livestock (Bhatnagar et al. 2006a, Bhatnagar et al. 2006b). Increased complaints of kiang (*Equus kiang*) competing with livestock have been noticed from the nomads and kiangs are being driven away from the pastures (Bhatnagar et al. 2006b). Tibetan gazelle is already on the brink of extinction in other parts of Ladakh with reasons attributed to livestock grazing (Bhatnagar et al. 2006a). Such decreasing tolerance towards wild herbivores in future may lead to a worsening willingness to preserve them. The current livestock use pattern of reserving the study area for winter grazing has likely facilitated the survival of existing populations of argali. In case of complete spatial and temporal overlap between livestock and argali, the risk of competitive exclusion of argali is real. Hence, livestock management strategies need to consider such policies while establishing livestock wildlife management plans.

Status and distribution

In India, nearly 15 years ago the number of argali was estimated at a little over 200; recent surveys that include additional areas suggest about 600 to 800, located in two widely separated areas. There seem to be c.400 to 540 individuals in 8 widely spaced locations in Ladakh and about 200 in northern Sikkim. Although information on population trends is uncertain as regular monitoring is lacking from the mentioned areas, it has been argued that the populations are small and scattered as a result of hunting in the past. The existing populations all over the range are probably most threatened by increasing livestock population and associated overgrazing and disturbance. Particularly in India, the modernization of livestock production, tourism

and other human activities in the areas where argali still thrive constitute the major future threats to argali. There is an urgent need for adjustments in livestock production and management strategies for conservation of argali in its range. For reliable population estimates, precise and efficient survey methods are required which reduce the bias in survey and sampling while following regular monitoring protocols using standardised methods.

Limitations

Paper 1

The first paper dealt with the resource selection by argali which was based mainly on physical environment and resources. However, with the progression of the work, we argue that livestock may affect the resource use by argali through resource exploitation. Incorporating the livestock use of the area based on grazing intensities when included into the habitat selection models could reveal if actually resource exploitation does affect argali habitat use in summer. Although we approximated grazing pressure experienced by the rangelands in the area based on nomad camp locations, it is difficult to assess the impacts unless actual livestock group locations and movements are studied.

Paper 2

We studied sexual segregation in argali and identified that spatial segregation contributed the most in explaining sexual segregation in argali. First of all, we were not able to monitor the year- round segregation pattern due to observations being restricted primarily to the summer months. We argued that changes in resource availability may lead to spatial segregation, suggesting that changes in NDVI over time may provide valuable insight. However, due to the non- availability of satellite imagery from our exact study period we could not provide evidence for it, and hence used only single image from 2007. These concepts could not be fully tested.

Paper 3

In the sampling study using resource selection functions, one possible explanation for the changes in habitat selection during the two sampling periods was annual variations in habitat selection by animals. However, we did not provide substantial evidence about changes in resource availability and precipitation patterns during the years which may strengthen this argument. Because, we argue projection of the habitat distribution models prepared for argali to larger areas in Ladakh and these models were made mainly using topographical characteristics and NDVI, and we did not include land use and cover changes along with livestock grazing, it is difficult to know how effective these models will prove to be.

Paper 4

In paper 4, we documented causes and changes in nomadic lifestyle and pastoral practices, and speculated on resulting consequences on wildlife and rangeland productivity. We could have increased the scope of the paper by adding more information on the nomads' future plans and aspirations, but this is social science research we hope to see undertaken.

Paper 5

Paper 5 was mainly an effort to initiate a discussion on the issue of competition among argali and livestock species. The main constraint in the paper was the dearth of observations for both argali and livestock in winter, which could have helped to understand and present the arguments better. We also did not have data on actual movement patterns of the livestock groups to estimate effectively the livestock impact on the area. Hence, the evidence for competition and negative impact of livestock on argali can not be strongly justified, and should be addressed further.

