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## Forage and security trade-offs by markhor *Capra falconeri* mothers

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Food acquisition and security from predators are primary determinants of habitat use in ungulates. There is usually a trade-off in the response of animals to these two factors, influenced by the individual's reproductive state. Females with vulnerable offspring, after parturition, are expected to compromise food acquisition for security. In temperate species such as the markhor *Capra falconeri*, however, the females give birth at a time when nutritious forage begins to

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become available after the long lean period of winter. The need to access quality forage in spring should, therefore, be significant even for new mothers, making the issue of female habitat choice particularly interesting and important to understand. We assessed habitat use patterns of the Pirpanjal markhor during the winter and parturition periods, to examine the response of markhor females to contrasting pressures of forage acquisition and neonate security. Markhor were observed during morning and evening hours along trails and vantage points in the Limber Wildlife Sanctuary, western Himalaya, India. Vegetation abundance and quality were assessed. Principal Components Analyses revealed that during winter, as expected, access to forage was the primary factor influencing habitat choice by female markhor. Following parturition, however, despite the low availability of quality forage throughout the preceding winter, markhor mothers predominantly used secure areas with steep slopes closer to cliffs, even though they were poorer in forage availability. Our results underscore the importance of neonate security in determining habitat use of markhor and the causes of low productivity of this population.

**Keywords:** Forage, habitat use, Kashmir, Markhor, mountain ungulates, parturition, security, trade-off.

Most ungulate species have coevolved with their predators<sup>1</sup>. The pressures of food acquisition and security from predators are often opposing, and the resultant trade-offs in ungulate habitat use have been well documented<sup>2-8</sup>. Many studies have shown that predation in ungulates determines their habitat use<sup>2,9</sup>. Predation by wolf, for example, has been reported to play an important role in the habitat selection by elk *Cervus elaphus*, which forces them to reduce use of preferred habitats due to higher predation risks<sup>4,10</sup>. Ungulates, therefore, may use habitats that are safe from predators even if the forage quality or/and quantity is low. Such trade-off, however, may vary with the individual's reproductive state and across age and sex.

Female ungulates are especially constrained by the physiological and forage demands of reproduction<sup>11</sup> on the one hand and vulnerability of young on the other<sup>2,3,8</sup>. This may compel females to trade-off between these two important constraints. Bighorn *Ovis canadensis* ewes are reported to select lambing sites with high security and low forage availability<sup>5</sup>. This trade-off between forage and predation risk has been reported in many other ungulates<sup>12</sup> and is also considered one of the major causes for sexual segregation<sup>12</sup>.

Temperate environments are characterized by temporal variability in the availability and quality of resources<sup>13</sup>. In summer, resources are abundant but in winter, they are very limited<sup>13</sup>. Seasonal changes in habitat use are thus expected with changes in resource availability and quality. Being the lean season, forage availability during win-

ter also depends on snow cover and snow depth<sup>14</sup>. Winter is the period when the offspring are relatively large, often having been born the previous spring, and the females are often in gestation with relatively greater energy demands<sup>15</sup>. The dynamics of habitat choice by females in winter and subsequent parturition is, therefore, particularly interesting. While in winter, females are expected to maximize intake of limited forage, their habitat use following parturition, is likely to be determined by the balance of the contrasting need to maximize neonate security with that of acquiring much needed forage. We studied how females in seasonal temperate ungulates respond to this conundrum by studying habitat use in the markhor Capra falconeri during two contrasting periods: parturition, when forage is abundant but females have vulnerable offspring, and winter, when forage is limited but their offspring are weaned.

