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Recent Population Trends of Mountain Goats in the Olympic Mountains, Washington

Abstract

Mountain goats (*Oreamnos americanus*) were introduced in Washington's Olympic Mountains during the 1920s. The population subsequently increased in numbers and expanded in range, leading to concerns by the 1970s over the potential effects of non-native mountain goats on high-elevation plant communities in Olympic National Park. The National Park Service (NPS) transplanted mountain goats from the Olympic Mountains to other ranges between 1981 and 1989 as a means to manage overabundant populations, and began monitoring population trends of mountain goats in 1983. We estimated population abundance of mountain goats during 18-25 July 2011, the sixth survey of the time series, to assess current population status and responses of the population to past management. We surveyed 39 sample units, comprising 39% of the 59,615-ha survey area. We estimated a population of 344 ± 72 (90% confidence interval [CI]) mountain goats in the survey area. Retrospective analysis of the 2004 survey, accounting for differences in survey area boundaries and methods of estimating aerial detection biases, indicated that the population increased at an average annual rate of 4.9% since the last survey. That is the first population growth observed since the cessation of population control measures in 1990. We postulate that differences in population trends observed in western, eastern, and southern sections of the survey zone reflected, in part, a variable influence of climate change across the precipitation gradient in the Olympic Mountains.

Key Words: population abundance, *Oreamnos americanus,* aerial survey, sightability, climate variation

Introduction

Mountain goats were introduced in the Olympic Mountains during the 1920s prior to the establishment of Olympic National Park (Houston et al. 1994a). Over the next several decades, the population increased in size and expanded throughout the Olympic Mountains leading to management concerns by the mid-1970s over the potential effects of overabundant mountain goats on endemic plants, soils, and erosion in high-elevation plant communities of Olympic National Park (National Park Service 1995). In 1983, the NPS conducted the first aerial survey to estimate mountain goat population size throughout the Olympic Mountains, returning an estimate of 1175 ± 171 (Standard Error [SE]) mountain goats (Houston et al. 1986). Other localized ground and aerial surveys conducted prior to 1983 did not provide comprehensive population estimates (Houston et al. 1994a).

During the early 1980s, the NPS transplanted mountain goats from Olympic National Park to other ranges throughout several western states to reduce the population (Houston et al. 1991a). From 1981 through 1989, 407 goats were captured by the NPS and removed (Houston et al. 1994b:195). An additional 119 mountain goats were legally killed

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during sport hunting seasons outside the park and three known illegal kills occurred within the park from 1983-1997. The aerial capture and removal program was halted in 1990 due to human safety concerns associated with aerial capture operations (Houston et al. 1994b). No mountain goats have been transplanted from the Olympic Mountains since 1990, and no mountain goats were legally harvested in the Olympic Mountains between 1997-2011.

Beginning with the first comprehensive survey conducted in 1983, the mountain goat population has been estimated in the Olympic Mountains every three to seven years to assess population status and responses to past management actions. The second survey, conducted in July 1990 following the cessation of NPS capture and transplant operations, produced an estimate of 389 ± 106 (SE) goats (Houston et al. 1991b). Subsequent surveys were conducted in 1994, 1997, and 2004, during a period in which no goats were removed by NPS managers. Here we report results from a sixth survey conducted in 2011, estimate population growth since 2004, and retrospectively examine spatial variation in population trends since last reported in 1991 (Houston et al. 1991b). This survey was the first since we developed a sightability model for use in estimating and correcting detection biases in aerial mountain goat surveys in western Washington (Rice et al. 2009).

Study Area

The survey encompassed high-elevation mountain goat habitat throughout the Olympic Mountains, of which about 87% is within Olympic National Park, and 13% in the adjoining Olympic National Forest (Figure 1). The Olympic Mountains rise abruptly from the coastal plains and foothills of

