Seasonal and Sex-specific Variation in Terrain Use and Movement Patterns of Mountain Goats in Southeastern Alaska

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Abstract: Fundamental differences in fitness requirements between male and female individuals result in sex-linked ecological variation within many species of large mammals. Determining the extent to which sex-specific requirements alter behavioral strategies and subsequent spatial use patterns has important implications for conservation and management of species such as mountain goats (*Oreamnos americanus*). In this study, location data were collected from 22 GPS radio-collared mountain goats (11 males, 11 females) during September 2005 to February 2006. These data were integrated with terrain data layers in a GIS framework to address questions about sex-specific variation in movement patterns and terrain use across a 600 km^2 study area located in southeast Alaska. Male mountain goats exhibited greater rates of movement than females during the rut but not during fall or winter. As a result, male home ranges were significantly larger than females during this period. Both males and females moved to lower elevations with the onset of winter but did not differ with respect to altitudinal distribution. Following the rut, the period when sexual aggregation occurs, females used areas in which slope was steeper, distance to escape terrain was less, and terrain ruggedness was greater than areas used by males. Overall, these preliminary findings detail differences in terrain and spatial use patterns between male and female mountain goats and suggest that vulnerability to anthropogenic disturbance factors may be sex-specific.

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Elucidating patterns of resource use and movement play an important role in our understanding of the ecology and conservation of many species. While many factors may influence variation in these fundamental ecological characteristics, the sex of individuals in a population represents one variable of principal interest (Clutton-Brock et al. 1982, Main et al. 1996). This is particularly evident among polygynous ruminants that display pronounced sex-specific contrasts in morphology, social behavior, and life history strategies (Clutton-Brock et al. 1982). These patterns arise because natural selection acts on males and females in disparate ways as a result of fundamental differences in their reproductive characteristics (Darwin 1871).

Mountain goats (*Oreamnos americanus*) provide an interesting example for evaluating sex-mediated differences in patterns of resource use and movement as a result of sexual body size dimorphism, social organization, and narrow constraints on habitat use requirements (Côté and Festa-Bianchet 2003). Adult male mountain goats are 40 to 60% larger than females (Houston et al. 1989). As a result, males are expected to experience greater nutritional requirements but may also be less prone to predation. In addition, energetic resources required for successful reproduction are partitioned differently between males and females. In particular, polygynous males do not participate in rearing of young and maximize reproductive success by utilizing behavioral strategies that optimize their ability to mate with many high quality females during a limited 4 to 6 wk rutting season (Brandborg 1955, Geist 1964). Females, on the other hand, maximize their reproductive success by selectively breeding with a single high quality male (Brandborg 1955) and, perhaps more importantly, optimizing foraging and habitat use decisions that enable acquisition of adequate nutritional resources required for survival and successful rearing of young (Cote and Festa-Bianchet 2001); a period that may span at least 10 months (Chadwick 1977).

Largely unique among North American ungulates, mountain goats exhibit distinct morphological adaptations that enable them to live in steep, rugged mountain environments characterized by extreme climate conditions. It is widely recognized that the preferential for use of such habitat types is primarily linked to avoidance of predation (Schaller 1977, Smith 1983, Fox and Streveler 1986). At smaller spatial scales, these environments are composed of a mosaic of forage-rich alpine meadows and barren cliffs that provide escape terrain. Because of this juxtaposition of habitat types, mountain goats likely face trade-offs between utilizing forage-rich but relatively dangerous alpine meadows and forage-poor but safe cliff habitats. Such sex-specific trade-offs in habitat use have been documented in other mountain ungulate species (Bleich et al. 1997) and provide a framework for interpreting resource use patterns in mountain goats.

In this paper two principal research questions were addressed: (1) do adult male and female mountain goat home range and movement patterns differ during and outside of the rut?, and (2) do adult male and female mountain goats differ in their use of "safe" terrain features during periods outside of the breeding season?

