Seasonal altitudinal movements are common among cervids such as roe deer (Capreolus capreolus; Mysterud 1999, Mysterud et al. 2001), elk (and red deer; Cervus elaphus; Morgantini and Hudson 1988, Poole and Mowat 2005), mule deer (Odocoileus hemionus; Nicholson et al. 1997, Poole and Mowat 2005, Sawyer et al. 2005), and sika deer (Cervus nippon; Igota et al. 2004) and Caprinae such as ibex (Capra ibex; Francisci et al. 1985, Parrini et al. 2003, Grignolio et al. 2004), bighorn sheep (Ovis canadensis; Festa-Bianchet 1988), chamois (Rupicapra rupicapra; Hamr 1985, Lovari et al. 2006), and mouflon (Ovis aries; Gonzalez 1985), as well as mountain goats (Oreamnos americanus; e.g., Rideout 1974, Chadwick 1983, Nichols 1985, Côté and Festa-Bianchet 2003, White 2006). Many altitudinal movements in these species are migratory in that distinct ranges are used during different seasons and are generally to enhance access to high quality food and to reduce predation risk (Festa-Bianchet 1988, Albon and Langvatn 1992, Mysterud et al. 2001, Pettorelli et al. 2007). Snow is also considered an important factor affecting altitudinal movements because it incurs higher energetic costs for locomotion and covers forage (Sweeney and Sweeney 1984, Dailey and Hobbs 1989, Nicholson et al. 1997, Parrini et al. 2003, Luccarini et al. 2006). Consequently, mountain goats selected terrain with snow-shedding characteristics in winter and avoided chest-deep snow, and altitudinal movements were related to amount of snow (Rideout 1974, 1977; Smith 1977).

Other authors have defined seasons by fixed dates (e.g., Parrini et al. 2003, Igota et al. 2004, Lovari et al. 2006, Luccarini et al. 2006), departure from seasonal ranges (Nicholson et al. 1997, Mysterud 1999, Sawyer et al. 2005), and periods of high movement rate (Nicholson et al. 1997, Johnson et al. 2002, Taylor et al. 2006). Fixed dates fail to account for interannual differences in ecological conditions, departure from seasonal ranges can only be used if ranges are discrete and are ambiguous when movements are temporary (Stevens 1983, Festa-Bianchet 1988, Nicholson et al. 1997, Rice 2006), and periods of greatest movement may reflect habitat patch distribution or weather events rather than seasonal movements per se.

Because there is potential for considerable variation temporally, geographically, and among individuals in their response to these factors affecting altitudinal movement, my objectives were to 1) delineate summer and winter elevations used by mountain goats based on altitudinal movements, 2) determine seasonal timing and patterns of altitudinal movements, and 3) determine if there are gender- and age-related differences in seasonal patterns of altitudinal movements.

STUDY AREA

In the Cascade Mountain Range, mountain goats typically inhabited elevations between 600 m and 2,400 m. Topography extended as high as 4,267 m on several volcanic peaks, but most terrain was below 2,100 m.

On the western slope of the Cascade Range, precipitation ranged from 1,300 mm to 3,600 mm, mostly during October to June, and precipitation ranged from 500 mm to 3,040 mm on the eastern slope (McNab and Avers 1994). Snow accumulation in the Cascades varied greatly with elevation, aspect, and among years as was evident from example accumulation records from Snotel sites (Fig. 1; Natural Resources Conservation Service 1997).

METHODS

I captured 45 mountain goats in the Cascade Mountain Range in Washington State (Fig. 2; Rice and Hall 2007). All captures were in compliance with Washington Department of Fish and Wildlife Policy on Wildlife Restraint or Immobilization (M6003). I fitted captured mountain goats

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with Global Positioning System (GPS) tracking collars (Vectronic GPS Plus-4; Vectronic Aerospace, Berlin, Germany), usually with a 3-hour fix interval (I used rotating 5-hr intervals for 7% of the fixes).