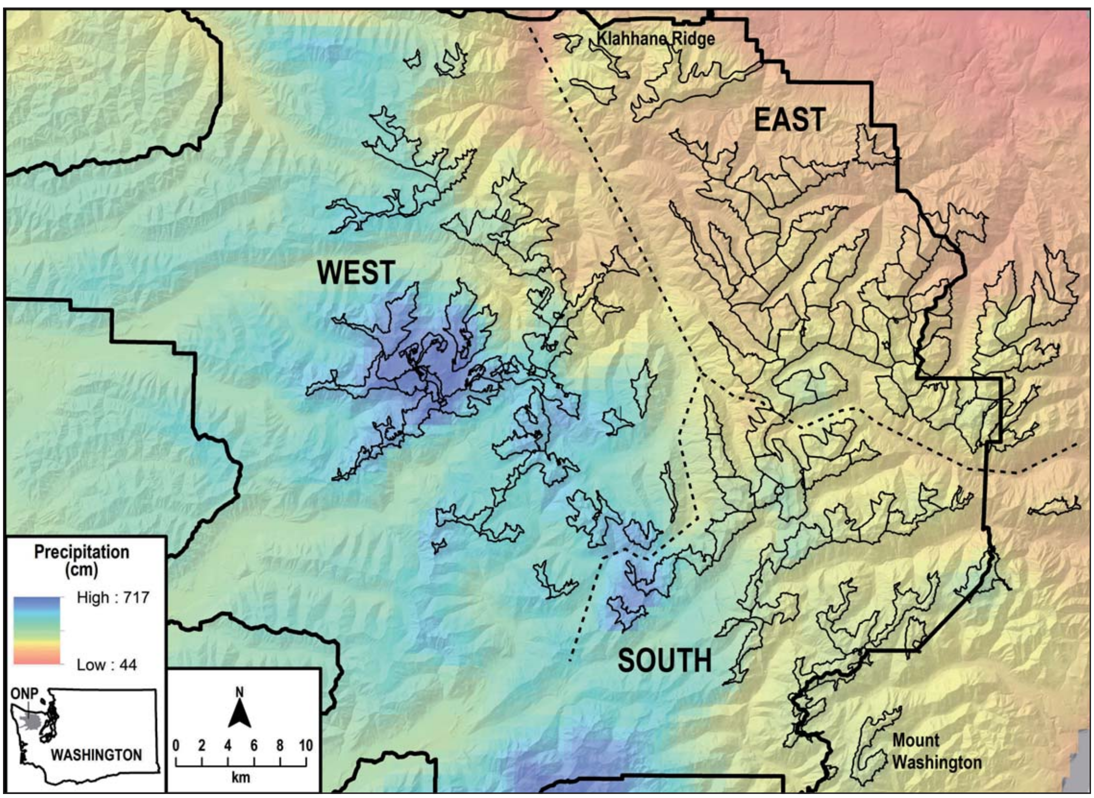

Figure 1. Mean annual precipitation in the Olympic Mountains, 1971-2000. The bold solid line represents the boundary of Olympic National Park (ONP), whereas the dashed lines delineate western, eastern, and southern sections of the Olympic Mountains. The medium solid lines delineate the survey unit boundaries (>1425 m in elevation in areas of suitable habitat). (Data source: PRISM Climate Group, Oregon State University, 1971-2000 precipitation normals; http://prism.oregonstate.edu)

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the Olympic Peninsula, culminating in Mount Olympus, the highest peak at 2430 m elevation, and 37 other major peaks exceeding 2130 m elevation, all within about 50 km of the sea. The Olympic Mountains are noted for steep gradients in elevation, vegetation, and precipitation within a context of highly convoluted topography and landforms (Tabor 1987, Henderson et al. 1989).

The Olympic Peninsula has both the wettest climate in the conterminous U.S. on the western slopes of the Olympic Mountains, which bear the brunt of the prevailing Pacific storms, and some of the driest climate of the Pacific Coast (outside of Southern California) in the mountains' rain shadow (Figure 1). Precipitation increases with elevation along the western slopes, reaching a peak in the interior mountains, and declining sharply in the leeward northeastern Olympic Mountains. Winter precipitation falls primarily as rain in lowlands below about 300-500 m and primarily as snow above 1000 m elevation. Median annual precipitation assessed across the survey zone was 174 (range 41-320), 266 (range 126-582), and 393 (range 136-717) cm in the eastern, southern, and western sections of the survey zone, respectively (Figure 1).

During 2011, snow water equivalent (SWE) measured on 1 April was approximately 167% of the 30-year normal (1971-2000). Late-season snows continued to augment the snowpack in April, resulting in a snowpack approximately 225% of normal on 1 May. Steep terrain was largely free of snow in July when the survey was conducted, particularly on southern aspects and in the drier northeast. Shaded areas such as north- and east-facing basins and forested areas, however, were predominately snow covered in much of the survey area.

Methods

Sampling

The survey zone used for previous mountain goat surveys in the Olympic Mountains, based on prior studies of mountain goat distribution, included all lands free of glacial ice above 1520 m (5000 ft) (Houston et al. 1986, 1991b). We made two adjustments to the survey zone for the 2011 survey. First, for unavoidable logistical reasons we omitted one 452-ha sample unit from the sampling frame in 2011 (Mount Washington Unit, Figure 2). Second, based on recent movement studies of GPS-collared mountain goats (Jenkins et al. 2011), we decreased the lower elevation boundary of the sampling frame to 1425 m in areas where suitable escape terrain comprised at least 50% of the elevation band between 1425 and 1520 m elevations. We defined escape terrain as area <111 m from any 25×25-m (0.0625 ha) raster cell classified as rock and with slope >33% (Olympic National Park Geographic Information System, Pacific Meridian Resources 1996). We chose the 111-m threshold because 90% of all locations of GPS-collared mountain goats below 1520 m in elevation were less than 111 m from escape cover during the July sampling window. The 50% classification was subjectively chosen based on cost and logistical considerations to minimize survey effort over relatively large areas of low quality habitats. The addition of lower elevations in 2011 increased the survey zone 18% from about 50,567 ha in 2004 (without the omitted survey unit) to the current 59,615 ha.