Study area

We studied mountain goats in a 600 km^2 study area in a mainland coastal mountain range east of Lynn Canal, a post-glacial fjord located near Haines in southeastern Alaska (Figure 1). The study area is oriented along a north-south axis and bordered in the south by Berners Bay (58.76N, 135.00W) and by Dayebas Creek (59.29N, 135. 35W) in the north. Elevations range from 1920 m to sea level. This area is an active glacial terrain underlain by late cretaceous-paleocene

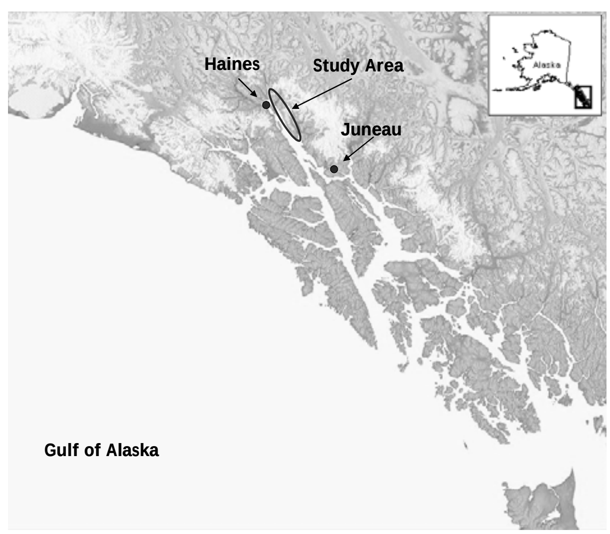

Figure 1. Mountain goat study area along the east side of Lynn Canal, Alaska.

granodiorite and tonalite geologic formations (Gehrels 2000). Specifically, it is a geologically young, dynamic, and unstable landscape that harbors a matrix of perennial snowfields and small glaciers at high elevations (i.e. above 1200 m) and rugged, broken terrain that descends to a rocky, tidewater coastline. The northern part of the study area is bisected by the Katzehin river, a moderate volume (~1500 c/fs; USGS, unpublished data) glacial river system that is fed by a tributary of the Juneau Icefield.

The maritime climate in this area is characterized by cool, wet summers and relatively, warm snowy winters. Annual precipitation at sea-level averages 143 cm and winter temperatures rarely are less than -15C and average -1C (Haines, AK; National Weather Service, Juneau, AK, unpublished data). Elevations at 800 m typically receive ca. 650 cm of snowfall, annually (Eaglecrest Ski Area, Juneau, AK, unpublished data). Predominant vegetative communities occurring at low-moderate elevations (<500m) include Sitka spruce (*Picea sitchensis*)-western hemlock (*Tsuga heterophylla*) coniferous forest, mixed-conifer muskeg, and deciduous riparian forests. Mountain hemlock (*Tsuga mertensiana*) dominated 'krummholtz" forest comprises a subalpine, timberline band occupying elevations between 500-750 m. Alpine plant communities are composed of a mosaic of relatively dry ericaceous heathlands, moist meadows dominated by grasses and forbs, and wet fens. Avalanche chutes are common in the study area, bisect all plant community types, and often terminate at sea-level.

Methods

During September and October 2005, we captured 22 adult mountain goats (11 male, 11 female) using standard helicopter darting techniques (Taylor 2000). Mountain goats were immobilized by injecting 3.0/2.7mg of carfentanil citrate (males/females, respectively) via projectile syringe fired from a Palmer dart gun (Cap-Chur, Douglasville, GA). During handling, all animals were carefully examined and monitored following standard veterinary procedures (Taylor 2000) and routine biological samples and morphological measures collected. Following handling procedures, the effects of the immobilizing agent was reversed with 100mg of naltrexone hydrochloride per 1mg of carfentanil citrate (Taylor 2000). All capture procedures were approved by the State of Alaska Animal Care and Use Committee.