Of the 45 collared mountain goats, I selected those that had fix records of ≥9 months of data. I removed outlier fixes by visually screening locations beyond the continuous distribution of distances of all fixes from the median for each individual and by visual inspection of travel paths (usually single fixes separate from temporal clusters). Because I was primarily interested in altitudinal movement as a response to seasonal changes in environment and habitat, and visits to mineral licks often involved excursions to low elevations that were not driven by these factors, I also removed fixes evidently associated with visits to mineral licks outside the usual range of the individual (fixes over 2–3 days several kilometers from all other fixes). I assigned each remaining fix an elevation by extraction from a 10-m digital elevation model (U.S. Geological Survey 1993) using ArcGIS 9.1.

As a framework for this analysis, I defined a season-year as the calendar year for summer, and the calendar year of the preceding summer for winter (e.g., Jan 2004 was in season-yr 2003), and stipulated that a season is a contiguous series of dates and only one summer and one winter were possible in any season-year. Furthermore, due to local spatial and temporal heterogeneity, seasons may be different among individuals and may vary among years due to differing weather patterns.

Terrain and habitat impose practical limits on the range of

Figure 1. Snow-water equivalent (snow depth is approx. snow-water equivalent × 3) over 4 winters at 4 Snotel sites in the Cascade Range in Washington, USA, 2002–2006, representing high elevation northern (Miners Ridge, 1,890 m) and southern (Corral Pass, 1,929 m) conditions and low elevation northern (Elbow Lake, 975 m) and southern (Tinkham Creek, 936 m) conditions.
elevations available to an individual mountain goat. For example, some mountain goats occupy mountain ridges with a maximum possible local elevation. For others, maximum elevations were constrained by transitions to permanent snow and ice. Minimum elevations were limited by habitat with suitable escape terrain. Because of this, I treated each animal individually. Also, the distribution of elevations used by an individual may be truncated where these limits were reached. Although distribution of elevations varied greatly among individuals, it generally could not be assumed to be normal but was not highly skewed. I chose the Van der Waerden Test (Conover 1980) for statistical evaluations for gross habitats by date with the seasonal classifications. For each point, I extracted the vegetation cover according to the Zone 1 coverage map (Sanborn 2007) reduced to 6 classes: bare, grassland, parkland, woodland, forest, and shrubland based on Comer et al. (2003). Bare cover was primarily North Pacific Montane Massive Bedrock Cliff and Talus, North American Alpine Ice Field, North Pacific Alpine and Subalpine Bedrock and Scree, and Rocky Mountain Alpine Tundra/Fell-field/Dwarf-shrub. Grassland was primarily North Pacific Alpine and Subalpine Dry Grassland. Parkland was primarily Northern Rocky Mountain Subalpine Dry Parkland. Woodland was primarily East Cascades Mesic Montane Mixed-Conifer Forest and Woodland and Rocky Mountain Subalpine Dry-Mesic Spruce–Fir Forest and Woodland. Forest was primarily North Pacific Dry-Mesic Silver Fir–Western Hemlock–Douglas fir Forest, Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest, and North Pacific Mountain Hemlock Forest. Shrubland was primarily Transitional Vegetation Short Shrub, Inter-Mountain Basins Big Sagebrush Steppe, and North Pacific Avalanche Chute Shrubland.

For each mountain goat for each day, I computed the expected frequency of occurrence for each cover class as the number of fixes each day (row total) times the total number of fixes for each class (column total) divided by the total for each mountain goat (grand total):

$$\text{Exp}_{ij} = \sum_{i=1}^{\text{classes}} \sum_{j=1}^{\text{days}} n_{ij} / \left( \sum_{i=1}^{\text{classes}} \sum_{j=1}^{\text{days}} n_{ij} \right)$$

where $\text{Exp}_{ij}$ is the expected frequency of occurrence in the $i$th cover class on the $j$th day, classes is the number of cover classes, days is the number of days in a year, and $n_{ij}$ is the number of GPS fixes recorded in the $i$th cover class on the $j$th day. I then computed the mean deviation from expected (obs – expected) for each day of the year and cover class. To more clearly illustrate the change in deviations from expected through the year, I fitted a local polynomial regression to the daily mean deviations with R (v2.3.0; R Foundation for Statistical Computing, Vienna, Austria; <http://www.r-project.org/>) package KernSmooth using the plug-in bandwidth selector (dpill) and compared these values with the proportion of fixes classified as summer for each day of the year.