We partitioned the survey zone into a 2041-ha Klahhane Ridge Unit and 108 sampling units ranging in size from 220-712 ha (Figure 2). These were the same sampling units as delineated in previous surveys, but we adjusted survey unit boundaries to accommodate the addition of lower elevations to the survey zone and to increase consistency in sample unit sizes. The Klahhane Ridge Unit was the site of intensive research and population reductions during the 1970s and 1980s and has been surveyed regularly in all previous surveys. We surveyed the Klahhane Ridge Unit and all the high-density survey units in their entirety. Remaining sampling effort was apportioned among low and medium density strata using standard optimal allocation methods (Cochran 1977) based on sampling variances from the most recent previous survey (Happe et al. 2005). Sampling strata were defined as:

High density: Units were assigned to this stratum if we expected to find 10 or more mountain goats per 500 ha based on previous surveys and field observations. The high-density stratum comprised 10 sample units covering 7606 ha.

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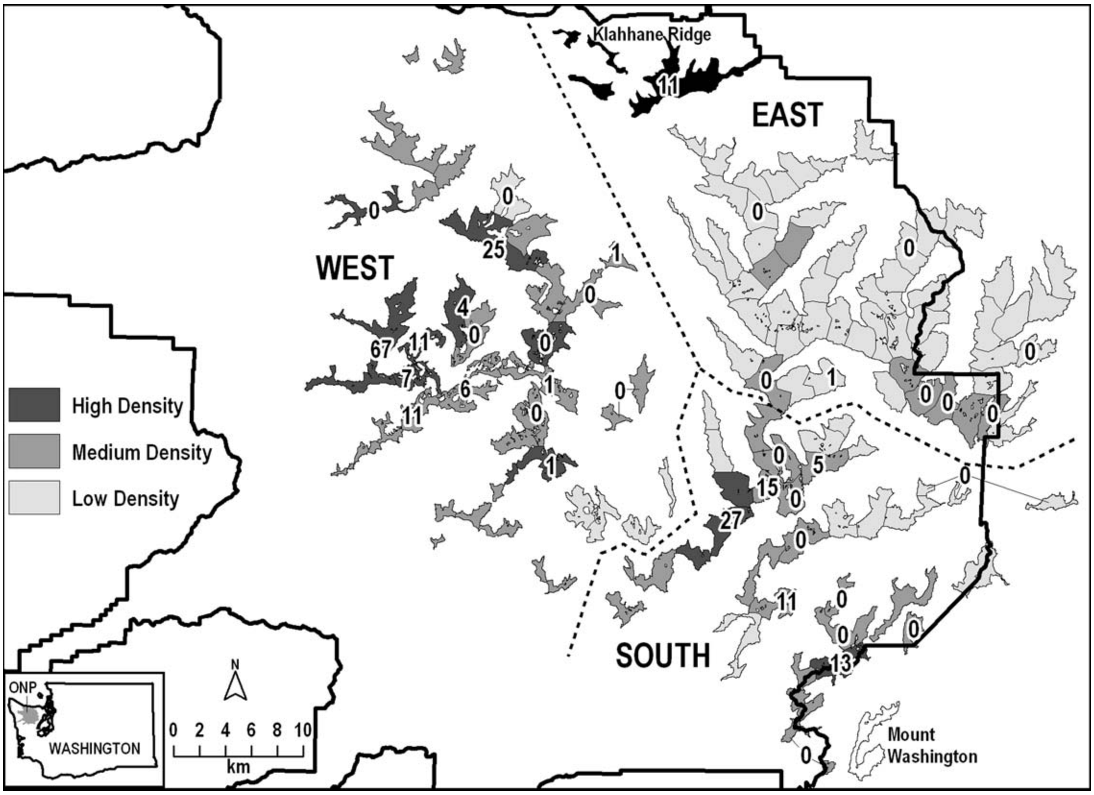

Figure 2. Sampling strata, units surveyed, and number of mountain goats counted during mountain goat surveys in the Olympic Mountains, Washington, July 18-25, 2011. Numbers show the observed count of mountain goats in the surveyed units. The bold solid line represents the boundary of Olympic National Park (ONP), whereas dashed lines delineate western, eastern, and southern sections of the Olympic Mountains.