Telonics TGW-3590 GPS radio-collars (Telonics Inc., Mesa, AZ) were deployed on all animals captured. Radio-collars were programmed to collect GPS location data at 6-hr intervals. During each location attempt ancillary data about collar activity (i.e. percent of 1-second switch transitions calculated over a 15-min period following each GPS fix attempt) was simultaneously collected. Complete data-sets for each individual were remotely downloaded (via fixed-wing aircraft) at 8-wk intervals. Location data were post-processed and filtered for "impossible" points and 2D locations with PDOP (i.e. position dilution of precision) values greater than 10, following D'Eon et al. (2002) and D'Eon and Delparte (2005).

Seasons were defined by using remotely collected activity sensor data as a proxy for defining behaviorally mediated changes in seasonal activity patterns. Specifically, GPS collars were deployed with mercury tip switches programmed to record the proportion of 1-sec switch transitions that occurred over a 15-min period coordinated with GPS location attempts (ie. 6-hr intervals). Previous research on comparable species documented reliable linkages between actual animal behavior and remotely collected activity switch data (Coulombe et al. 2006). As a result, I assumed that the proportion of switch transitions correlated positively with animal activity. Thus, distinct changes in activity patterns were used to define biologically relevant seasons for mountain goats.

Location data were integrated into a GIS (ArcView 3.2, ArcGIS 9, ESRI, Redlands, CA) in order to derive spatial attribute information for each data point. Digital elevation models (30-m resolution; NASA 2004) were used to estimate elevation (m), slope (degrees), distance (m) to slopes greater than 40 degrees (hereafter "distance to cliffs") and standard deviation of elevation within a 60 m radius of point locations (hereafter "topographic roughness"). Distance moved between successive locations was calculated at different time steps (1-d and 5-d intervals). Fixed-kernel home ranges (95% isopleths) were calculated using the least-squares cross validation (LCSV) technique to parameterize the smoothing function (Seaman and Powell 1999, Seaman et al. 1999). Both movement distance and home range area were calculated using surface area rather than planimetric area functions (following Jenness 2004). This approach enabled more precise estimates of space use parameters; planimetric area calculations tended to underestimate actual space use by 20.3%, on average (K. White, unpublished).

To compare seasonal and inter-sexual differences in male and female home range sizes, I used analysis of variance (ANOVA) and Tukey HSD pair-wise comparisons (Zar 1999). To evaluate seasonal and sex-specific differences in movement distances (1-d and 5-d intervals), elevation, slope, distance to cliffs and topographic roughness, daily mean values, and 95% confidence intervals were estimated for each sex category. Confidence intervals for population means were estimated using the variance among the individual animal mean values, which were based on all observations for each goat within the relevant season (Steel and Torrie 1980). Confidence intervals that did not overlap were considered to be evidence of sex differences. This analysis emphasized estimation of variable means (i.e. elevation, distance, etc.), rather than explicitly testing hypotheses; this approach was used because it provided a more descriptive assessment of variability in male-female differences at short time intervals.

Results

During September 27 to October 15, 2005, 22 adult mountain goats (11 male, 11 female) were captured and deployed with GPS radio-collars. Between September 27, 2005 and February 10, 2006 a total of 8576 GPS locations (mean ± SE = 389 ± 4 locations/animal) were acquired and used in subsequent analyses.

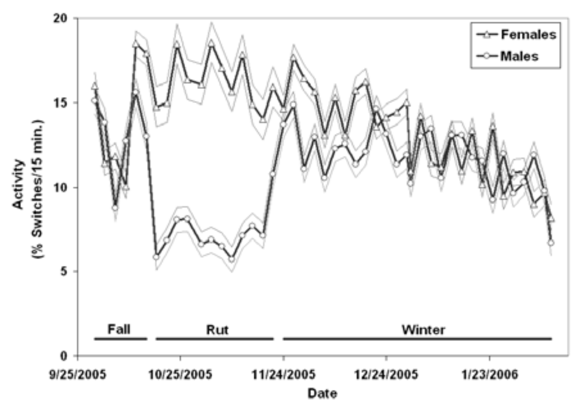

Figure 2. Activity patterns for male and female mountain goats between September 27, 2005 and February10, 2006. Activity data derived from tip-switch sensors located on Telonics TGW-350 GPS radio-collars. Daily mean ± 95% confidence intervals.