Future avenues

Argali habitat use in high altitude rangelands and climate change scenarios

Through the research reported here, we identified factors affecting habitat selection of argali. Snow free areas seem to be preferred by argali in winter and spring at the broad landscape scale, and feeding patches associated with higher green tissue of vegetation are selected. The dependence of argali and livestock on snow-free areas can be clearly investigated in the context of climate warming and changes in precipitation regimes. Climate change models predict an increase of extreme weather events in high altitude ecosystems, especially winter precipitation, which is in the form of snow (Miehe and Miehe 2000, McCarthy et al. 2007). During the initial stages of the study, we initiated observational and experimental studies to understand the likely impacts of climate warming on rangeland vegetation in the argali preferred areas and general rangeland health, but logistical constraints prevented their completion. Future observational studies should be aimed at understanding differences in vegetation characteristics by comparing areas with early and delayed snow melt. Snow melt regimes (early, delayed and control) need to be established to observe the effects of these scenarios on vegetation biomass, species composition, phenological changes such as plant height, number of leaves, date of budding, duration of flowering and percent of green tissue. Such studies have great potential in understanding the impacts of warming on rangeland vegetation and implications for forage availability to both wild and domestic herbivores, especially when fine scale plant species selection is based on forage quality. These experiments need to be restarted and continued.

Additionally, impacts of different levels of livestock grazing on rangeland productivity and health need to be studied to identify clearly the competition threat imposed by livestock on wild herbivores through excess resource exploitation.

Sexual segregation and life history of ungulates in extreme environments

Causes of sexual segregation are still debated in the literature after over 200 studies (Main 2008). We identified that predation risk associated with the reproductive strategy is likely the ultimate factor causing sexual segregation in our study population of Tibetan argali along with other proximate factors varying with species and their environments. Till now, very few studies have considered the issue of impact of evolutionary history on defining sexual segregation in wildsheep. Among the wild sheep species, argali inhabit one of the most extreme and resource-limited environments. In terms of life history comparisons, unlike other wild sheep species, argali are relatively short lived (10-13 years for males and 8-10 years for females),

thus need to grow faster and age physiologically and behaviourally, earlier than do mountain sheep (Geist 1971, Schaller 1977). With pressures of sexual selection, resource availability as a limiting factor, may play a crucial role in determining sexual segregation in argali. These results assumptions however, could not be tested due to the unavailability of either demographic data on argali or measurements of year-round resource variability. Such studies on demography of ungulate species and resource variability in extreme environments could help to understand the phenomena of sexual segregation, at least in such systems.

Argali distribution at a broad scale

The different elements of habitat use and selection by argali can now be put, in a larger context by building general habitat models of argali over larger areas as well as for other herbivores inhabiting remote areas and mountain ecosystems. To strengthen the conclusions about the impact of predation risk on habitat selection of wild and domestic ungulates, further research should be directed towards understanding the habitat selection and movement patterns as well as prey selection of their predators. To begin with, the impact of predation on argali needs to be assessed.

Conservation of argali

Animal movement should be investigated in response to ecological and human-induced barriers. Many changes in land use have taken place in the last decades, including habitat fragmentation, livestock management, road construction, human disturbance (e.g. tourism). From a conservation perspective, all these changes could affect available habitat for argali. This may also provide an opportunity for assessing large-scale manipulations by following changes of an ungulate's habitat selection in response to an increase disturbance and competition for resources and space. Areas that have undergone relatively low levels of disturbance can be compared to those with high fragmentation. Such approaches can be combined in an integrative conservation and management plan. We have initiated the surveys of argali using stratified random sampling and demonstrated reductions in sampling efforts. Future sampling and monitoring programs can be planned using the initial observations collected in the study to produce argali population estimates and distribution maps. We have also identified the suitable habitat for argali in the area, and these maps can now be improved using winter data to identify the year round use of the area. Use of such maps may help choosing the appropriate scale for conservation of argali in the area.