Medium density: Units were assigned to this stratum if we expected one to nine mountain goats per 500 ha. The medium-density stratum comprised 20,599 ha in 41 sample units ranging in size from 220 to 712 ha, from which we randomly sampled 22 units (54%) for surveys.

Low density: Units were assigned to this stratum if we expected no mountain goats. The low-density stratum comprised 29,369 ha in 56 sample units ranging in size from 363 to 659 ha. We randomly selected six low-density sample units (11%) for surveys.

Aerial Surveys

Aerial survey procedures were similar to those described previously (Houston et al. 1986, 1991b). Surveys were conducted within about four hours of dawn by a pilot and three-person crew aboard an MD-500D helicopter. We counted mountain goats within the selected survey units by flying multiple contours about 100 m from the terrain (i.e., above flat terrain or horizontally away from vertical terrain) at elevations spaced 90-150 m apart vertically. Flight speed was maintained between 56 and 72 km h^{-1} (35-45 mi h^{-1}). Lower elevations of each unit were flown first and then the helicopter progressively worked upslope until the entire unit was searched. We searched adjacent units sequentially to minimize the chance of double counting mountain goats that moved across sample unit boundaries between surveys. We used a GPS unit aboard the helicopter to assist with navigation, mapping flights, and recording locations of mountain goat observations.

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Upon spotting mountain goats, we recorded the total number within the group, number of young of the year, the percentage of vegetation cover capable of obscuring a mountain goat within a 10-m buffer around the group (0, 1-25, 26-50, 51-75, 76-100), and whether terrain obstruction was present within a 10-m buffer around the group when it was first seen. We defined terrain obstruction, a binary variable (equal to 1 if present and 0 otherwise), as any landform potentially capable of obscuring an aerial view of a mountain goat. We treated percent vegetative cover as a continuous variable and used mid-points of the observed class intervals to approximate the value for each group. The group size, vegetation, and terrain obstruction covariates were used to estimate group-specific detection probabilities for bias correction (Rice et al. 2009). We also recorded whether each observed group was in the newly added lower elevation zone within each survey unit (i.e., between 1425 and 1520 m elevations) to facilitate comparisons of abundance estimates between years.

Population Abundance

We estimated mountain goat abundance using the sightability modeling approach developed by Steinhorst and Samuel (1989) and the mountain goat sightability model recently developed for application in the study area (Rice et al. 2009). This approach combines counts of animals, or groups of animals, in a set of randomly sampled survey units with a model for their probability of detection. For a stratified random sample of survey units, the estimate of population size ($\hat{\tau}$) is given by:

$$\hat{\tau} = \Sigma\Sigma\Sigma \left(\frac{N_h}{n_h}\hat{\Theta}_{h,i,j}\,Y_{h,i,j}\right) \qquad (1)$$

where the sums are over strata (h), sampled survey units (i), and observed groups (j); n_h and N_h are, respectively, the number of stratum h plots in the sample and in the population; the $\hat{\Theta}$'s are estimated sightability correction factors associated with each observed group (≈ the inverse of each group's detection probability); and $Y_{h,i,j}$ gives the number of animals in the j^{th} observed group (within the i^{th} survey unit in stratum h). The best fitting sightability models all included some combination of group size, presence of terrain obstruction, and percent vegetative obstruction. As suggested by Rice et al. (2009), we used model averaged regression parameters and their unconditional variance covariance matrix to estimate group-specific sightability correction factors following Steinhorst and Samuel (1989).

Three random processes create uncertainty in the estimated abundance ($\hat{\tau}$): (1) the random sampling of survey plots; (2) random detection (and failed detection) of independent groups within surveyed plots; and (3) variation in estimation of parameters used to model sightability. Wong (1996) developed consistent (asymptotically unbiased) estimators of each of these variance components. We used code written in R (R Development Core Team, 2011; available from J. Fieberg, Minnesota Department of Natural Resources, Forest Lake, Minnesota) to estimate total abundance using the Steinhorst and Samuel (1989) estimator (eq. 1), and Var($\hat{\tau}$) using equations from Wong (1996).

Population Trends

Changes in methods used to estimate detection biases for the 2011 survey precluded direct comparison with previous population estimates. But because we recorded sightability covariates (group size, terrain obstruction, percent vegetative obstruction) during the 2004 survey, we estimated abundance for the 2004 survey using the same bias correction methods as used in 2011, and evaluated trends in population growth between 2004 and 2011.