As defined by the proportion of switch transitions, male and female mountain goat activity patterns were similar except between October 18 and November 23, 2005, when male activity patterns were significantly less than females (Figure 2). Based on Geist (1964), I assumed this period of reduced male activity coincided with the rut. The period between September 27 and October 18 was defined as fall while the period between November 23, 2005 and February 10, 2006 was defined as winter (Figure 2).

Movement rates for males and females were similar during fall and winter; however, rates significantly deviated during the rut. Specifically, movement rates were significantly greater for males than females, particularly when analyzed over 5-d time intervals (Figure 3, 4). During the shorter 1-d time step, movement rate overlap between males and females was evident for brief periods but overall was greater for males despite greater variability in estimates at this time scale (Figure 5). Significant differences were detected in seasonal home range estimates for males and females ($r^2 = 0.32$, $F_{5,52} = 12.71$, $P < 0.001$; Figure 6, 7). Specifically, males used larger home ranges than females during the rut; however, home range estimates did not differ by sex during other seasons. Altitudinal distribution did not differ between males and females (Figure 8). An overall decline in mean elevation of all goats occurred with the onset on winter conditions at high elevations, though variability was evident in this relationship and coincided with the occurrence of an abnormally warm, late-season storm system November 17 to 25, 2005.

Overall, I estimated mean differences in slope, distance to cliffs, and terrain ruggedness were significantly different between males and females during the post-rut, winter period (Figure 9 to 11). Specifically, my findings indicate that females used steeper slopes that were more rugged and closer to cliffs than males. No differences were detected in terrain use comparisons between males and females during the breeding aggregation period, or rut.

Discussion

Adult male and female mountain goats face differential selection pressure as a consequence of variation in morphology and associated life history strategies. By comparing behavioral differences between males and females during the breeding season, it is possible to characterize mechanisms each sex employs to maximize chances for increasing individual fitness.

Similar to previous research in southeast Alaska (Schoen and Kirchhoff 1982, Smith and Raedeke 1982), male and female mountain goats in this study exhibited substantial differences in movement rates and home range sizes. Males moved widely across the landscape during the breeding season, presumably in search of receptive females, while females used relatively small areas and moved less. These differences in space use and movement patterns suggest males exhibit behavioral strategies during the rut that enable increased chances to successfully breed with as many females as possible. Females, on the other hand, exhibit space use strategies that encompass relatively small areas that, possibly, maximize chances of discovery by high quality males during the breeding season.