Herbivores and rangelands

A large body of information exists on plant-herbivore interactions in the low-productive arctic ecosystems. These simple systems allow the estimation of the fine-scale plants' response to herbivory, and its application to high-altitude rangelands needs to be assessed. In our system, a setting with exclosures of different types of herbivores (livestock vs. equids vs. bovids vs. rodents) could disentangle the differential response of plants to a large gradient of within the browser-grazer community.

Finally

I hope this thesis has contributed to the existing ecological information base on the little studied Tibetan plateau ungulate species, especially the argali which occurs all

across the Tibetan plateau and is under a threat of extinction. I also hope this work carries forward the studies on resource competition between wildlife and livestock, which was initiated by (Bhatnagar 1998) and (Mishra 2001). The thesis also reflects the issues related to harmonious coexistence between pastoralism and wildlife and how future socio economic and political changes in the region could affect the survival of wildlife. I conclude here with the hope that the present thesis will be able to contribute towards a better understanding of the ecological processes and factors that affect the wildlife and nomadic pastoralism in the rangelands of Transhimalaya and the Tibetan plateau. It may also assist in formulating species- based and area-based conservation and management plans.

References

- Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management* **69**:298-310.
- Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. *Ecology* **77**:215-227.
- Bagchi, S., C. Mishra, and Y. V. Bhatnagar. 2004. Conflicts between traditional pastoralism and conservation of Himalayan ibex (*Capra sibirica*) in the Trans-Himalayan mountains. *Animal Conservation* **7**:121-128.
- Bangs, P. D., P. R. Krausman, K. E. Kunkel, and Z. D. Parsons. 2005. Habitat use by desert bighorn sheep during lambing. *European Journal of Wildlife Research* **51**:178-184.
- Bhatnagar, Y. V. 1998. Ranging and habitat utilization by the Himalayan Ibex (*Capra ibex*) in Pin valley national park. Saurashtra University, Gujarat.
- Bhatnagar, Y. V., and R. Wangchuk. 2001. Status survey of large mammals in eastern Ladakh and Nubra. In *Conserving Biodiversity in the Trans-Himalaya*, Technical Report (1999–2000).
- Bhatnagar, Y. V., R. Wangchuk, and C. Mishra. 2006a. Decline of the Tibetan gazelle (*Procapra picticaudata*) in Ladakh, India. *Oryx* **40**:229-232.
- Bhatnagar, Y. V., R. Wangchuk, H. H. T. Prins, S. E. Van Wieren, and C. Mishra. 2006b. Perceived conflicts between pastoralism and conservation of the kiang *Equus kiang* in the Ladakh trans-Himalaya, India. *Environmental Management* **38**:934-941.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: Resources or predation? *Wildlife Monographs*:3-50.
- Bonenfant, C., L. E. Loe, A. Mysterud, R. Langvatn, N. C. Stenseth, J. M. Gaillard, and F. Klein. 2004. Multiple causes of sexual segregation in European red

- deer: enlightenments from varying breeding phenology at high and low latitude. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**:883-892.
- Bowyer, R. T. 2004. Sexual segregation in ruminants: Definitions, hypotheses, and implications for conservation and management. *Journal of Mammalogy* **85**:1039-1052.
- Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* **10**:421-431.
- Chundawat, R. S., and Q. Qureshi. 1999. *Planning Wildlife Conservation in Leh and Kargil Districts of Ladakh, Jammu and Kashmir*. .
- Conradt, L. 1998a. Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**:1359-1363.
- Conradt, L. 1998b. Measuring the degree of sexual segregation in group-living animals. *Journal of Animal Ecology* **67**:217-226.
- Edwards, T. C., D. R. Cutler, L. Geiser, J. Alegria, and D. McKenzie. 2004. Assessing rarity of species with low detectability: Lichens in Pacific Northwest forests. *Ecological Applications* **14**:414-424.
- Edwards, T. C., D. R. Cutler, N. E. Zimmermann, L. Geiser, and J. Alegria. 2005. Model-based stratifications for enhancing the detection of rare ecological events. *Ecology* **86**:1081-1090.
- Fox, J. L. 2004. The Tso Kar basin; conservation of a Tibetan plateau ecosystem in the Changthang highlands of Ladakh, India.1-30.
- Fox, J. L., C. Nurbu, and R. S. Chundawat. 1991. The Mountain Ungulates of Ladakh, India. *Biological Conservation* **58**:167-190.
- Fox, L. J., and A. J. T. Johnsingh. 1997. Wild sheep and goats and their relatives. *in* D. M. Shackleton, editor. *Status survey and conservation action plan for Caprinae*, Gland, Switzerland and Cambridge, UK: IUCN.
- Fryxell, J. M., and P. Lundberg. 1994. Diet choice and predator-prey dynamics. *Evolutionary Ecology* **8**:407-421.
- Fryxell, J. M., J. F. Wilmshurst, A. R. E. Sinclair, D. T. Haydon, R. D. Holt, and P. A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters* **8**:328-335.
- Geist, V. 1971. *Mountain sheep: a study in behavior and evolution*. The University of Chicago Press, Chicago.