The study was carried out in the Limber Wildlife Sanctuary in Kajinag Range, western Himalayas, Baramulla district of Jammu and Kashmir, India (Figure 1) during the years 2006–2007. The sanctuary covering c. 40 sq. km is mountainous, encompassing an altitudinal gradient of c. 2000-3900 m interspersed by cliffs and rocky outcrops. It is a temperate system, with cold winters and warm summers, with a temperature range of -10to +30°C. Precipitation is mainly in the form of snow in winter and rains in March with occasional showers during summer. Four distinct seasons can be classified during a year: winter (December to February) with very low temperatures and snow covering most of the area, spring (March to May) when temperatures begin to rise and sprout appears at lower elevations, summer (June to August) when temperatures rise further and the area contains abundant forage and receives some monsoon showers. During autumn (September to November) senescence sets in plants. Late spring (May end) and early summer (first half of June) are the parturition period of markhor<sup>16</sup>.

Vegetation is dominated by coniferous forests of kail-Pinus wallichiana, fir Abies pindrow, spruce Picea smithiana, and deodar Cedrus deodara. Birch Betula utilis forests occur near the tree line in combination with fir and kail, whereas the other broad leaf forests are mainly confined to areas along nullahs (hill streams). The subalpine area is dominated by juniper scrub Juniperus squamata.

Markhor is a medium sized, sexually dimorphic mountain ungulate. It exhibits sexual segregation, which is very prominent during summer (parturition and lactation period). Parturition occurs in late spring and early summer (mid-May to mid-June) when forage availability starts increasing after a lean winter. The potential predators of markhor are common leopard *Panthera pardus*, yellow-throated martin *Martes flavigula* and golden eagle *Aquila chrysaetos*. Sightings and indirect evidences such as pug marks, scrapes, scats, etc. of these predators have been recorded in our study area. Other wild ungulates in

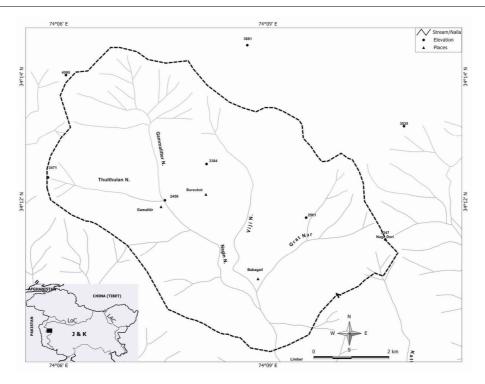


Figure 1. Map of the study area in the Limber Wildlife Sanctuary, Kajinag, Kashmir, India.

the area include Kashmir musk deer *Moschus leucogaster* and goral *Nemorhaedus goral*.

About 7000 sheep and goats belonging to migratory *Bakkarwals* and local *Chopans* use the study area between June and September<sup>17</sup>. Livestock is an important source of income for the local people and the primary source of income for *Bakkarwals*.

We collected data on habitat selection by female markhor for parturition (and lactation) (May 2006-August 2006) and winter (December 2006–January 2007) periods. Observations were made on markhor groups with the aid of  $8 \times 40$  binoculars and 15–45x spotting scopes along predetermined trails (n = 12) and vantage points (n = 6) selected to extensively cover the study site. The observations along trails were made for c. 3 h during early mornings and evenings and for c. 40 min at each vantage point. These observations were repeated three times each during the winter and parturition periods. All the sightings were marked on 1:50,000 topographic maps with elevation contour interval of 40 m. The time and date of all the sightings and age-sex of the groups were also recorded along with the following variables: vegetation type (open conifer, moderate conifer, dense conifer, broad leaf, riparian scrub, sub-alpine scrub, alpine meadows), vegetation cover (ground cover, shrub cover), slope, aspect, altitude, shortest (straight line) distance from escape terrain (cliffs). The vegetation variables (type and cover), snow cover and distance from escape terrain were visually estimated. Topographic variables, altitude, aspect were recorded through global positioning systems (GPS, Garmin Inc.). The topographic variable, aspect was classified into north (N, NW), south (S, SE), east (E, NE) and west (W, SW) for analysis.