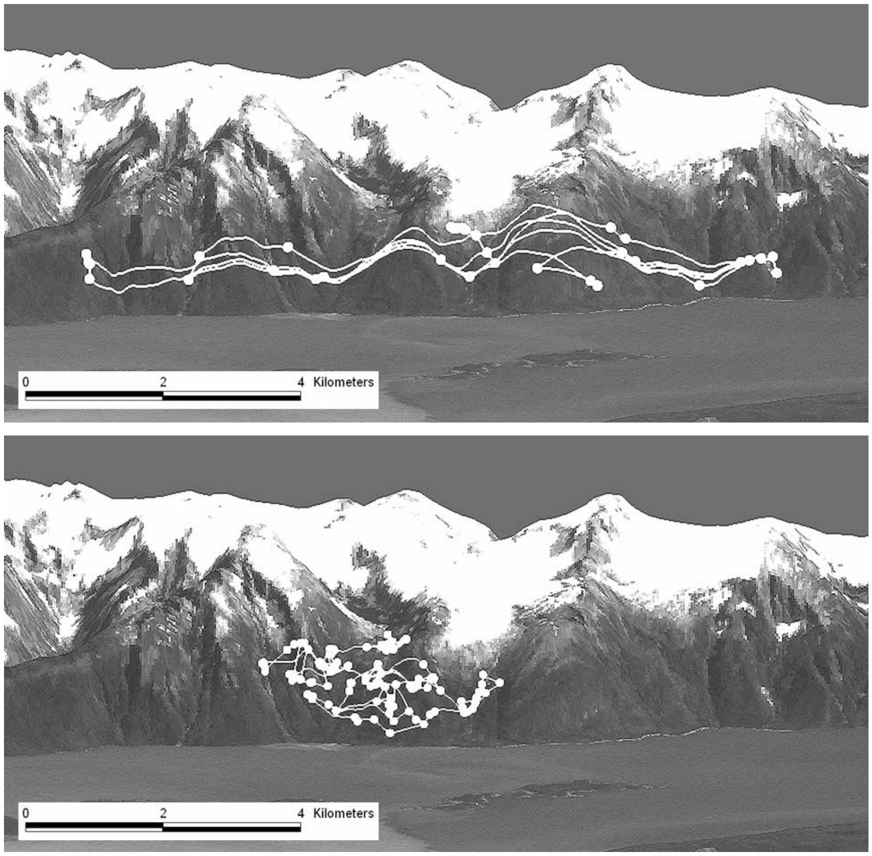

Figure 3. Representative 1-day interval movement patterns for radio-collared male (Goat #16; upper) and female (Goat #10; lower) mountain goats during the rut (October 18 to November 23, 2005).

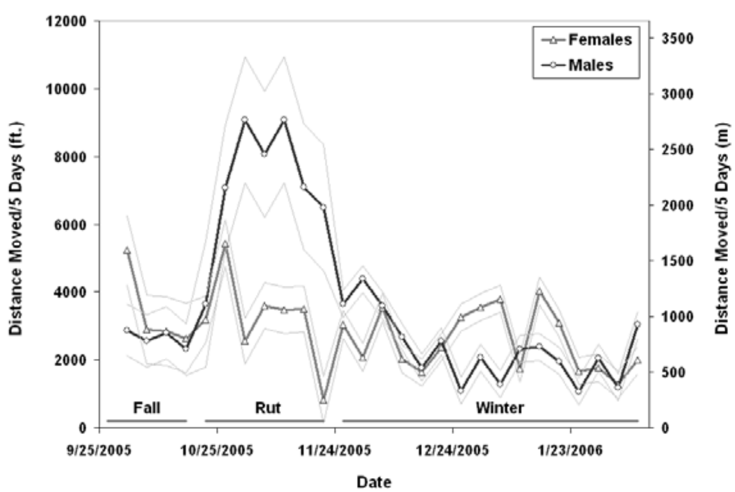

Figure 4. Distance moved by male and female mountain goats between September 27, 2005 and February 10, 2006: 5-d mean ± 95% confidence intervals.

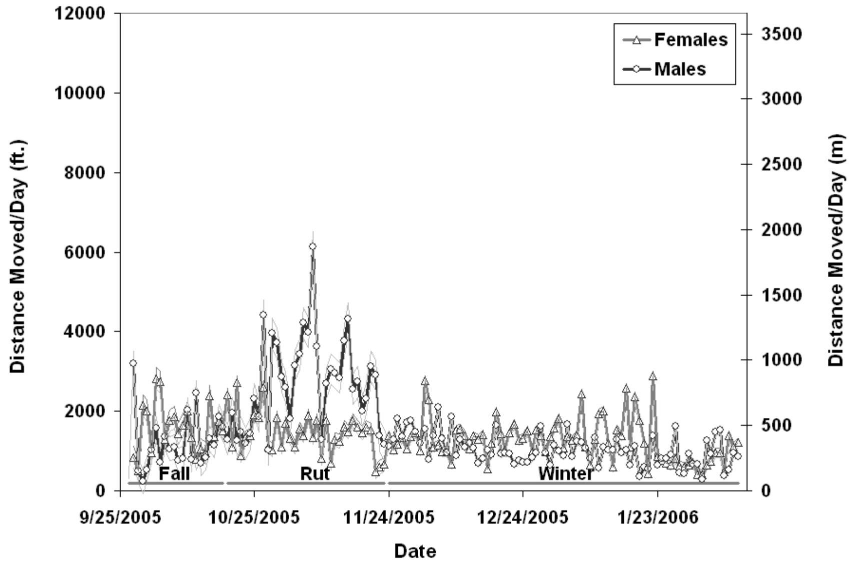

Figure 5. Distance moved by male and female mountain goats between September 27, 2005 and February 10, 2006: daily mean ± 95% confidence intervals.