- Geist, V., and R. G. Petocz. 1977. Bighorn sheep in winter - do rams maximize reproductive fitness by spatial and habitat segregation from ewes. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **55**:1802-1810.
- Green, R. H., and R. C. Young. 1993. Sampling to detect rare species. *Ecological Applications* **3**:351-356.
- Guisan, A., O. Broennimann, R. Engler, M. Vust, N. G. Yoccoz, A. Lehmann, and N. E. Zimmermann. 2006. Using niche-based models to improve the sampling of rare species. *Conservation Biology* **20**:501-511.
- Hagalia, W. 2004. Changing rangeland use by the nomads of Samad in the highlands of eastern Ladakh, India. MS Dissertation, Agricultural University of Norway, Ås, Norway.
- Hill, N. M., and P. A. Keddy. 1992. Prediction of rarities from habitat variables: coastal plain plants on Nova Scotian lakeshores. *Ecology* **73**:1852-1859.
- Johnson, D. H. 1980. The comparison of use and availability measurements for evaluating resource preference. *Ecology* **61**:65-71.
- Kie, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy* **80**:1114-1129.
- Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology* **83**:530-544.
- Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure - a hierarchical framework for the study of heterogeneity. *Oikos* **59**:253-260.
- Main, M. B. 2008. Reconciling competing ecological explanations for sexual segregation in ungulates. *Ecology* **89**:693-704.
- Main, M. B., and B. E. Coblenz. 1996. Sexual segregation in Rocky Mountain mule deer. *Journal of Wildlife Management* **60**:497-507.
- Main, M. B., F. W. Weckerly, and V. C. Bleich. 1996. Sexual segregation in ungulates: New directions for research. *Journal of Mammalogy* **77**:449-461.
- Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London.
- McCarthy, J. J., O. F. Canziani, N. A. Leary, D. J. Dokken, and K. S. White. 2007. Climate change 2007: Impacts, adaptations and vulnerability, contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) Intergovernmental Panel on Climate Change Cambridge University Press, UK.