To place the 2004 and 2011 population estimates in historical context, we also computed population indices from all counts conducted from 1983 to 2011. These indices were constructed from counts of mountain goats prior to any adjustments for detection biases. Population indices were computed using Jolly's (1969) method for stratified random samples of unequal sized sample units as outlined by Norton-Griffiths (1978) and used previously by Houston et al. (1986, 1991b). Consequently, these indices are minimum population estimates because they do not account for animals present but not seen during surveys. Moreover, the comparison of population indices over time assumes that sightability of mountain goats did not change over time. To evaluate that assumption,

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we examined trends in group size over time using a one-way ANOVA on square-root transformed group sizes (Zar 1980). We examined changes in group size because this variable is most closely associated with aerial detection probabilities (Rice et al. 2009).

In comparing 2011 population estimates and indices to all previous surveys we made the following adjustments to account for differences in survey boundaries among years: (1) all observations of mountain goats from the new survey areas added in 2011 were removed from the 2011 dataset (i.e., observations between 1425 and 1520 m elevations), (2) observations from the Mount Washington Unit, which was not surveyed in 2011, were removed from the 1983-2004 datasets. Hence, abundance estimates and indices compared among years reflected comparable land areas and numbers of mountain goats estimated on lands free of permanent snow and ice above 1520 m elevation and excluding the Mount Washington Unit (Figure 2).

We used a 2-tailed *z*-test to determine whether or not the 2004 and 2011 abundance estimates differed statistically from a null hypothesis of zero change (Thompson et al. 1998). We also estimated the instantaneous rate of exponential population growth and the average finite rate of growth from the 2004 and 2011 abundance estimates (Caughley 1977:151). Population estimates compared between 2004 and 2011 were formed using the same sightability model and, thus, were not independent. Therefore, we wrote code in R to take into account the covariance between years in the estimation of population growth rates (R Development Core Team, 2011; available from J. Fieberg, Minnesota Department of Natural Resources, Forest Lake, Minnesota).

To examine recent geographic trends in minimum population indices of mountain goats within the Olympic Mountains, we divided the survey zone into eastern, southern, and western sections (Figure 1). The section boundaries partitioned gradients in rainfall and primary productivity, from the wet western zone to the dry eastern zone, with an intermediate transitional zone in the south.

Results

We conducted aerial surveys during six mornings from 18-25 July 2011. We surveyed mountain goats within 39 sample units totaling 23,458 ha (Table 1). That area is similar to area surveyed in 2004 (i.e., 41 sample units comprising 24,524 ha in 2004; Happe et al. 2005), but we sampled a lower proportion of the total sampling frame in 2011 (39%) than in 2004 (48%) because of the larger frame used in 2011. Survey intensity averaged 4.7 min km^{-2} across all surveyed units, ranging from 3.6 to 5.3 min km^{-2} in the low and high-density strata, respectively (Table 1). Survey intensity in 2011 was comparable to that of past surveys (4.4 min km^{-2}; Houston et al. 1991b, Happe et al. 2005). Differences in survey intensity among sample units and strata reflected variation in habitat complexity and the time required to record observations, rather than variation in our expectation of finding goats.

Population Abundance

We counted a total of 217 mountain goats in the Klahhane Ridge Unit and the three sampling strata (Table 1, Figure 2). We estimated a population

TABLE 1. Mountain goat survey characteristics and raw counts of mountain goats in the Klahhane Ridge Unit, and high, medium, and low density strata, Olympic Mountains, Washington, July 18–25, 2011.

Stratum	Area (ha)	Number of units	Area sampled (ha)	Units sampled	Percentage of stratum surveyed	Survey time (min)	Survey intensity (min km^{-2})	Number of goats seen
Klahhane Ridge	2041	1	2041	1	100	74.5	3.7	11
High	7606	10	7606	10	100	406.0	5.3	155
Medium	20,599	41	10,811	22	52	514.4	4.8	50
Low	29,369	56	3001	6	10	111.4	3.7	1
Total	59,615	108	23,458	39	39	1106.3	4.7	217

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TABLE 2. Population estimates of mountain goats, associated components of variance, and 90% confidence intervals (CI) in the Olympic Mountains, Washington, 2004–2011. To allow comparison between years, estimates in 2011 were computed for the expanded survey boundaries, which included suitable habitats above 1425 m elevation, and the original boundaries, which were limited to lands above 1520 m elevation. Both survey definitions exclude the Mount Washington Survey Unit in the southeastern Olympic Mountains, which was not surveyed in 2011.

			Variance Component				
Year	Survey boundaries	Population estimate (N)	Total	Sampling	Detection	Modeling	90% CI
2011	Expanded	344	1924	1212	432	280	± 72
2011	Original	303	1668	1048	388	231	± 67
2004	Original	217	375	137	160	78	± 31

of 344 ± 72 (90% CI) mountain goats within the sampling frame at the time of the survey (Table 2). The total variance of the population estimate, Var($\hat{\tau}$), was 1924, which accounts for variance associated with random sampling of survey units ($Var_{sampling}$ = 1212 or 63% of the total), random detections of independent groups ($Var_{detection}$ = 432 or 22%), and uncertainty in model estimation (Var_{model} = 280 or 15%).

