Simulation Modeling of Population Expansion for Introduced Mountain Goats in the Olympic Mountains of Washington State

By

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Melissa Marie Oscarson
August 8th, 2017

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A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Completion
Of the Requirements for the Degree
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Abstract

Mountain goats (*Oreamnos americanus*) are not native to the Olympic Peninsula as they are to other regions of Washington State. A total of eleven or twelve animals were translocated from Alaska and British Columbia between 1925 and 1929 then released in the foothills of Mount Storm King. By 1970 these founding goats had colonized the entire Olympic range and concerns about the management of this introduced species developed as damage to alpine soil and vegetation was noted. An aerial census of the Olympic range conducted in July 1983 estimated the mountain goat population at 1,175 (95% CI 840 – 1510). A series of removals reduced the population to 389 (95% CI 181 – 597) goats by 1990, with a period of stasis occurring during the following decade. The most recent two aerial surveys (2011 and 2016) indicate positive growth, and a variety of efforts to mitigate damage to fragile alpine ecosystems are again under consideration.

I parameterized an existing population model, CDPOP, for use with mountain goats. CDPOP is a simulation program that uses individual-based movement (including dispersal), reproduction, and mortality to predict the influence of landscape heterogeneity on population dynamics and genetic exchange. Population parameters for the model were derived from published literature. I successfully calibrated the model and simulated the population trajectory for Olympic mountain goats from establishment through the 1983 census. Modeled population dispersal closely tracked anecdotal reports of dispersal. However, observed heterozygosity for the modeled population did not align with previous research. I suspect genetic diversity for the true founding goats was not as great as that of the individuals used to initialize the model. Sensitivity analyses showed that changes in annual reproductive rate had the greatest influence on population trajectories, followed by juvenile mortality and adult female mortality, respectively. These findings differ from those in two related studies, likely due to the early primiparity within the modeled population. I validated the model by simulating the period from 1990 to 2016. The modeled population showed that approximately 75% to 80% of the total animals removed during the 1980's needed to be female in order for the observed population stasis to occur. Finally, I discuss avenues for future model development and applications. This model could be utilized to inform current management decisions regarding the impact of removals from the Olympic mountain goat population and proposals to use these animals to augment reduced native populations in the Cascade Mountain Range.

Acknowledgments

This work was part of a collaboration involving Washington Department of Fish and Wildlife (WDFW), Olympic National Park, North Cascades National Park and Western Washington University (WWU). Funding for this project was provided by Seattle City Light, Rocky Mountain Goats Foundation, Aquatic Lands Enhancement Account (ALEA), and the Mazamas. I would like to thank my advisor, David Wallin, for his unwavering support and expert guidance, as well as my committee members Peter Homann (WWU), Erin Landguth (University of Montana), and Cliff Rice (WDFW) for their mentorship and expertise. I am also grateful to Stephan Freelan, Scott Wilkinson, and Robin Matthews, all of Western Washington University, for their technical and statistical support. Research by Andrew Shirk and Leslie Park laid much of the foundation for my project. Additional thanks go to Richard Harris (WDFW), Adam Wells and Samuel Cushman (U.S. Forest Service) for their advisement and collaboration. The steadfast support and encouragement from my "parent-trio", family, and friends throughout this project was essential to my work and infinitely appreciated. Shannon Call, thanks for your formatting prowess and comic relief as we navigated graduate school together. Finally, I would like to express my gratitude to the interns – Chris Trinies, Erin McVoy, Devon Hamblett, Tatsu Ota, Moureen Moschel, and Mitchell Gellhaus -- who worked tirelessly and enthusiastically as we collected samples across the North Cascades.

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2.0 Introduction

Mountain goats (*Oreamnos americanus*) were introduced to the Olympic Mountains as a joint effort of state wildlife agents, United States Forest Service (USFS), and local sportsman's clubs, likely with the intention of establishing a harvestable population on the Olympic Peninsula (Hutchins and Stevens 1981). In 1909 president Theodore Roosevelt declared Mount Olympus a national monument under the jurisdiction of USFS in an effort to preserve the then declining Roosevelt elk (*Cervus elaphus roosevelti*) and their habitat (Moorhead and Stevens 1982). Areas surrounding this new preserve were identified by federal and state land managers as suitable habitat for mountain goat. In 1925, four goats were transported from the Selkirk Mountains in British Columbia and released near Lake Crescent, at the base of Mount Storm King, in the northwestern corner of the Olympic Mountains (Scheffer 1949, Moorhead and Stevens 1982, Johnson 1983). The sex of these goats is unclear with one record referring to them as "two pairs" and another labeling them "three nannies and a billy" (Scheffer 1949).

Roosevelt elk populations began increasing as a result of the aforementioned conservation efforts and state agencies from other areas started requesting elk, inspiring the potential for trade. In 1929 eight young Roosevelt elk were delivered to Afognak Island, Alaska in exchange for eight mountain goats who were released in the Olympic Mountains near the first release site (Webster 1932, Scheffer 1949, Moorhead and Stevens 1982). Early records for both releases were sparse and, especially in relation to this second introduction, contained some contradictory information which is presented in more detail by Moorhead and Stevens (1982). Briefly, some accounts cite 1927 as the second release date while others cite 1929 and 1930 (Scheffer 1949). Six of the goats came from southeast Alaska, likely near

Juneau, while the other two were from the Chugach Mountains near Cordova (Scheffer 1949, Moorhead and Stevens 1982). It is unclear whether all eight of these goats were released. A correspondence signed by the Olympic Park Superintendent in 1947 states that one of the eight Alaskan animals died during transport (Moorhead and Stevens 1982) while other accounts cite the release of all twelve animals (Webster 1932). At least six of these goats were released at the base of Mount Storm King while two were potentially released slightly to the west on Baldy Ridge (Scheffer 1949). Thus, with certainty, we know that eight animals were shipped from Alaska, six from southeast Alaska and two from the Chugach Mountains, and seven or eight were released near Mount Storm King and Baldy Ridge between 1927 and 1930.

These founder goats dispersed from the introduction site near Mount Storm King in a southeastern direction, traveling approximately two to three kilometers per year, and successfully colonized the entire Olympic range by the late 1960's (Moorhead and Stevens 1982). In 1929 mountain goats were reported on Mount Appleton, approximately 13 kilometers south of the release site (Figure 2-1). By 1935 goats had dispersed to the eastern portion of the range, with sightings on Mount Constance, sixty kilometers southeast of the introduction site. In 1938 Olympic National Park (ONP) was established, encompassing most of the Olympic range within its boundaries. Because hunting is prohibited within National Parks, harvesting opportunities intended for the newly introduced goats were now virtually eliminated. Small numbers of goats continued establishing themselves in the northern and eastern areas of the park over the next several years. In 1946 observations were reported on Mount Anderson, fifty-three kilometers from the introduction site, indicating southwestern movement. By 1960 mountain goats reached the southern park boundary and were sighted south of this boundary annually thereafter. The western and central interior portions of the Olympic range were slow to be inhabited. Goats were not reported on Mount Olympus, the tallest mountain in the range, until 1952, with sparse sightings until the early 1960's. Mount Ferry, located in the central Bailey Range near Mount Olympus, had no documented sightings until 1968. Moorhead and Stevens (1982) theorized this relatively late colonization was a result of deep and persistent snowpack characterizing the area, with the peak of Mount Olympus receiving an average of greater than 15 meters of snow annually (Davey et al. 2006). Dispersal into this final portion of the range marked complete colonization of the Olympic Mountains.