Figure 2. Minimum convex polygons for Global Positioning System fixes showing the locations of the 42 mountain goats in Washington, USA (26 Sep 2002 to 22 Sep 2006), with >9 months tracking.
Based on the summer and winter start and end dates I computed additional statistics: duration of summer and winter (months), median elevations for summer and winter and their difference, and distance between summer and winter median centroids. I estimated overlap of summer and winter elevations by estimating the one-dimensional kernel density (Silverman 1986, Jones et al. 1996) of elevations for each mountain goat and season with the R package KernSmooth using the plug-in bandwidth selector (dpik).

I transformed kernel densities to sum to one and took the overlap as the sum of the minimum of the summer and winter transformed densities. For each mountain goat, I also calculated the 5th and 95th percentiles of the elevation distributions, their differences being the 90% ranges.

I classified individual mountain goats as (ad) female, dispersing male, and nondispersing male. Dispersing males were those that moved long distances (>24 km between first and last fix) in a nonseasonal manner and did not return to previously occupied areas. Nondispersing males occupied consistent areas among successive seasons (as did females). I aged mountain goats by counting horn annuli at time of capture (Smith 1988).

To examine effects of these categories on season and elevation I used a multivariate equivalent of the Van der Waerden Test by transforming independent variables to normal percentiles for use in a least-squares analytic framework (Conover 1980) using an $\alpha$ level of 0.05. I included individual mountain goat as a random effect in this analysis due to repeated measures on individuals across years and I considered no interactions due to the low sample size.

Where effects were found, I used records from 23 Snotel stations of snow water equivalent (related to snow depth) and temperature to look for comparable differences to assess the extent that these differences could be explained by weather conditions. Snotel stations I selected were within rectangles defined by latitude and longitude limits of 4 regional groups of mountain goat collar GPS fixes.

**RESULTS**

Of the 42 mountain goats with GPS records >9 months, one covered 1 year, 16 covered 2 years, 23 covered 3 years, and 2 covered 4 years. Number of fixes per mountain goat ranged from 979 to 5,340 (median $\bar{x} = 3,295$, 25th percentile $= 2,349$, 75th percentile $= 4,449$). Thirty-one were females, 9 were nondispersing males, and 2 were dispersing males.

Estimated ages during years of tracking were typically intermediate ($\bar{x} = 4.8$ yr, SD = 1.5 yr) with the bulk of the sample being for ages 3–6 years (86 summer starts and 67 winter starts) with less representation for younger (1–2 yr of age, 4 summer starts and 4 winter starts) and older (7–10 yr of age) animals (11 summer starts and 8 winter starts). Age was undetermined for animals covering 6 summer starts and 4 winter starts.

Of the 197,285 fix attempts by collars on the 42 mountain goats, 143,296 were successful, and 141,759 of these were not obvious errors (beyond the continuous distribution of distances from the median location). Examination of fix plots identified an additional 193 outliers, which I removed along with 324 fixes associated with visits to known or suspected mineral licks outside the individual animal's...
normal range. Of the remaining 140,890 fixes I used in the analysis, 80.1% were 3-dimensional fixes.

Elevations recorded ranged 335–3,089 m and varied considerably among individuals (Fig. 3). Median elevations were 1,037–2,171 m and the interquartile ranges were 119–939 m. Short-term fluctuations in elevation were considerable, but even mountain goats using low ranges of elevation showed a tendency for higher elevation records to be in summer months and lower elevation records to be in winter months (e.g., Fig. 4).

Across all mountain goats and years, proportion of fixes classified as summer increased beyond 0.5 on 31 May, at almost the same time selection for bare terrain and parkland changed from negative to positive and selection for forest, grassland, and shrubland changed from positive to negative (Fig. 5). In the fall, transitions were more complex, with proportion of fixes classified as summer declining below 0.5 during a stable region of selection for bare terrain, slightly before selection for parkland changed from positive to negative, slightly after selection for grassland and shrubland changed from negative to positive, and about a month before selection for forest changed from negative to positive.