Population Trends

Population estimates corrected for detection biases and adjusted for comparable survey areas were 217 ± 31 (90% CI) mountain goats in 2004 and 303 ± 67 (90% CI) mountain goats in 2011 (Table 2, Figure 3). Compared with the abundance estimate of 344 mountain goats for the expanded survey zone, the estimate of 303 mountain goats pertains to the more restricted survey zone used in previous years (i.e., areas above 1520 m elevation).

Based on population estimates of mountain goats within the comparable survey zone, mountain goat abundance was greater in 2011 than in 2004 (z = 2.04, P = 0.04). The estimated population of mountain goats increased at an instantaneous rate (r) of 0.048 ± 0.034 (90% CI) between 2004 and 2011, representing an average 4.9% finite rate of population increase annually (i.e., λ = 1.049 ± 0.036 [90% CI]).

Minimum population indices of mountain goats ranged from a high of 755 ± 191 (90% CI) in 1983, to lows of 171 ± 25 (90% CI) in 1997 and 179 ± 16 (90% CI) in 2004 following the experimental removals. The population index increased to 232 ± 44 (90% CI) in 2011 (Figure 3). Mean group sizes ranged between 1.9 and 2.3 (standard deviations ranged between 1.8 and 2.0) during the current and previous surveys. We did not detect a significant difference in mean group sizes between surveys ($F_{4,404}$ = 1.17, P = 0.32), suggesting that there were no obvious shifts in mountain goat grouping behavior that would alter the relationship between the index and population size appreciably.

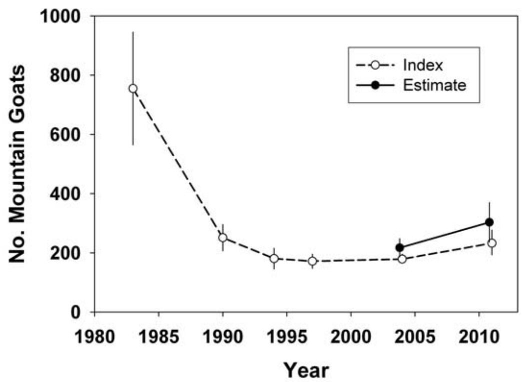

Figure 3. Population trends of mountain goats in the Olympic Mountains above 1520 m in elevation, Washington, 1983-2011. The solid black line connects the 2004 and 2011 sightability-adjusted abundance estimates of mountain goats (error bars indicate ± 90% CI), excluding the Mount Washington survey unit. The dashed line connects the minimum population indices (± 90% CI), excluding the Mount Washington survey unit. Confidence intervals of the population estimates account for sampling variation, random detection, and sightability model estimation. Confidence intervals of the minimum population indices account for sampling variability only; some have been truncated on the lower bounds at the number of mountain goats seen during the survey.

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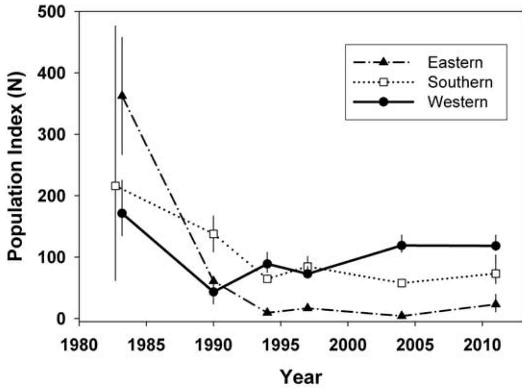

Figure 4. Trends in minimum population indices (± 90% CI) of mountain goats in the eastern, southern, and western Olympic Mountains above 1520 m in elevation, 1983-2011. Estimates exclude the Mount Washington survey unit in the southern zone. Confidence intervals account for sampling variability only; some have been truncated on the lower bounds at the number of mountain goats seen during the survey.

Minimum population indices have varied both temporally and regionally within the Olympic Mountains (Figure 4). In the early 1980s prior to most of the mountain goat removals, indices were greater in the eastern than in the western Olympic Mountains. Substantial uncertainty associated with the population index in the southern section prevents the reliable comparison of mountain goat populations between that area and the eastern or western Olympics. Populations of mountain goats have remained very low in the eastern Olympics since the population culling of the 1980s. From 1990 to the present, population indices have increased primarily in the western Olympics, where population indices are currently greatest.

Discussion

After a relatively long period of population stasis during the 1990s the mountain goat population increased in the Olympic Mountains between 2004 and 2011. The observed increase, averaging about 4.9% annually, represents the first population increase since the population reductions of the 1980s and the cessation of sport hunting outside the park in 1997.