Concerns about the management of this introduced species began to develop in the late 1970's as damage to alpine soil and vegetation was noted. Mountain goats are generalist herbivores, consuming grasses, sedges, forbes, shrubs, and deciduous or coniferous trees (Stevens 1983, Fox et al. 1989, Côté and Festa-Bianchet 2003). Chadwick (1974) identified 163 forage species utilized by goats. Often more deleterious than grazing, trampling and digging can also negatively impact fragile alpine vegetation and soil. Mountain goats repeatedly utilize the same preferred areas for activities such as bedding or mating (Chadwick 1977), trampling vegetation and creating large wallow and rutting pits of bare, eroded ground (Rideout and Hoffmann 1975, Chadwick 1977, Hutchins and Stevens 1981). Studies by Pfitsch (1985) and Schreiner and Woodward (1994) demonstrated the "direct and indirect impacts" ONP goats have on the vegetation including reduced cover and disruption of competitive relationships between species. As a result of long-term geographic isolation, the diverse Olympic biota includes a number of endemic plants and animals. Of eight total endemic plant taxa, the distribution of seven overlap with mountain goat summer range (Schreiner and Woodward 1994) making them particularly vulnerable to these impacts.

While mountain goats are noted for their heightened sensitivity to anthropogenic disturbance in comparison to other ungulates (Lentfer 1955, Chadwick 1974, Festa-Bianchet and Cote 2008), they seem to habituate to human presence over time, perhaps in part due to access to desired nutrients gained by these interactions. Alpine forage is low in sodium, a beneficial mineral of particular importance to females during lactation (Ayotte et al. 2006), and the concentration of nutrients in alpine soil is relatively poor (Slabach et al. 2015). Given the great distances goats are willing to travel to access natural licks rich in sodium (Brandborg 1955, Singer 1978, Poole et al. 2010, Rice 2010), it is apparent that this mineral is a coveted resource. Human sweat and urine are also sources of sodium and result in the attraction of goats to areas accessed regularly by people for outdoor recreation (Stevens 1983), such as the many trails of Olympic National Park. Mountain goats will dig up and ingest soil containing this sodium, further contributing to the soil erosion and vegetation degradation discussed above (Hutchins and Geist 1987). Additionally, shared use of these ONP trails has resulted in trail closures due to incidents of goat aggression toward people, with two reported gorings (1999 and 2010), the worst of which was fatal (Happe 2011).

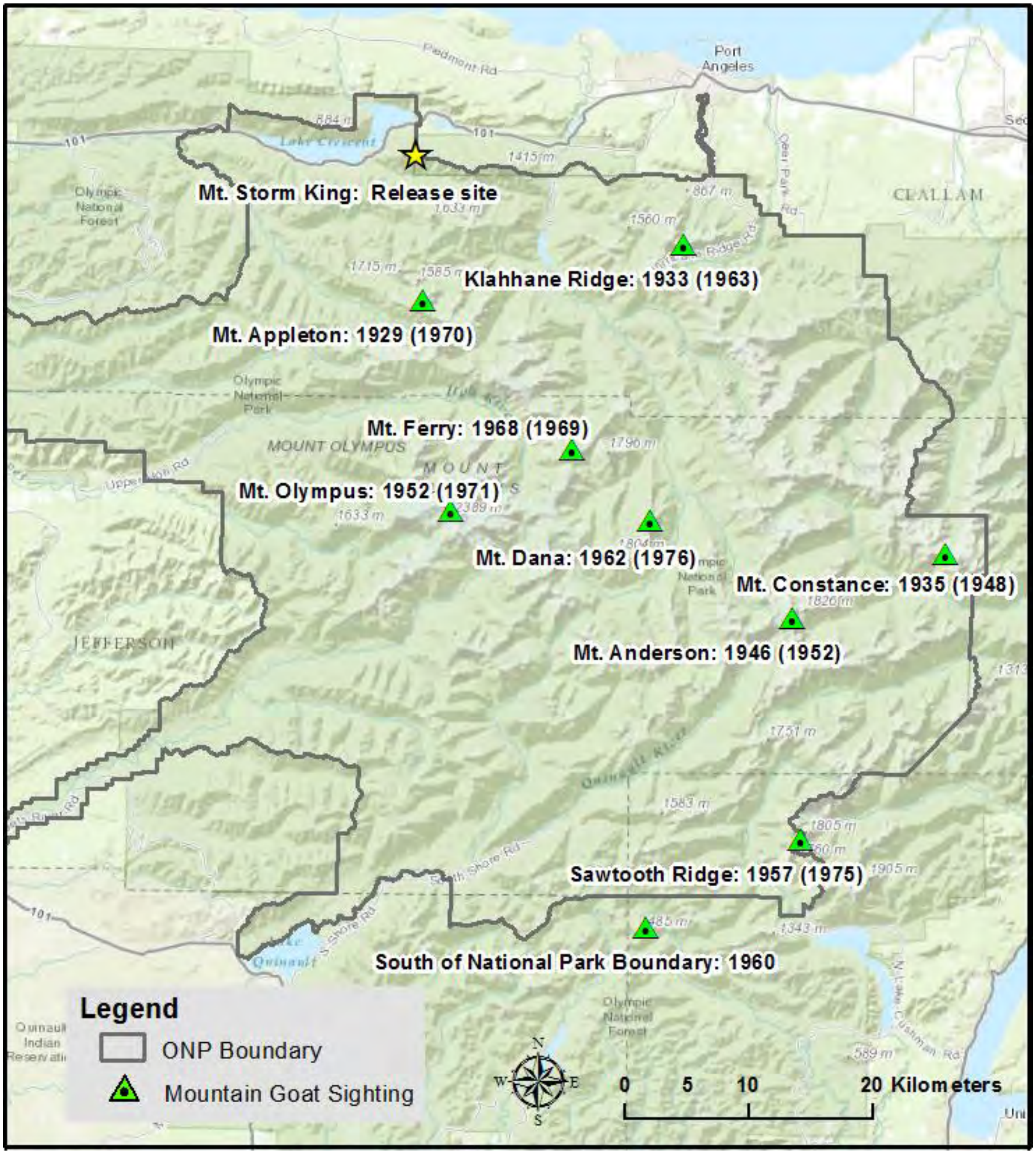


Figure 2-1. Mountain goat dispersal progress in the Olympic Range. Movement occurred in a southeasterly direction from the release site near Lake Crescent in the foothills of Mount Storm King (starred). The year a goat was first reported in specific areas of the range are listed (initial date) followed by the year that a nanny with kid-at-heel was first reported (parentheses). Modified from Moorhead and Stevens (1982).