- Michelena, P., P. M. Bouquet, A. Dissac, V. Fourcassie, J. Lauga, J. F. Gerard, and R. Bon. 2004. An experimental test of hypotheses explaining social segregation in dimorphic ungulates. *Animal Behaviour* **68**:1371-1380.
- Michelena, P., K. Henric, J. M. Angibault, J. Gautrais, P. Lapeyronie, R. H. Porter, J. L. Deneubourg, and R. Bon. 2005. An experimental study of social attraction and spacing between the sexes in sheep. *Journal of Experimental Biology* **208**:4419-4426.
- Miehe, G., and S. Miehe. 2000. Environmental changes in the pastures of Xizang. *Marburger Geographische Schriften* **135**:282-312.
- Miller, D. 1999. Nomads of the Tibetan plateau rangelands in western China. Part two: pastoral production practices. *Rangelands* **21**:16-19.
- Mishra, C. 2001. High altitude survival: conflicts between pastoralism and wildlife in the Trans-Himalaya. Wageningen University, The Netherlands.
- Mishra, C., S. E. Van Wieren, P. Ketner, I. M. A. Heitkonig, and H. H. T. Prins. 2004. Competition between domestic livestock and wild bharal (*Pseudois nayaur*) in the Indian Trans-Himalaya. *Journal of Applied Ecology* **41**:344-354.
- Namgail, T., Y. V. Bhatnagar, C. Mishra, and S. Bagchi. 2007a. Pastoral nomads of the Indian Changthang: Production system, landuse and socioeconomic changes. *Human Ecology* **35**:497-504.
- Namgail, T., J. L. Fox, and Y. V. Bhatnagar. 2007b. Habitat shift and time budget of the Tibetan argali: the influence of livestock grazing. *Ecological Research* **22**:25-31.
- Namgail, T., J. L. Fox, and Y. V. Bhatnagar. In press. Status and conservation of the endangered Tibetan argali in Ladakh, India. *Oryx*.
- Perez-Barberia, F. J., E. Robertson, and I. J. Gordon. 2005. Are social factors sufficient to explain sexual segregation in ungulates? *Animal Behaviour* **69**:827-834.
- Perez-Barberia, F. J., D. M. Walker, and I. J. Gordon. 2004. Sex differences in feeding behaviour at feeding station scale in Soay sheep (*Ovis aries*). *Behaviour* **141**:999-1020.
- Rawat, G. S., and B. S. Adhikari. 2005. Floristics and distribution of plant communities across moisture and topographic gradients in Tso Kar basin, Changthang plateau, eastern ladakh. *Arctic, Antarctic and Alpine Research* **37**:539-544.
- Rosenzweig, M. L. 1981. A theory of habitat selection. *Ecology* **62**:327-335.
- Ruckstuhl, K. E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour* **56**:99-106.

- Ruckstuhl, K. E. 2007. Sexual segregation in vertebrates: proximate and ultimate causes. *Integrative and Comparative Biology* **47**:245-257.
- Ruckstuhl, K. E., and P. Neuhaus. 2005. Sexual segregation in vertebrates: ecology of the two sexes, 1st edition. Cambridge University Press, Cambridge.
- Sabharwal, A. 1996. Changpas, the nomads of Rupshu: a study of ecology, economy and exchange, M.Phil. Dissertation, Department of Anthropology, University of Delhi.
- Schaefer, J. A., and F. Messier. 1995. Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* **18**:333-344.
- Schaller, G. B. 1977. Mountain Monarchs. University of Chicago Press, Chicago and London.
- Schaller, G. B. 1998. Wildlife of the Tibetan Steppe. University of Chicago Press, Chicago and London.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* **37**:789-799.
- Shackleton, D. M. 1997. Wild Sheep and Goats and their relatives: Status Survey and Conservation Action Plan. .
- Wallis de Vries, M. F., and P. Schippers. 1994. Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. *Oecologia* **100**:107-117.
- Wiser, S., R. K. Peet, and P. S. White. 1998. Prediction of rare-plant occurrence: a southern Appalachian example. *Ecological Applications* **8**:909-920.