We caution that the current estimate of 344 ± 72 (90% CI) mountain goats should be considered a conservative estimate. Extensive snow cover that existed in 2011 may have excluded some mountain goats from parts of the survey zone, despite our efforts to sample more comprehensively in lower elevation habitats in 2011 than in previous surveys. Furthermore, although we previously assessed and did not observe significant effects of snow on aerial sighting probabilities (Rice et al. 2009), uncharacteristic snow cover during 2011 might have resulted in lower detection probabilities than estimated by our models. Any such biases, however, would underestimate the true population size in 2011, strengthening our conclusion that the mountain goat population recently increased.

Changes made in both the aerial sampling frame and methods of estimating detection biases preclude the direct comparison of current to previous population estimates. Previous estimates were based on an assumed 66% sighting efficiency of aerial surveys (Houston et al. 1986, 1991b). This sighting efficiency was based on comparisons between raw aerial counts of mountain goats and population estimates determined from counts made before and after a known number of mountain goats was removed in the Klahhane Ridge Unit (i.e., Index manipulation method of Caughley [1977]). The average 66% sighting efficiency translated to multiplying raw counts of all mountain goats observed from the helicopter by 1.52 (i.e., 1/0.66) as an effort to more accurately reflect the actual number of mountain goats in the population. This multiplier was meant to adjust for mountain goats that were not detected during the aerial survey either because they were outside the survey zone or because they were not seen within the zone. Use of a constant multiplier does not account for all components of sampling variability associated with sightability modeling, and it fails to account for changes in environment or goat behavior that may affect sighting efficiency either spatially or temporally.

We reduced bias in population estimation by increasing the survey zone area to more accurately encompass the entire population and by estimating sightability bias as a function of mountain goat group size, vegetation cover, and the presence of terrain capable of obstructing visibility (Rice et

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al 2009). We detected about 14% more mountain goats by expanding the survey zone to include lower elevation habitats (an 18% increase in area). Moreover, our application of the sightability model to groups of mountain goats observed within the survey zone adjusted the population indices (i.e., those based on raw counts) upwards by an average factor of about 1.30 (i.e., 271 [index] versus 303 [estimated] mountain goats within the 2004 survey boundary, Figure 3). We caution against comparing this average multiplier to the constant (i.e., 1.52) used in previous studies because the formerly used method adjusted for mountain goats outside the survey zone (<1520 m in elevation) and those not seen within the zone, whereas our model only accounts for animals not seen within the survey zone. Collectively, the redefined survey boundaries and application of the sightability model resulted in a cumulative upward adjustment of the raw counts made above 1520 m in elevation by over 40%, which is more comparable to the 52% upwards adjustment used previously. The discrepancy between past and present correction ratios illuminates the problem associated with comparing the past and present population estimates directly. Notwithstanding these relatively small discrepancies, the current population estimate provides a more reliable estimate of precision than past estimates, because it includes complete accounting of all components of uncertainty (Steinhorst and Samuel 1989, Wong 1996).

In addition to the direct comparison of population abundance estimates made between 2004 and 2011, we examined long term trends and patterns of population growth from 1983-2011 based on minimum population indices derived from raw counts. Population indices examined at the scale of the entire mountain range revealed a static population during the 1990s until 2004 (Figure 3). Reasons for the lack of population growth following cessation of NPS transplanting operations in 1990 and sport hunting outside the park in 1997 are poorly understood, but likely reflected complex interactions between stochastic demographic processes, genetic factors, and climate. Mountain goats are sensitive to high rates of removal, such as those implemented during the NPS transplanting operations, due to their relatively low rate of reproduction and the combined additive effects of natural and human-caused mortality or management removals (Côté and Festa-Bianchet 2003, Hamel et al. 2006). Population recovery from overharvest or culling is highly individualized among different populations, but is hindered most in small populations that may be more susceptible to stochastic events such as density-independent mortality (Hamel et al. 2006; Rice and Gay 2010). Moreover, recent genetic studies that indicated low allelic diversity and evidence of inbreeding among mountain goats in the Olympic Mountains (Shirk 2009), suggest that genetic factors may also have affected population growth negatively (Shirk 2009). The interaction between population growth and genetic diversity of mountain goats in Washington remains speculative, but a negative relationship between survival of sub-adult mountain goats and genetic diversity has been demonstrated previously in Alberta (Mainguy et al. 2009).