In an effort to manage the rapidly expanding population and mitigate the environmental degradation and public safety threat imposed by the goats, a management plan was enacted in 1981 with the primary objective of population reduction, via translocation from within the park and hunting outside the boundaries of the park (Houston et al. 1994). The plan, described in Houston et al (1991b, 1994), occurred in two phases beginning with the experimental phase that ran through 1987 and concluding with the operational phase that was scheduled to terminate in 1992. Objectives for the experimental phase were to determine current population density and distribution, evaluate various goat removal techniques, and to monitor the effect of reductions on vegetation and soil. Two hundred sixty removals by ONP officials occurred during the experimental phase. While completing this phase, land managers determined that full extirpation was necessary in order to preserve the alpine ecosystem (Schreiner 1987 as cited in Houston et al. 1991b). Thus, the primary objective of the operational phase was to eliminate mountain goats from the core area of the park. This objective fell under intense public scrutiny and was the subject of much controversy (Anunsen and Anunsen 1993, Scheffer 1993, Lyman 1994, Hutchins 1995, Wright 1996). An additional 147 goats were removed during the operational phase (Houston et al. 1994). During the extent of the management plan, 407 goats were removed by park officials and 114 goats were harvested (total population reduction of 521). Operations were prematurely canceled in 1990 by the superintendent of Olympic National Park. Risks to the capture team had become too great and the publication of a full environmental impact statement addressing mounting public concerns was deemed necessary before additional action was taken (Houston et al 1994).

In the midst of removal operations, an aerial census of the Olympic range conducted in July of 1983 during the experimental phase estimated the mountain goat population at 1175 (95% CI 839 – 1510; Houston et al. 1986). Subpopulations were distributed nonuniformly, with densities, population dynamics, and individual body conditions varying widely between these groups (Stevens 1983). The subpopulation on Klahhane Ridge, located at the north end of the park, exhibited a particularly high density (14 goats / km^2) in relation to other subpopulations within the range (0.6-4 goats / km^2; Stevens 1983). Mountain goats in this high-density group displayed later primiparity, decreased fecundity, and reduced body mass in relation to nine other subpopulations examined by Stevens (1983). Based on these indicators, Klahhane Ridge was determined to have reached ecological carrying capacity while other subpopulations within the range still displayed characteristics indicative of expanding populations. As such, Klahhane Ridge was the area used for density reduction experimentation during the first phase of the management plan with a population decrease of 82% (230 to 41) from 1981 to 1986. This reduction resulted in subpopulation dynamics more closely resembling those exhibited by the expanding groups elsewhere in the Olympic range (Houston and Stevens 1988).

In 1990, after the Olympic-wide removal efforts were terminated, a second aerial census was conducted, yielding an estimate of 389 (95% CI 181 – 597; Houston et al. 1991a), a reduction in total population substantially greater than the actual number of individuals removed (Figure 2-2). Between autumn 1983 and 1989 (after the first census and prior to the second), a total of 326 mountain goats were removed from the Olympics, with

245 (75.2%) moved for translocation and the remaining 81 harvested (Houston et al 1991a). Assuming both censuses were accurate, this leaves 460 individuals unaccounted for when ignoring regular birth and mortality that occurred between the 1983 and 1990 censuses. Houston et al. (1991b, 1994) suggests several possible sources of mortality that may have occurred in addition to the removals. During the period from 1985 to 1989, 66% of the 102 adult females captured were lactating. Only in rare cases were kids captured with the nannies. While cases of orphaned kids surviving mild winters have been documented (Chadwick 1974, Hutchins 1984), probability of survival is greatly reduced (Brandborg 1955) and most of those orphaned during the removal process probably would have died. Furthermore, it is likely that increased mortality during relatively more severe winters (1984 and 1987) further reduced the population (Houston et al 1991b).