Capra uses cliff and steep slopes to escape predators<sup>7</sup>. We used proximity to cliffs and the steepness of slope as measures of security. For forage availability, we quantified ground cover (grass and herbs) and shrub cover through line intercept and point intercept sampling respectively, on and around cliffs (20 plots) and 50-300 m away from cliffs (23 plots). For each plot the slope, terrain type, altitude and aspect were also recorded. At each plot, five 10 m lines were placed parallel to each other, 2.5 m apart. For point intercept sampling, we recorded the item on the ground at 30 cm intervals yielding 33 points on each line and 165 points for each plot. In total we had 3300 points close to cliffs and 3795 points in areas away from cliffs. For line intercept sampling, we measured the length of the line touched by each shrub on the first, third and fifth line. Palatability of the recorded plants was ascertained from the direct observation and feeding signs of markhor, domestic sheep and goats and also the traditional knowledge of palatability obtained through interviews of 20 key informants, largely herders.

We performed Principal Component Analysis (PCA) of habitat use data to identify the significant variables that correlated best with the observed locations of female markhor. PCA identifies groups of interrelated variables and generates the principal components. The first component captures the highest amount of variation and

successive components extract the maximum residual variation. Distance to cliff (m), slope (°), tree cover (%), shrub cover (%), ground cover (%), snow cover (%) were used in PCA.

We observed 143 female markhor groups which included 49 in winter and 94 during parturition. The first three components of PCA explained 66% of variation in the data. Component 1 reflected a security axis, with distance to cliff, elevation and snow cover being the important variables loaded on *X*-axis (Table 1). Components 2 and 3 reflect forage availability, with shrub, ground and tree cover being the important variables loaded on *Y*-axis.

Perusal of the PC scores (Figure 2) showed that mark-hor females used a gradient of elevation, tree cover and shrub cover categories during both periods, but were clearly confined to areas offering greater security (steeper areas closer to escape terrain) during the parturition period. In winter, female markhor appeared to use a variety of habitats along both axes, including areas farther away from the cliffs, on gradual slopes and with higher shrub and ground cover. Habitat use during parturition appeared to be associated with security whereas winter habitat use seemed to be more associated with forage availability (high shrub and ground cover) as revealed by the PC scores along the two axes.

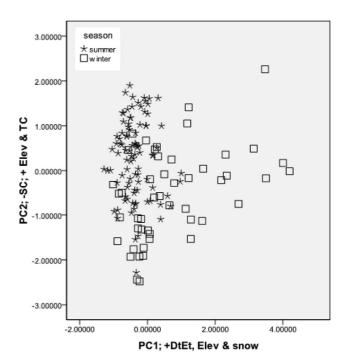
As distance to cliff, elevation, slope and vegetation cover were revealed to be important factors governing seasonal use by markhor (Figure 2), we studied their individual contributions (Table 2). Most of the sightings were very close to cliffs (0–30 m; 93.6%) and merely 1% was farther than 60 m during parturition. In winter, the use of areas farther than 60 m from cliffs increased to 36% (Table 2). Majority of the sightings (77%) of markhor were in rugged terrain (cliffs, interspersed rocky slopes and broken) during parturition while, in winter, it came down to half (53%). During parturition 90% of sightings were on the steeper slopes (>40°), whereas in winter this reduced to 33%, and the use of more gentle slopes (<40 degrees) increased to 67%. This indicates the importance of security during summer when females give

Table 1. Principal component analysis of the variables describing Markhor locations in Limber wildlife sanctuary (WLS), Kashmir, India. The table shows the varimax rotated factor scores of the first three Principal Components Axes. Distance to escape terrain which relates to the security, is loaded on the first component whereas the shrub and ground cover designating the forage cover is loaded as 2nd and 3rd components respectively