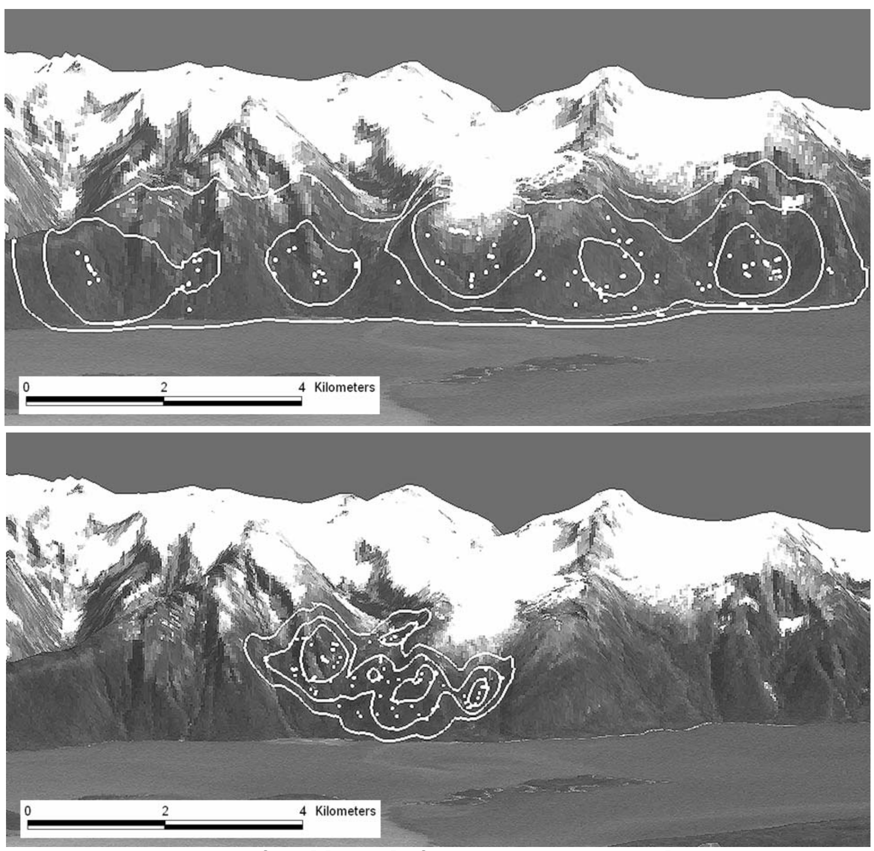

Figure 6. Home range size (95% fixed kernel) for representative male (Goat #16; upper) and female (Goat #10; lower) mountain goats during the rut (October 18 to November 23, 2005).

Since body size of males is substantially larger than females, females may be potentially more vulnerable to attacks by large mammalian predators (Curio 1976). Additionally, females also are more likely to be associated with related young or sub-adults, than males; a factor that further predisposes them to increased predation-risk. Findings from this study, consistent with previous mountain goat research in southeast Alaska (Schoen and Kirchhoff 1982), suggest females use safe terrain features to a greater extent than males. This pattern was specifically evident during the post-rut period when females used steeper more rugged terrain in areas closer to cliffs than did males. While largely consistent with expectations associated with predation-mediated habitat-use trade-offs, the affinity for use of steep, rugged terrain by females also may be due to lower snow depths in these habitat types during winter (Fox 1983).