Mechanisms behind the observed geographic variations in population growth are also poorly understood. Winter climate, however, appears to have influenced mountain goat populations differentially across the precipitation gradient of the Olympic Mountains in the past, and may help to explain recent patterns. Snowpack has declined throughout the Pacific Northwest since the late 1970s reflecting complex interactions between anthropogenic warming forces and the Pacific Decadal Oscillation (PDO) (Mote 2005, Meehl and Hu 2009), an atmospheric and oceanic condition that produces 20-30 year cycles in precipitation and temperature in the Pacific Northwest (Mantua et al. 1997). Recent analyses of snowpack measurements in the Olympic Mountains clearly demonstrate an overall downward trend suggestive of anthropogenic warming as well as a stepwise decrease in snowfall coinciding with a major shift in the PDO in 1976/1977 (Barry and McDonald 2012). Specifically, mean SWE of snowpack in the Hurricane Ridge area of Olympic National Park from the late 1940s to middle 1970s was nearly double that measured during the 1980s and 1990s (Barry and McDonald 2012).

Houston et al. (1994a) postulated that the western Olympic Mountains were marginal habitat for

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mountain goats during a period of high snowpack that persisted prior to the middle 1970s. Mountain goats colonized the eastern and southern Olympic Mountains by the 1950s but were not commonly seen in the western Olympics until the late 1960s (Houston et al. 1994a). Prodigious accumulations of heavy snow that characterized the late 1940s to middle 1970s may have exerted a strong density-independent influence on reproduction and mortality in the western Olympic Mountains (e.g., large-scale additive mortality due to winter weather). This interpretation is supported by studies that have shown a negative association between mountain goat reproduction and severe winter weather in the Rocky Mountains (Adams and Bailey 1982, Swenson 1985, Bailey 1991), as well as greater mortality associated with severe snow conditions in southeastern Alaska (Smith 1984, White et al. 2011).

By contrast, mountain goats in the comparatively dry eastern Olympic Mountains appear to have been less influenced by snow during the primary population expansion phase from the 1930s to 1960s. By the 1970s, mountain goats had built up to high numbers in some subpopulations of the eastern and southern Olympics (Houston et al. 1994a). Evidence of density-dependent variations in body weight and reproductive indices suggested that the Klahhane Ridge subpopulation was resource limited by the 1980s (Stevens 1983, Houston and Stevens 1988). Although density independent effects of weather may have added variation to the observed density-dependent relationships, severe winter weather was not limiting to mountain goat populations in the eastern Olympic Mountains as was once the case in the snowy west side of the range (Houston et al. 1994c).

Recent population trends are consistent with the hypothesis that climate continues to influence mountain goat populations differently across the precipitation gradient. Mountain goat subpopulations increased primarily in the western Olympic Mountains during the period of low snowpack that persisted during the 1990s until recently, supporting the notion that mountain goats were formerly limited by severe winter weather on the west side of the Olympics. In contrast, mountain goat abundance in the eastern and southern Olympic Mountains did not increase in response to the milder conditions. We cannot rule out potential effects of limited sport hunting that continued until 1997 in the eastern and southern Olympics outside the park or the effects of random demographic processes (Hamel et al. 2006) as possible explanations for these geographic differences, but climate differences across the precipitation gradient may also have played a role.

We postulate that the recent period of low winter snowpack that benefited the subpopulation of mountain goats on the western flank of the Olympic Mountains has limited subpopulation growth in the dry eastern Olympics. Summer drought conditions have been shown to negatively affect survival of mountain goats in southeastern Alaska, most likely through the influence of summer temperatures on snowpack, forage conditions, and foraging budgets of mountain goats, and ultimately, physical condition of mountain goats at the end of summer (White et al. 2011). Moreover, Stevens (1983) reported a strong correlation between 1 April snow depth and mountain goat reproductive rates the following year in the Klahhane Ridge area of the eastern Olympic Mountains. She hypothesized that the availability and nutrient content of green forage depends on snowfield persistence in the subalpine zone during summer, which may affect nutritional condition of mountain goats as well as ovulation and parturition rates the following fall and spring, respectively. The hypothesis is supported by similar positive correlations that have been shown between reproduction and pre-breeding snowpack in Colorado (Bailey 1991), and studies showing that prolonged snowpack on summer ranges extends the availability of high quality herbaceous vegetation in Alaska (Fox 1991).

Although current evidence now points to an increasing population of mountain goats overall, uncertain effects of climate, nutrition, and genetic factors hamper the prediction of future trends. If the estimated average rate of population growth were to remain constant, however, the population could increase by 50% in the next eight to nine years and double in 14-15 years. Now that the population has begun to increase following control

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measures of the 1980s and a period of relative stasis in the 1990s, more frequent surveys would better inform mountain goat management in the future. Continued monitoring of mountain goats across future climate changes, either inherent or human-forced, may provide additional correlative support for the winter severity and summer drought hypotheses in the western and eastern Olympic Mountains, respectively. Moreover, research on the effects of summer snowpack, forage qualities, and nutrient status of mountain goats across the precipitation gradient in the Olympic Mountains would help to clarify potential relationships between population trends and climate variation.

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