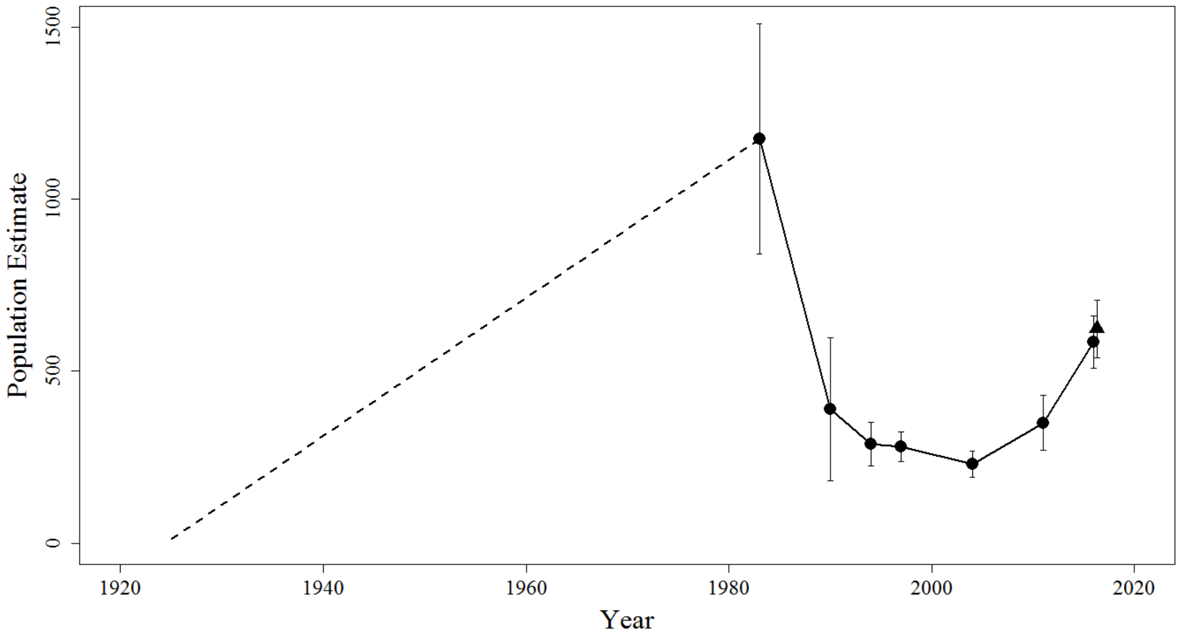


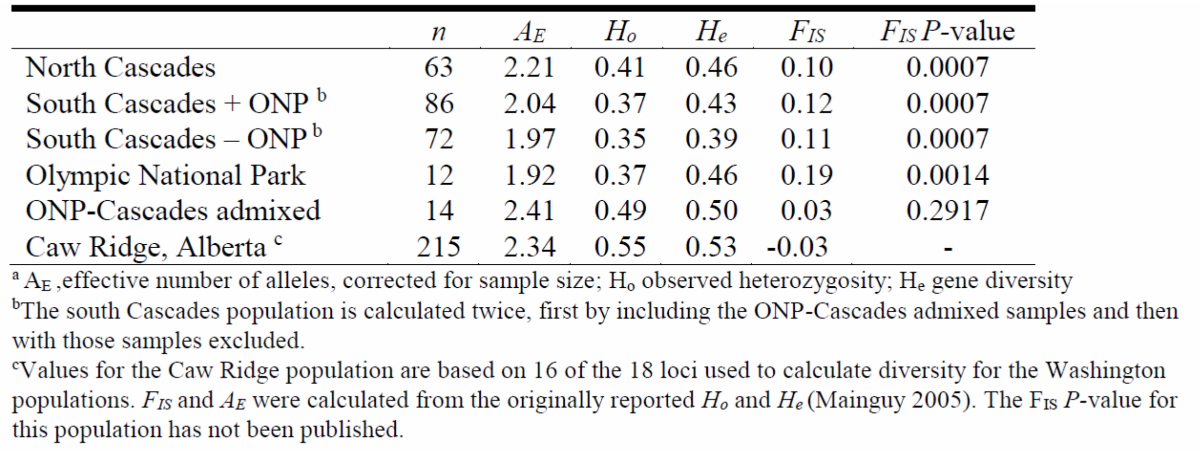
Figure 2-2. Mountain goat population estimates from introduction in the 1920's through 2016. Population estimates from 1983 and beyond were derived from counts obtained by aerial helicopter surveys based on stratified random sampling procedures. Filled circles represent estimates acquired in survey areas above 1,520 meters while the closed triangle represents the 2016 estimate using an expanded survey area (>1,425 meters). Error bars show 95% confidence limits of estimates from 1983 and beyond.

After the 1990 aerial survey, population growth exhibited a period of stasis that lasted through 2004 before an increase was observed in 2011 (Jenkins et al. 2011). Explanations for this period of slow growth are merely speculative but climate, low genetic diversity, and changing demographic processes are all potential factors. Survey methodology was improved in 2011 (Jenkins et al. 2011*b*) with an expansion of the survey zone (suitable habitat at elevations above 1,425 meters rather than 1,520 meters) based on movement data for GPS collared goats and application of a recently-developed, detection bias model (Rice et al. 2009). This methodology was applied during the most recent, 2016 survey, producing a population estimate of 623 (95% CI 539 – 707; Jenkins et al. 2016). To facilitate direct comparison, the 2011 and 2016 population estimates were adjusted to reflect survey boundaries comparable to years prior (>1,520 meters). The most recent census estimates mountain goat abundance at elevations above 1,520 meters to be 584 (95% CI 508 – 660), representing an average finite rate of growth of eight percent annually from 2004 to 2016 (Jenkins et al. 2016). This population growth has reinvigorated the need for action and ONP is considering a number of management solutions similar to those examined in the 1980s including zero action (with management such as hazing), translocation, lethal removal, or a combination of the former two (National Park Service 2017).

In the Cascade range to the east, mountain goat populations have suffered a 90% decline since 1961 (Rice and Gay 2010) and the Olympic goats have been identified as a potential augmentation source. Over-hunting has been identified as the cause of the Cascade population decline but, despite a 90% reduction in hunting permits since the early 1990s and subsequent recovery in several areas, some historical habitat remains unoccupied (Rice personal communication). Approximately 150 of the animals removed from ONP during the 1980's were released in the Cascades. Monitoring of the outcome of these translocations was limited but recent genetic work (Shirk 2009, Shirk et al. 2010, Parks 2013) has demonstrated that at least some of these animals survived and interbred with native Cascade animals. Evidence of this previous translocation success and revived management concerns in the Olympics have motivated plans for a second, large translocation effort. Olympic National Park, working with the United States Forest Service (USFS), Washington Department of Fish and Wildlife (WDFW), and several Indigenous tribes, is actively engaged in planning for this project with the goal of beginning translocation work during the summer of 2018 (Happe, pers. com.).

Although it is not feasible to capture the entire Olympic population of approximately 623 mountain goats, 200-250 animals could be available for translocation, offering potential for an increase in not only population size in the Cascades, but genetic diversity as well. Shirk (2009) found that both the Cascade and ONP populations have low genetic diversity compared to core populations in Alberta, Canada (Table 2-1). However, as a result of the combination of unique alleles, ONP-Cascades admixed individuals showed diversity indicators much closer to that of the genetically rich, core population. These data provide a strong indication that additional translocations from ONP to the Cascades could be quite beneficial. If translocation efforts can result in an increase in both the number of goats and genetic diversity in the Cascades, this could play a significant role in restoring the population. These data also suggest that a large reduction of the ONP population could have a profound impact on the long-term viability of the remnant population, with the potential to push this population to extinction.

Table 2-1. Genetic diversity summary statistics[a] for mountain goat populations in Washington and Alberta, Canada. Sample size (n), genetic diversity, inbreeding coefficient (F_{IS}), and significance test for inbreeding also shown. All statistics are based on microsatellite DNA (from Shirk 2009).



	n	A_E	H_o	H_e	F_{IS}	F_{IS} P-value
North Cascades	63	2.21	0.41	0.46	0.10	0.0007
South Cascades + ONP [b]	86	2.04	0.37	0.43	0.12	0.0007
South Cascades – ONP [b]	72	1.97	0.35	0.39	0.11	0.0007
Olympic National Park	12	1.92	0.37	0.46	0.19	0.0014
ONP-Cascades admixed	14	2.41	0.49	0.50	0.03	0.2917
Caw Ridge, Alberta [c]	215	2.34	0.55	0.53	-0.03	-

[a] A_E ,effective number of alleles, corrected for sample size; H_o observed heterozygosity; H_e gene diversity

[b] The south Cascades population is calculated twice, first by including the ONP-Cascades admixed samples and then with those samples excluded.

[c] Values for the Caw Ridge population are based on 16 of the 18 loci used to calculate diversity for the Washington populations. F_{IS} and A_E were calculated from the originally reported H_o and H_e (Mainguy 2005). The F_{IS} P-value for this population has not been published.

Note. Reprinted from "Mountain goat genetic structure, molecular diversity, and gene flow in the Cascade Range, Washington", by A. Shirk, 2009. MS Thesis, Western Washington University, Bellingham, WA.

Population modeling can be used to gain better understanding of a system and to predict future trends, thereby enhancing management efficiency and potential (Pojar 1981). My objective was to parameterize an existing population genetic model (Landguth and Cushman 2010) for use with mountain goats. Population parameters for the model were derived from published literature. I calibrated the model by simulating the population trajectory for Olympic mountain goats from establishment in 1925 through the first census in 1983. Additionally, I validated the model by simulating the period of stasis and growth that occurred between 1994 and 2016. This model could be used to inform management decisions related to removals and could later be applied to the Cascade population in order to evaluate a variety of augmentation scenarios. To my knowledge, this is the first spatially explicit individual-based introduction model calibrated and validated with empirical data.