The iterative search designated start dates with a median of 6 June for summer and 19 October for winter across all individuals and years (n = 66 and 83, respectively), with a median duration of summer of 4.60 months and 7.32 months for winter (n = 41 and 66, respectively). Individuals varied considerably from these medians (Fig. 6).

Summer median elevations for individual mountain goats had a median of 1,591 m, which for winter was 1,353 m. Whereas many summer medians were 1,500–1,599 m, these ranged from 1,200 m to 2,257 m. Winter medians were more widely dispersed between 808 m and 2,103 m (Fig. 6). The difference between summer and winter medians also varied widely (median = 316 m, range 60–770 m; Fig. 6). The upper and lower extent of elevations also varied across individuals with the fifth percentile having a median of 1,101 m (range 569–1,757 m) and the 95th percentile having a median of 1,835 m (range 1,435–2,613 m; Fig. 6). Similarly, the central 90% range varied from 322 m to 1,562 m (median = 754 m; Fig. 6).

The proportional elevation overlap between summer and winter varied widely (Fig. 6) with a median of 0.39 (range 0.09–0.84). The nature of overlap also varied among individuals with some showing distinct peaks for each season that overlapped little (e.g., 050GRM; Fig. 7), somewhat (e.g., 045MRF), or highly (e.g., 024KRF). Other individuals showed a peak of elevation use for summer, but
not winter (e.g., 003SCF; Fig. 7), and vice versa (e.g., 047LMF) or a complex distribution of elevation use (e.g., 035NRF). Median distance between summer and winter median centroids was 1.8 km (range 0.1–19.8 km), most (83%) being <5 km (Fig. 6).

The date of the start of summer was affected by sex-dispersal class ($P = 0.049$; Fig. 8). Median date that females started summer was 14 days earlier than that of non-dispersing males (5 Jun and 19 Jun, respectively; Fig. 8). Median start of summer was much earlier for dispersing males (23 Apr) but is based on a small sample size for this group (5 summers for 2 individuals).

The date of the start of winter was affected by season-year ($P < 0.001$; Fig. 8). Median dates for 2003, 2004, and 2005 were 1 November, 18 October, and 17 October, respectively. The median date for 2002 of 17 December was based on only 2 individuals. Summer median elevation was not affected by any of the mountain goat classes considered ($P > 0.100$; Fig. 8). Distance between summer and winter centroids varied by sex-dispersal class ($P = 0.013$; Fig. 8) with a median distance of 1.4 km for females, 3.4 km for nondispersing males, and 11.5 km for dispersing males ($n = 2$).

Other measures (winter start, winter duration, summer duration, summer median, winter median, median difference, 90% range, overlap) were not related to sex-dispersal class ($P > 0.100$), nor were summer start, winter duration, or summer duration related to season-year, and age was not related to any of the measures ($P > 0.100$).

Metrics of altitudinal movements of mountain goats were often related. For instance, winter duration was correlated with summer and winter start dates (Table 1), which is not very informative. Other relationships can help in our understanding of altitudinal movements of mountain goats. Summer medians were correlated with winter medians. The difference in summer and winter median elevations was not correlated with the summer median elevation but was correlated with winter median elevation (Table 1). Notably, distance between summer and winter centroids was not correlated with any of the other measures.

**DISCUSSION**

This study area encompassed nearly all suitable mountain goat habitat in the Cascade Range so our results can be taken to represent the range of responses for the entire region. Nevertheless, the Cascade Range in Washington represents the southern limit of the distribution of mountain goats (Côté and Festa-Bianchet 2003) and patterns may be different in more northern coastal locations (BC and AK) and interior locations (the Rocky Mountains of Canada and the United States).

Visual inspection of the distribution of the measures I used to evaluate altitudinal movements (Fig. 6) showed a considerable range of values indicating a wide range of response among individuals. For the measures that most clearly define seasonal altitudinal migration, there is little evidence of central tendency (Fig. 6). Nor is there evidence in these distributions of a bimodal pattern that would be expected if individuals were naturally partitioned into migratory and nonmigratory groups. Rather, there is a continuous response among individuals in the degree of their altitudinal migration.