Variable	PC1	PC2	PC3
Distance to escape terrain	0.868	0.058	0.109
Elevation	0.643	0.523	0.078
Snow cover (Sqrt)	0.626	-0.042	-0.509
Slope	-0.509	0.517	0.154
Tree cover (Sqrt)	0.084	0.744	0.098
Ground cover (Sqrt)	0.055	0.003	0.905
Shrub cover (Sqrt)	-0.046	-0.657	0.402

birth and are lactating. Female markhor primarily used the mid-elevations (2700–3000 m) during both parturition (78%) and winter (46%), but the use of the lowest elevations (<2700 m) increased during winter (from 21% in birthing to 38% in winter). In summer the higher elevations (>3000 m) were not used at all, but their use in winter constituted 14%. Most of these differences were statistically significant (Table 2). Areas away from cliffs had higher ground cover (58.1%) than areas on and close to cliffs (41.9%). Similarly, the cover of palatable species was higher (78.4%) in areas farther from cliffs than in areas closer to cliffs (61.2%; t = -4.279; P < 0.001) but the difference in unpalatable cover was not significant (t = -1.506; P < 0.140). Barren cover (rock and soil) was much higher in areas which are on and close to cliffs.

Our observations on female markhor indicate that habitat use was predominantly associated with security during parturition period, despite the fact that parturition follows a long winter of lean resource availability. On the other hand, during winter, their habitat use, expectedly, was determined by forage availability. The parturition sites of markhor are in cliffs, interspersed with trees and caves providing cover for young ones from predators, inclement weather and disturbance from livestock herders. However, we found that the palatable forage availability/abundance was significantly lower in these markhor parturition sites



**Figure 2.** Ordination of female markhor habitat use during parturition and winter. PC1 represents a 'security' axis with increasing distance to escape terrain (DtEt), elevation (Elev) and snow cover (snow), while the PC2 represents a forage axis with declining shrub cover (SC) and increasing tree cover (TC). The female markhor strictly used areas very close to cliffs during parturition, whereas in winter, they also used areas away from cliffs. See table 1 for PC scores or variables.

(on and around cliffs) than in areas away from cliffs. Safer areas often have less forage availability (abundance and/or quality) compared to risky ones<sup>18,19</sup> compelling the female parturient ungulates to compromise on forage abundance and/or quality for the security of their young<sup>20</sup>. Female alpine ibex *Capra ibex* provide evidence for such trade-offs, using grasslands with newly emergent vegetation in gentle slopes during pre-parturition and habitats with steep escape terrain during parturition to increase offspring security<sup>7</sup>.

In winter markhor females selected areas away from cliffs with relatively greater forage availability. Since the offspring are larger and weaned during this period, and the forage availability (quality and quantity) is generally low, forage availability becomes the primary determinant of habitat use. As a result, markhor females tend to move wider for exploiting areas with forage even if they are less secure, hence compromising on safety for forage acquisition.

Interestingly, our results show that female markhors did not use the elevation zone above 3000 m during parturition and lactation period (summer), despite our

**Table 2.** Proportionate use of the important habitat and vegetation variables by markhor females during the two periods of parturition (May-August) and winter (December-January) Limber WLS

Variables	Parturition (%) $N = 94$	Winter (%) N = 49	$\chi^2$	P value
Distance to ET* (m)			46.21	0.0001
0–30	93.6	52.9		******
30-60	5.4	10.2		
>60	1.1	36.6		
Elevation (m)			43.315	0.0001
2400-2700	21.2	38.6		
2701-3000	78.8	46.4		
3000-3300	0	14.1		
Slope (deg)			84.775	0.0001
20–40	9.6	67.2		
40-60	46.8	30.5		
>60	43.6	2.0		
Tree cover (%)			12.872	0.005
0	25.3	50.8		
1-30	54.8	29.3		
31-60	18	16.9		
>60	2.1	3.0		
Shrub cover (%)			4.295	0.0116
0-20	74.4	85.7		
20-40	20.2	10.2		
40-60	5.4	4.0		
Ground cover (%)			26.276	0.0001
0-40	17.1	32.5		
41-80	52.1	63.2		
>80	30.8	4.1		
Snow cover (%)			36.2	0.0001
0	100	69.2		
1-30	0	15.3		
31-60	0	12.3		
>60	0	3		