3.0 Study Area

The study area covers the Olympic Mountain range on the Olympic Peninsula of northwestern Washington; encompassing approximately 15,000 square kilometers. This range is bounded on three sides by the waters of the Pacific Ocean to the west, the Strait of Juan De Fuca to the north, and Puget Sound to the east. The Chehalis River lowlands extend along the southern portion of the range and, in combination with the aforementioned marine features, isolate the Olympic Mountains from other ranges. The Olympic range rises steeply and abruptly from sea level with more than 70 peaks extending above 2,000 meters. Mount Olympus, the highest of these peaks, has an elevation of 2,430 meters. Eleven major rivers, fed by expansive glaciers and snowfields, originate in these jagged cliffs and drain radially into the surrounding bodies of water (Tabor 1987). The many peaks of the Olympic Range create a barrier for oceanic weather generated by the Pacific resulting in a stark contrast in annual precipitation between the western side of the range and the northeastern corner, which is situated in the rain shadow of the great mountains (Figure 3-1). The western slopes of the Olympic Mountains possess the wettest climate in the continental United States (Tabor 1987) receiving an average of 600 centimeters (236 inches) of precipitation annually. The northeastern corner, near the town of Sequim, experiences some of the driest conditions on the Pacific Coast with an average of 43 centimeters (17 inches) of precipitation annually, second only to southern California (PRISM Climate Group 2016). Below 500 meters precipitation falls primarily as rain while areas above 1,000 meters generally receive precipitation as snow.

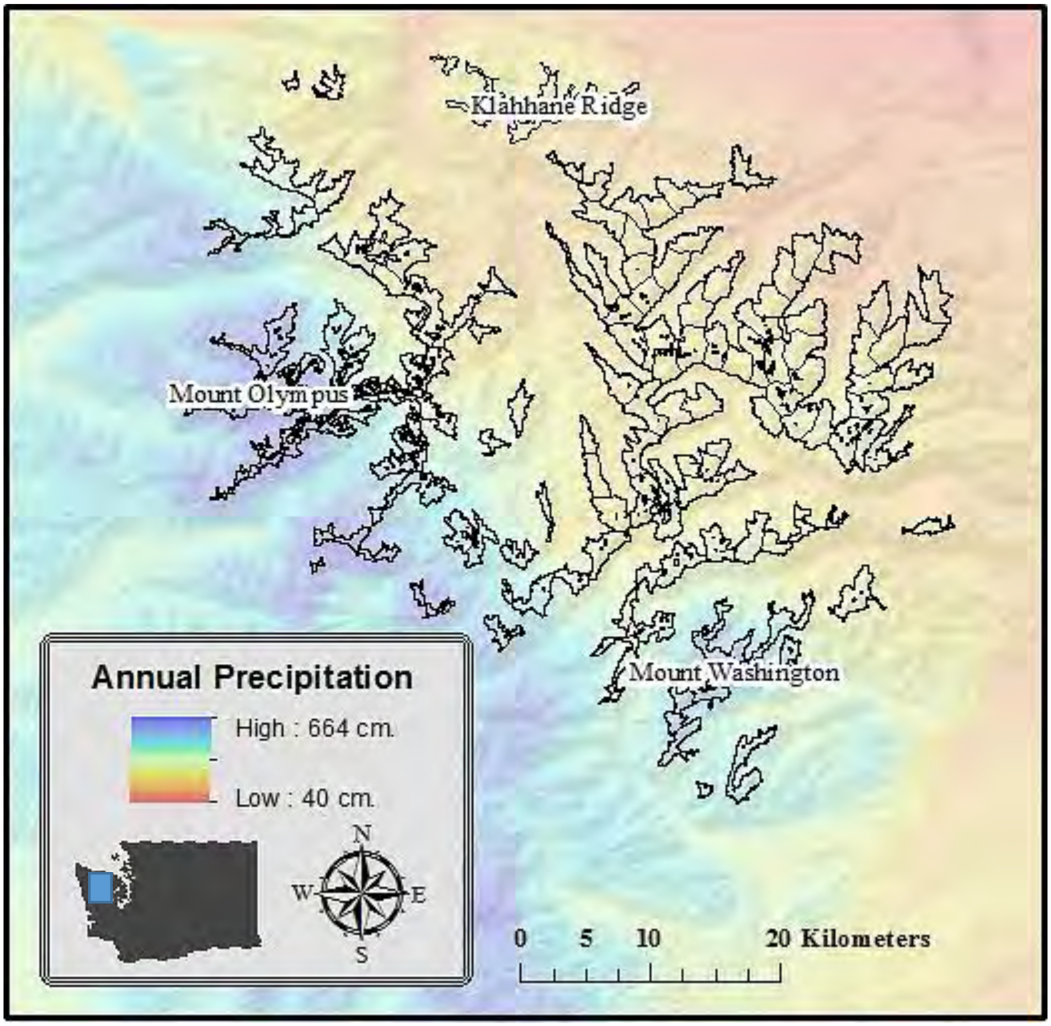


Figure 3-1. Study area map showing mean annual precipitation in the Olympic Mountains, 1981 – 2010. Polygons delineate mountain goat survey unit boundaries (>1,425 meters in elevation in areas of suitable habitat). (Data source: PRISM Climate Group, Oregon State University, 1981 – 2010 precipitation normal, http://prism.oregonstate.edu)

The steep changes in slope, elevation, and precipitation across the Olympic range create a diversity of ecosystems that support uniquely rich biota. Below approximately 1,500 meters forests are dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Above 1,500 meters forests transition to predominantly subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). These are interspersed among subalpine and alpine meadows largely comprised of grasses, forbes, and sedges (Rideout and Hoffmann 1975, Johnson 1983). Mountain goats inhabit these alpine and subalpine zones during summer and early fall then move to cliff bands at lower elevations in response to snowfall during the colder months. Fauna with the potential to prey upon mountain goats in the Olympics include mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), American black bears (*Ursus americanus*), bald eagles (*Haliaetus leucocephalus),* and golden eagles (*Aquila chrysaetos*) (Rideout and Hoffmann 1975, Johnson 1983). Mountain lions are thought to be the most frequent predator on mountain goats while success of the other four species is limited to kids or adult goats who are weak from malnutrition or illness (Johnson 1983, Festa-Bianchet and Cote 2008). The Columbian black-tailed deer (*Odocoileus hemionus columbianus*) and the Roosevelt elk (*Cervus elaphus roosevelti)* potentially compete with mountain goats for resources during winter months when the ungulates share forested ranges at lower elevations (Jenkins and Starkey 1984).