Distributions of summer and winter start dates (medians of 6 Jun and 19 Oct, respectively) exhibited several outliers (Fig. 6). Those at the start of summer included one of the dispersing males (009GRM), where he had his highest elevations in the spring of 2004 (around 2,650 m). These locations were on the flanks of Mt. Adams and were the
Figure 6. Frequency distributions of measures of seasonal altitudinal movements of mountain goats in Washington, USA (26 Sep 2002 to 22 Sep 2006).
highest locations for any of the collared mountain goats. Two other summer start date outliers occurred for females in 2006, when Snotel data showed that snow melt-off was 4–5 weeks earlier than other years. There were 2 extremely late values for the start of winter (Fig. 6). These were also in 2006, when there was little snow until mid-March, so some of these extreme values are associated with unusual movements by an individual or associated with low snow cover depth and duration, but some may be considered estimation error.

Notably, summer start dates did not vary consistently by season-year. Given that weather and snow cover vary and hence snow melt-off and vegetative resurgence vary greatly among years in the Cascade Range (Mote et al. 1999), parturition, predator avoidance, or possibly some other factor evidently determined when females returned to higher elevations.

Winter start dates did vary among years (Fig. 8) with medians of 1 November, 18 October, and 17 October for 2003–2005, respectively. Although patterns of snowfall vary greatly in the Cascade Range, records from Snotel sensors within mountain goat range typically recorded first snow accumulation later in 2003 (1 Nov) than in 2004 and 2005 (21 and 24 Oct, respectively), indicating a rough relative correspondence between initial snow accumulation and the start of winter. A detailed examination of relationships between date, elevation, and snow cover is beyond the scope of my analysis, but would further our understanding of the relationship between altitudinal movements of mountain goats and snow cover. Mountain goats apparently showed a similar pattern snow-induced synchrony in fall movements in Montana (Smith 1977) and eastern British Columbia (Poole and Heard 2003).

The correlation of the difference between summer and winter median elevations with winter median elevation, but not with summer elevation (Table 1), indicated that greater altitudinal movement was a consequence of utilization of lower elevations during winter and not due to utilization of higher elevations during summer.

It is noteworthy that the distance between summer and

Figure 7. Example distributions of elevation use (kernel densities) by season for 6 mountain goats in Washington, USA (26 Sep 2002 to 22 Sep 2006). I transformed kernel densities to sum to one for each season for each individual.
winter centroids showed almost no relationship with the measures of altitudinal movement (Table 1). Horizontal movements have been the typical focus of seasonal movements of animals in mountain environments, including ibex (Parrini et al. 2003, Grignolio et al. 2004), mule deer (Nicholson et al. 1997), roe deer (Mysterud 1999) sika deer (Igota et al. 2004), elk and red deer (Hebblewhite et al. 2006, Luccarini et al. 2006) and coyotes (Canis latrans; Gantz and Knowlton 2005), even when altitudinal movement is considered to be the primary characteristic of these movements (Lovari et al. 2006; chamois). Using horizontal distance would appear to be a poor measure upon which to base analysis of this phenomenon and may be misleading.

Although the extent of horizontal movement has definite implications for conservation and management of these species and their habitats, in mountain environments elevation is closely tied to meteorological conditions, plant communities, and plant phenology and thus has greater ecological significance than distance. Therefore, I considered horizontal movement to be a consequence of altitudinal movement, not the reverse. Although longer distance movements incur greater energetic costs, energetic expenditures for altitudinal movements are also substantial (Dailey and Hobbs 1989).