In coastal mountain regions mountain goats typically migrate from high elevation summer ranges to lower elevation, forested winter ranges (Hebert and Turnbull 1977, Fox et al. 1989). However, whether males and females maintain similar altitudinal distributions during winter in southeast Alaska is less clear (Schoen and Kirchhoff 1982, Smith 1986). In this study I documented sex-independent altitudinal migrations by mountain goats that coincided with the onset of the first winter storms. Overall, 80% of all winter locations were at elevations less than 600 m above sea-level. These findings represent an interesting contrast to those of Hundertmark et al. (1983) which documented mountain goats inhabiting an upper tributary of the Chilkat river valley, approximately 55 km north, wintered primarily in windswept, high elevation habitats. Consequently, it appears that over-wintering strategies of mountain goats can vary over relatively small spatial scales and are not likely related to different sex ratios in each population.

The extent to which the sexes segregate or employ different strategies for utilizing resources in their environment and avoiding mortality have important implications for conservation and management of species. For instance, differences in sex-specific movement patterns during the rut likely result in increased vulnerability of males to hunting pressure as a consequence of increased movement and visibility. Disparities in visibility of males relative to females also may alter their observability during routine population monitoring surveys. Extensive landscape-level movements of males during the rut appear to be an important element of rutting behavior. If habitat connectivity is altered by industrial activity and inhibits movement of male goats, reproductive success and population productivity may be diminished due to lower copulation rates and/or increased incidence of second estrous mating events. Thus, acquisition of information about sex-specific variability in habitat use and movement patterns may help resolve key challenges associated with management and conservation of mountain goats.

Differences in sex-specific patterns of terrain use and movement were not always evident. Such findings are nonetheless significant for conservation of mountain goats. In particular, the observation that both sexes utilized low-elevation areas extensively during the critical winter period is important in devising conservation strategies that limit the effects of human disturbance on mountain goats. In southeast Alaska, industrial activity (i.e. mining, road construction,

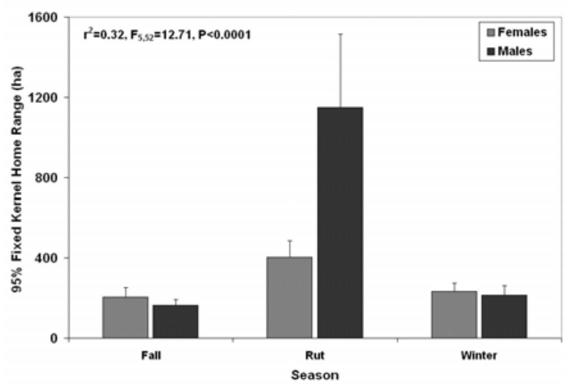

Figure 7. Seasonal home range sizes (95% fixed kernel) for male and female mountain goats. Mean ± SE.

timber harvest) is primarily confined to low elevation habitats, and identifying the extent to which such activity is sympatric with mountain goat winter range can help guide policy decisions that strive to ensure adequate protection of mountain goat populations in this region.

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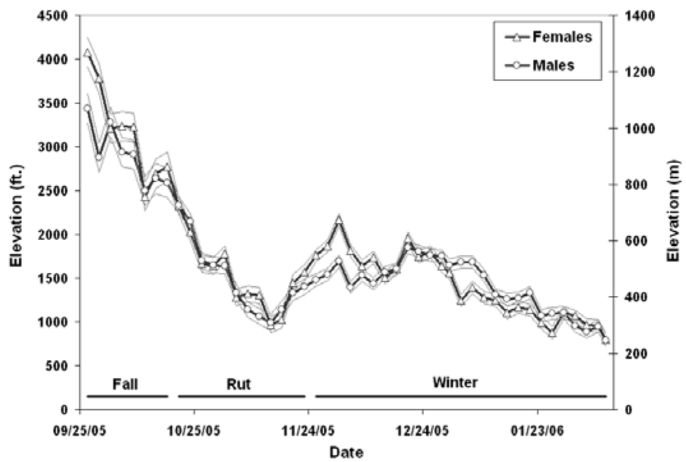

Figure 8. Mean daily elevation for male and female mountain goats between September 27, 2005 and February 10, 2006. Mean ± 95. % confidence intervals.