Adverse anthropological impact in the Olympic range is relatively low compared to surrounding areas because approximately 90% of the study area is inside Olympic National Park and the remaining 10% is within the adjoining Olympic National Forest. A major highway runs the circumference of most of the Olympic range but the interior is uninterrupted by major roadways or agricultural lands. The park receives a substantial number of annual visitors (Figure 3-2). The park was established in 1938, with 75,310 people visiting the park in this first year. This number has grown exponentially since then. From 1971 on, ONP has received more than two million visitors annually and over 3 million annually nearly every year since 1994.

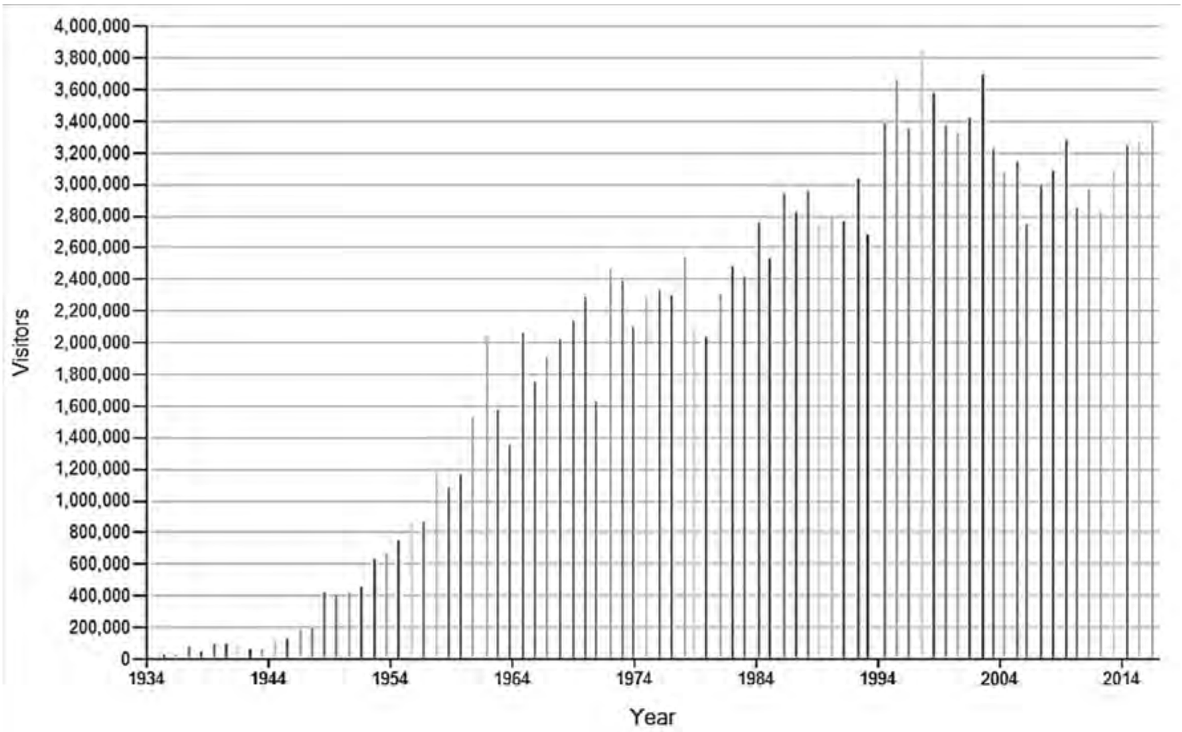


Figure 3-2. Number of annual recreation visitors to Olympic National Park, 1935 – 2016. From https://irma.nps.gov/Stats/Reports/Park/OLYM.

4.0 Methods

4.1 Model Structure

I used CDPOP for all population modeling. A full description of the CDPOP model is provided in Landguth and Cushman (2010). Briefly, this simulation program uses individual-based movement (including dispersal), reproduction, and mortality to predict the influence of landscape heterogeneity on population dynamics and genetic exchange. Mate selection and dispersal are simulated across a resistance surface, with each pixel value representing the species-specific, unit cost of crossing that pixel cell (Dunning et al. 1992, Cushman et al. 2006, Spear et al. 2010). To begin, CDPOP reads in a table of input parameters including age-specific reproduction and mortality, mate movement, dispersal, and genetic processes. The model then reads in potential (x,y) locations for every individual, including the founding population, with genotype, age, and sex specified for every member of this initial group. Individual animals move to locate mates based on a user-specified function with resulting offspring inhabiting the mother's home cell. After the application of mortality to all individuals followed by the dispersal of offspring, the first modeled time period concludes. CDPOP has been applied to simulations involving a variety of plant (Kitchen and Allaby 2013), mammal (Castillo et al. 2014, Row et al. 2014), fish (Cooke et al. 2014), amphibian (Prunier et al. 2014), and reptile (DiLeo et al. 2013) species.

The CDPOP model requires a data layer that specifies landscape resistance; the ease with which animals can move across the landscape. Landscape resistance can be influenced by a range of different natural and anthropogenic features. In previous studies of mountain goats in the Cascades, Shirk et al. (2010) and Parks et al. (2015) found that landscape resistance was influenced by major roadways, water/wetlands, agriculture, urban land cover, elevation, and in some contexts, distance to escape terrain. Because the Olympic Range is predominantly contained within the boundaries of ONP and thereby protected from development, major roadways, agriculture, and urban land cover are not features contributing to landscape resistance. Additionally, the range's isolation results in a large patch of connected habitat surrounded by features impassable to goats. Wetlands and most large bodies of water occur in the foothills on the outer edges of the range and are beyond habitat accessed by the goats. Landscape resistance related to rivers originating in the range is largely influenced by the correlated elevation gradient. Distance to escape terrain was found to have minimal influence on individual movement (Shirk et al. 2010) except in areas where it was a limited resource (Parks et al. 2015), a feature which does not apply to the craggy peaks of the Olympic Range. Therefore, for the Olympic Range, I calculated landscape resistance based solely on elevation.

I utilized a 30 meter resolution digital elevation model (DEM) of western Washington (obtained from United States Geological Survey) to create a resistance surface. In ArcGIS I calculated landscape resistance based on elevation for mountain goats using the following Gaussian function from Parks et al. (2015):

$$R = R_{max} + 1 - R_{max} * e^{\frac{-(elevation - E_{opt})^2}{2 * E_{SD}^2}}$$

where R is pixel resistance, R_{max} dictates maximum resistance, E_{opt} is the optimal elevation, and E_{SD} is the standard deviation of elevation. As elevation moves away from $E_{opt,}$ resistance increases from 1 to R_{max} at a rate dictated by E_{SD}. Based on the most highly supported models for the entire Parks et al. (2015) study area, R_{max}, E_{opt}, and E_{SD} were defined as 5, 1600 meters and 1500 meters respectively. I clipped the DEM to the extent of the Olympic Mountains and resampled the cells to 100 square meters to obtain the same cell size* used by Parks et al. (2015). I then rescaled the DEM to achieve cell values from one (low resistance) to two (high resistance), thereby creating the final resistance surface model (Figure 4-1).