Some mountain goats in my study showed little altitudinal movement, whereas other mountain goats showed considerable altitudinal movement. Likewise some moved several kilometers in the course of seasonal movements, others quite little. Also, some individuals moved frequently between elevations within the range they used, whereas others had more discrete distributions of elevation use (Fig. 7). In the latter case, altitudinal movements may be considered primarily facultative (Hahn et al. 2004), in response to conditions varying over short durations. To some extent, seasonal movements (altitudinal migration) may be considered long-term facultative movements, merely being a long-term response to a long-term change in conditions. In mountain goats, the distinction between facultative altitudinal movements and altitudinal migration is far from clear. Presumably, costs and benefits of remaining at a given elevation and costs and benefits of traveling to a new elevation in response to varying conditions are balanced over a wide range of conditions among years, locations, and individuals. Seasonal movement decisions are therefore more appropriately considered in the context of how much, rather than yes or no. The yes or no are instead a special case

### Table 1. Pearson correlation coefficients for median values among individuals for mountain goat altitudinal movements in Washington, USA (26 Sep 2002 to 22 Sep 2006).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Start date</th>
<th>Duration</th>
<th>Elevation</th>
<th>Elevation difference</th>
<th>90% range</th>
<th>Overlap</th>
<th>Distance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Summer</td>
<td>Winter</td>
<td>Summer</td>
<td>Winter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer start date</td>
<td>0.011</td>
<td>0.654</td>
<td>0.645</td>
<td>0.560</td>
<td>0.103</td>
<td>0.235</td>
<td>0.189</td>
</tr>
<tr>
<td>Winter start date</td>
<td>0.016</td>
<td>0.645</td>
<td>0.654</td>
<td>0.560</td>
<td>0.168</td>
<td>0.186</td>
<td>0.091</td>
</tr>
<tr>
<td>Summer duration</td>
<td>0.654</td>
<td>0.645</td>
<td>0.875</td>
<td>0.875</td>
<td>0.294</td>
<td>0.054</td>
<td>0.315</td>
</tr>
<tr>
<td>Winter duration</td>
<td>0.770</td>
<td>0.560</td>
<td>0.856</td>
<td>0.875</td>
<td>0.160</td>
<td>0.039</td>
<td>0.306</td>
</tr>
<tr>
<td>Summer elevation</td>
<td>0.103</td>
<td>0.168</td>
<td>0.294</td>
<td>0.160</td>
<td>0.011</td>
<td>0.826</td>
<td>0.012</td>
</tr>
<tr>
<td>Winter elevation</td>
<td>0.235</td>
<td>0.186</td>
<td>0.054</td>
<td>0.039</td>
<td>0.826</td>
<td>0.555</td>
<td>0.395</td>
</tr>
<tr>
<td>Elevation difference</td>
<td>0.086</td>
<td>0.091</td>
<td>0.315</td>
<td>0.306</td>
<td>0.011</td>
<td>0.555</td>
<td>0.719</td>
</tr>
<tr>
<td>90% elevation range</td>
<td>0.189</td>
<td>0.092</td>
<td>0.381</td>
<td>0.373</td>
<td>0.012</td>
<td>0.395</td>
<td>0.719</td>
</tr>
<tr>
<td>Elevation overlap</td>
<td>0.288</td>
<td>0.012</td>
<td>0.286</td>
<td>0.265</td>
<td>0.044</td>
<td>0.394</td>
<td>0.0765</td>
</tr>
<tr>
<td>Horizontal distance</td>
<td>0.035</td>
<td>0.045</td>
<td>0.003</td>
<td>0.009</td>
<td>0.062</td>
<td>0.081</td>
<td>0.052</td>
</tr>
</tbody>
</table>
of a more generalized response that is seen when suitable conditions (i.e. habitat) are spatially separated.

MANAGEMENT IMPLICATIONS

Land managers need to recognize that seasonal altitudinal movements of mountain goats are highly variable. Consequently, the management needs of each population must be considered separately, and consequences of these movements for forest practices (e.g., logging, road and trail construction, and management of recreation) that can impact mountain goat habitat will be specific to each setting.

The general perception of mountain goats as an inhabitant of the alpine and subalpine zones would appear to be highly biased by the frequency of summer observations. In reality, mountain goats typically spent the majority of the year in shrubland, forests, and grasslands. Much of our knowledge of mountain goats is based on research conducted during the summer, but managers should encourage investigations emphasizing mountain goats during winter and in winter habitats.

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