<sup>\*</sup>ET, Escape terrain.

expectations to the contrary. During parturition and lactation period, the higher elevation zones have younger and more nutritious forage, and we had expected the females to use them disproportionately after a prolonged preceding period of lean forage access. It appears that the presence of livestock in higher altitudes during the postparturition period prevented markhor females from using higher elevations. This is reinforced by our observation that 14% of our markhor sightings were in this zone during winter when there is no livestock in the study area. The use of sub-optimal habitats by wild ungulates in presence of livestock has been reported from other studies also<sup>21,22</sup>. It therefore appears that while winter is the period of lean forage availability, female markhor are prevented from accessing areas with nutritious forage even post-winter. This is likely to affect their reproductive performance as forage limitation imposed by high level of livestock grazing has been reported to negatively affect the population performance of mountain ungulates<sup>23</sup>. Indeed, we have recorded a relatively low ratio of kids to adult female markhor (60:100) during repeated population surveys in our study area, compared to the 102:100 kids to adult female ratio of markhor population in Pakistan<sup>24</sup>. Our study suggests that protection of key parturition sites from livestock grazing and other disturbance, and livestock grazing management of markhor habitat especially at higher elevations during summer months will be key to increasing the productivity of this endangered population.

Markhor females are trying to prioritize the habitat use to increase their reproductive success by using secure areas during parturition and compromising on forage. They do the opposite during winter. But the presence of livestock during the parturition and lactation period does have negative impact. The parturition sites and summer habitats of female markhor should be released from livestock grazing at least during these periods to increase the productivity of this markhor population.

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## Alkaline phosphatase activity in developmental stages of Asia I and Asia II-1 populations of whitefly, *Bemisia tabaci* (Gennadius)

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The whitefly, Bemisia tabaci (Aleyrodidae, Hemiptera), regarded as a species complex comprising over 34 genetic groups, is a serious insect pest of several crops. The aim of this study was to find out the difference in alkaline phosphatase (ALP) activity between developmental stages of two populations of B. tabaci belonging to Asia II-1 and Asia I genetic groups. There was a rise in ALP activity from first to second instar followed by gradual decline through third and fourth instars. ALP activity reached its peak during the adult stages of both Asia I and Asia II-1 populations. The specific activity of ALP in nymphal instars of Asia II-1 was significantly higher than that of Asia I.

The kinetics of ALP revealed that Asia I population showed significant increase in  $V_{\rm max}$  value compared to Asia II-1 in the second instar, fourth instar and adult stages, whereas the opposite is seen in the first and third instars. Also, the Asia I population showed significant decrease in  $K_{\rm m}$  value compared to Asia II-1 in the first and fourth instars; the opposite was seen in second instar. No significant differences were observed between the  $K_{\rm m}$  values of the third instar and adult stages of both the populations. The possible physiological role of ALP and its implications in management of this pest are also discussed in this communication.

**Keywords:** Alkaline phosphatase, *Bemisia tabaci*, developmental stages, genetic groups.

WHITEFLY, *Bemisia tabaci* (Hemiptera: Aleyrodidae), one of the world's top 100 invasive pests with a host range of well over 900 plants (<a href="http://www.issg.org/database">http://www.issg.org/database</a>) causes serious damage directly as sap-sucking pest and indirectly as vector of plant pathogenic viruses. *B. tabaci* is regarded as a species complex comprising about 34 morphologically indistinguishable genetic groups<sup>1</sup>. There is a great amount of diversity of *B. tabaci* in Asia with the presence of 19 of the 34 genetic groups recorded so far. The Indian subcontinent represents an important Old World centre of diversification and evolution of *B. tabaci* with Asia 1 and Asia II-1 being the two dominant genetic groups widely distributed in India<sup>2,3</sup>.

Alkaline phosphatase (ALP, EC 3.1.3.1; a ubiquitous hydrolase enzyme present in animals, fungi and bacteria)

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