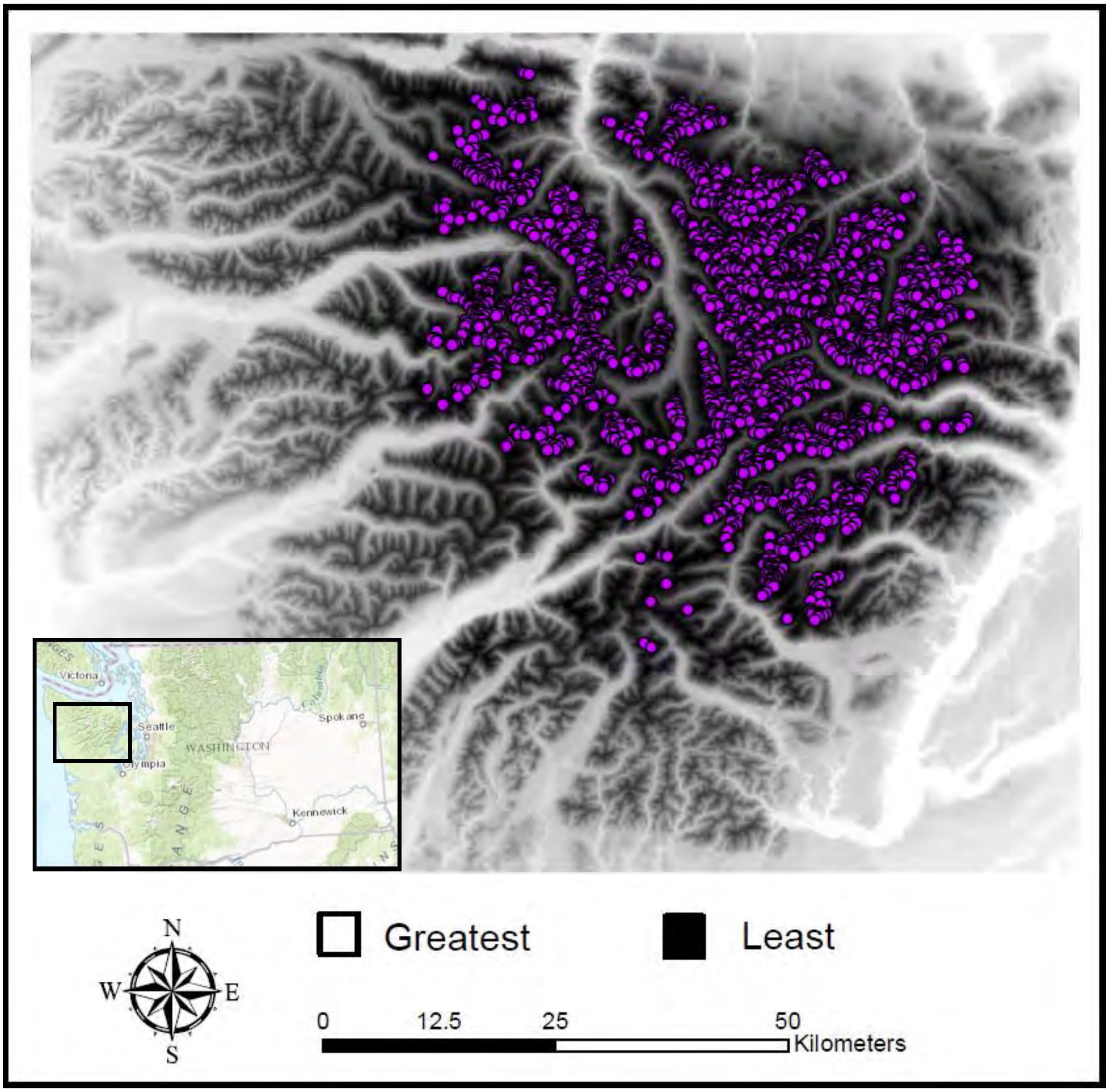


Figure 4-1. Landscape resistance based on elevation and potentially inhabitable points within the Olympic Range. Light colored areas correspond to areas of substantial resistance to movement while darker areas correspond to areas of low resistance. Each purple dot represents a landscape location that has the potential to be filled by an individual mountain goat in the model. A weighted selection was used to distribute points based on habitat suitability (the inverse of resistance; see text for details).

CDPOP requires the designation of XY coordinates for sites that could potentially be occupied by an individual animal. These potential sites are then used to create a cost distance matrix between sites. I determined that approximately 3,000 points or greater would be sufficient to encompass the maximum observed population (approximately 1,200 animals in 1983) while not limiting growth by lack of open space and allowing me to observe populations trends for several modeled years after the maximum observed population was attained. I used the inverse of the DEM-based resistance surface, prior to rescaling, to create a movement suitability model (Mateo-Sánchez et al. 2015). The movement suitability model was then rescaled to achieve suitability values from zero (low movement suitability) to one (high movement suitability). Random points representing potentially inhabitable spaces in areas of high movement suitability were generated by creating a raster of random floating-point values between 0.0 and 1.0 within the extent of my study area. After I subtracted the random floating point raster from the movement suitability model, I began selecting sites for potential occupancy beginning with the highest value. I found that using a minimum value of 0.931 resulted in 3,231 potentially occupied cells concentrated in areas of high habitat suitability. I then converted these cells to XY coordinates available for inhabitation by individual goats in the model. I created a cost distance matrix in UNICOR (Landguth et al. 2012*a*) simulator using the landscape resistance surface and the 3,231 point locations. UNICOR simulator uses a modified Dijkstra's algorithm (Dijkstra 1959) to calculate the least cost path from every specified location on a landscape to every other location (Landguth et al 2012). This cost distance matrix was used to inform mate movement and natal dispersal, as discussed in 4.2.3.

Genotypes for the founding goats were generated using genetic data recently collected by Shafer et al (2011) from locations near the original 1920's capture sites. Of 157 total samples selected by location, 50 were from the Selkirk Mountains in British Columbia and the remaining 107 were from the Coast Mountains near Juneau, Alaska (Figure 4-2).

Samples were not collected in the Chugach Mountains near Cordova, where two of the founder goats originated, and the nearest samples collected were southeast of the Chugach range on the Kenai Peninsula. The Kenai population is on the periphery of the range and exhibits particularly low measures of genetic variability (A. B. Shafer et al. 2011). Samples from that area would not represent the diversity within the Chugach range and as such were omitted. Because only two of the eight Alaskan founder goats were from the Chugach area, I decided to assign all of the Alaskan genotypes based on Juneau samples. Individual genotypes for each of the founder goats were randomly generated within CDPOP using the allele frequencies I calculated for 109 unique alleles at 19 loci from the dataset for each location.