Paper 1

**Scales and selection of habitat and resources:
Tibetan argali in high altitude
rangelands**

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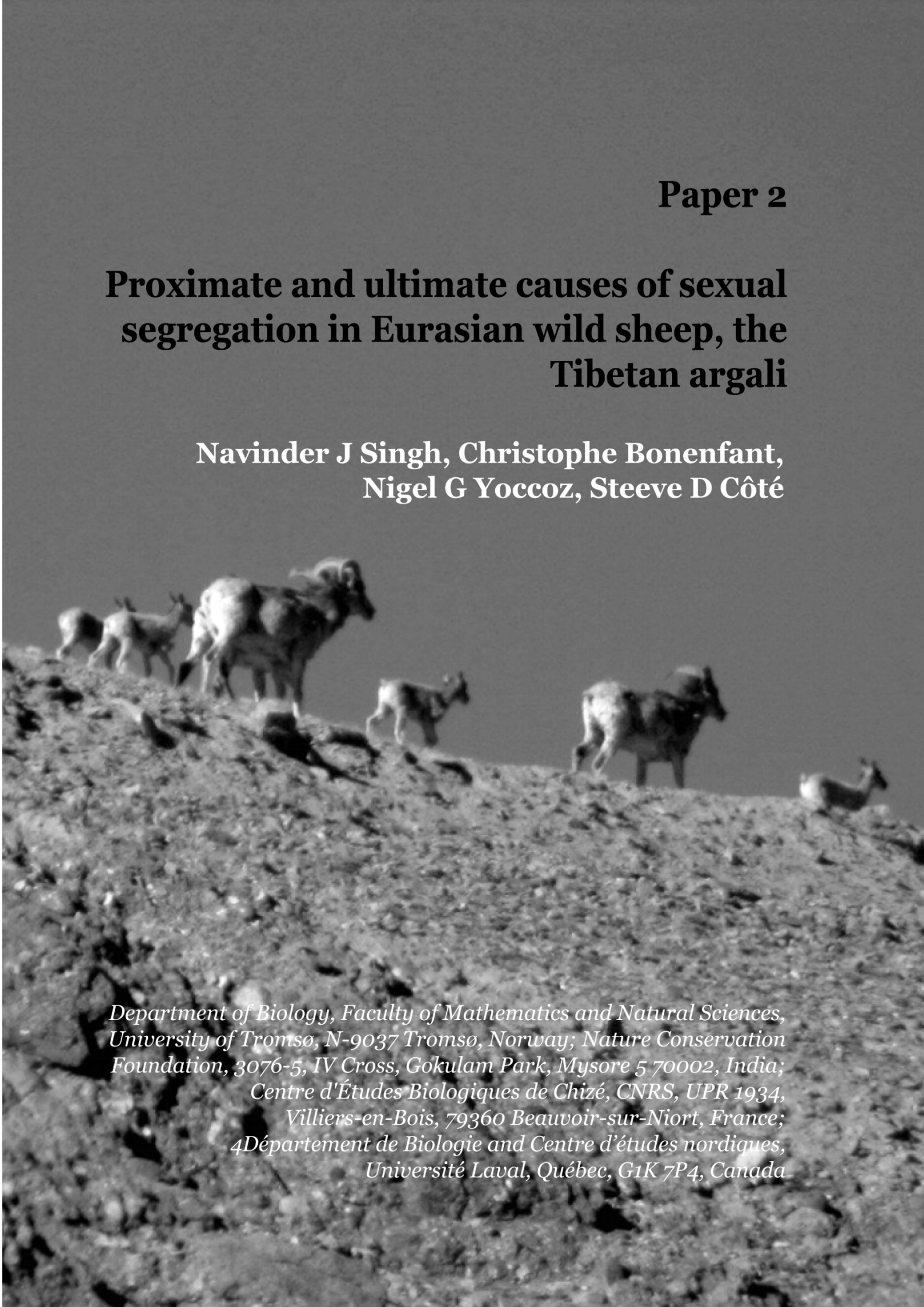


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Paper 2

Proximate and ultimate causes of sexual segregation in Eurasian wild sheep, the Tibetan argali

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Paper 3

**Using resource selection functions to
sample rare species in high altitude
ecosystems: a case study with
Tibetan argali**

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Paper 4

**Changing nomadic pastoralism in
Transhimalayan rangelands of India:
Causes and consequences**

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Paper 5

**Assessing wildlife-livestock
interactions in Indian Transhimalaya:
Tibetan argali as a case study**

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Paper 6

**Tibetan argali in India, Nepal and western
Tibet Autonomous Region, China**



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