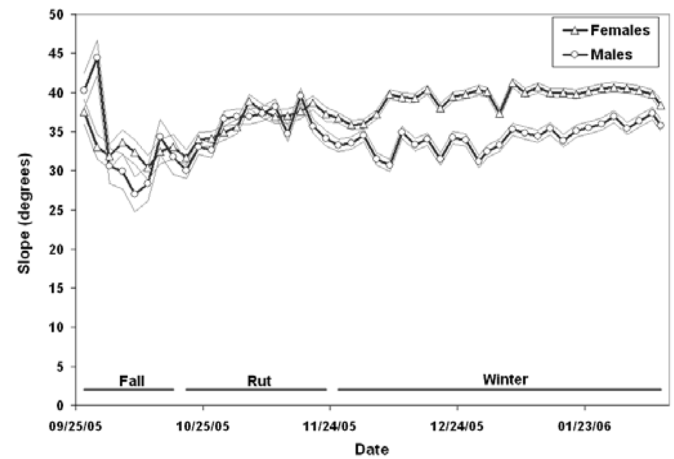

Figure 9. Mean daily slope used by male and female and mountain goats between September 27, 2005 and February 10 2006. Mean ± 95% confidence intervals.

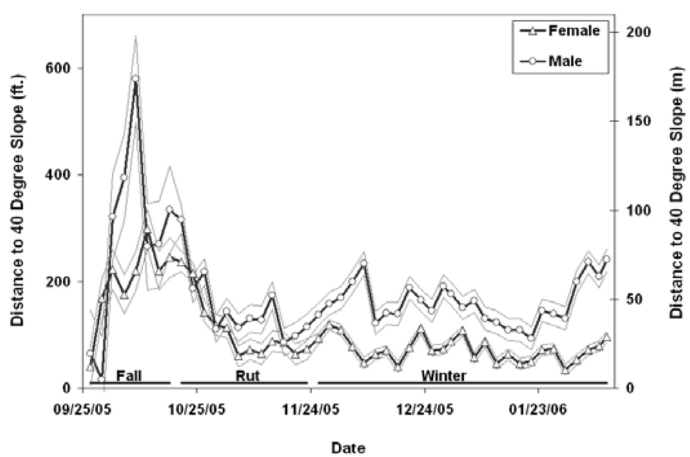

Figure 10. Mean daily distance to cliffs for male and female mountain goats between September 27, 2005 and February 10, 2006. Mean ± 95% confidence intervals..

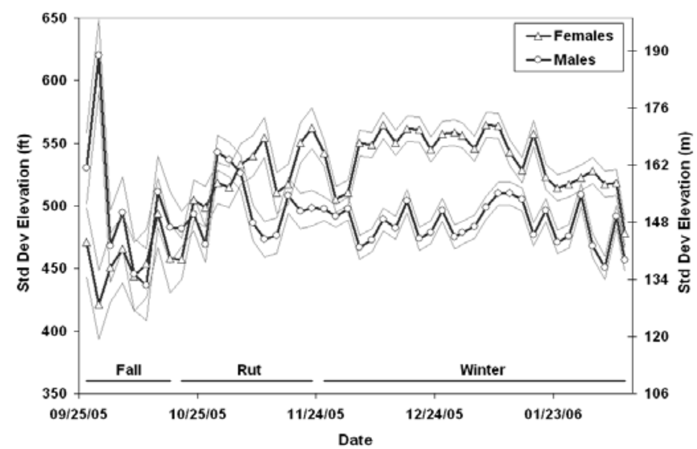

Figure 11. Mean daily terrain ruggedness used by male and female mountain goats between September 27, 2005 and February 10, 2006 Mean ± 95% confidence intervals.