Genetic diversity for the modeled population was evaluated using observed heterozygosity. Observed heterozygosity refers to the percent of loci containing heterozygous alleles for every individual goat. As a result of genetic drift (random fluctuations in allele frequencies), observed heterozygosity decreases over time at a rate correlated with population size (Hartl 2000, Gillespie 2004, Halliburton 2004, Templeton 2006). Mainguy et al. (2005) documented observed heterozygosity of 0.56 at Caw Ridge. Shirk (2009) reported considerably lower genetic diversity for the mountain goats within ONP (H_o 0.37). Modeled mean observed heterozygosity for the entire population was calculated within CDPOP for every modeled year.

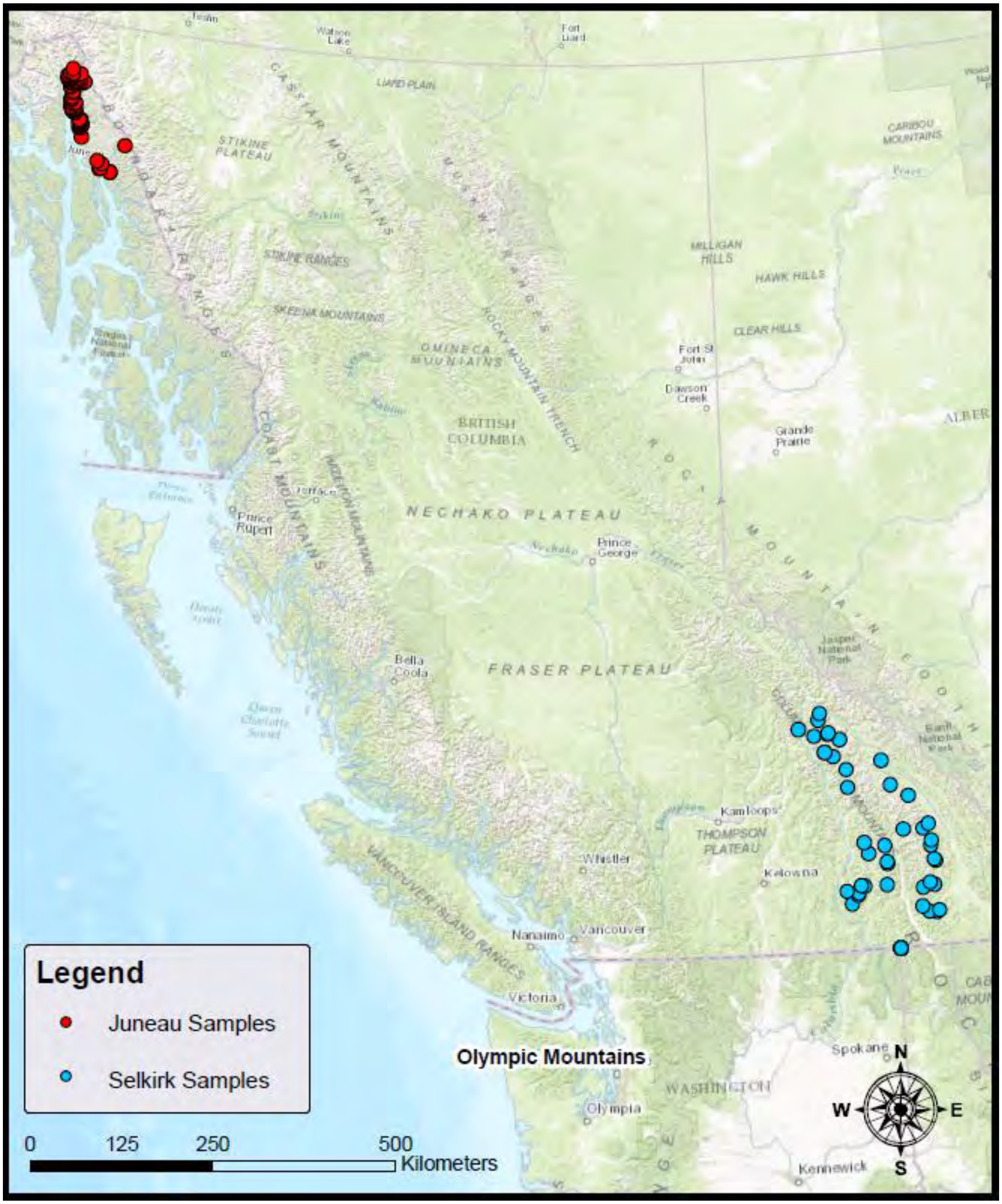


Figure 4-2. Allele frequency source samples from Alaska and British Columbia. Samples are a subset from Shafer et al (2011).

A single start date was necessary for initializing the model. Introductions potentially occurred over a five year period (1925 – 1930), with the largest number of goats being introduced toward the end of this period, so I chose 1928 as the initialization date. As such, the first population estimate in 1983 would have occurred at simulated year 55. I simulated 70 consecutive years (to 1998) in order to model population trends beyond this timeframe. Klahhane Ridge was the only subpopulation that reached carrying capacity. As such, I chose an exponential growth function as opposed to one limited by carrying capacity. It is likely that the vast expanse of connected prime habitat within the Olympic Range provides abundant unexploited areas for goat inhabitation, alleviating over-crowding and over-grazing, thereby moderating progress toward ecological carrying capacity (Varley 1996). Population dynamics over this 70 year period were simulated for three different scenarios. The first and second scenarios used parameter estimates specific to expanding populations, with one representing each plausible extreme for sex and total-animal combinations based on historical records. A total of 12 goats with a bias toward females (8 females and 4 males), hereafter referred to as "12 Founders", and a total of 11 goats with a bias toward males (6 males and 5 females), hereafter referred to as "11 Founders", were used to initialize these two simulations. The third simulation scenario was parameterized based on data from Caw Ridge (Festa-Bianchet and Cote 2008) and represents established population dynamics for comparison purposes. It was initialized using the 12 founding goats described above and hereafter will be referred to as "Caw Parameters". To asses variability in population growth, I performed ten replicate runs for each of the three scenarios. For every reported factor, I calculated confidence intervals around each year for the entire study period using the mean from the 10 replicate runs.

4.2 Model Parameterization

4.2.1 Mortality

Festa-Bianchet and Cote (2008) conducted the most extensive and well-documented mountain goat demographic study to date, spanning sixteen consecutive years in a marked population at Caw Ridge in Alberta, Canada. This study provides the only available sex- and age-specific survival data for mountain goats. The most frequent causes of mortality for mountain goats are predation (Rideout and Hoffmann 1975, Johnson 1983, Festa-Bianchet and Cote 2008) and incidences of natural mortality, with the latter occurring most often during the winter months due to greater susceptibility to starvation, accidents, and disease (Chadwick 1977, Johnson 1983, Stevens 1983, Swenson 1986). Juvenile survival, especially of kids, is highly variable (Stevens 1983, Gaillard et al. 1998, Festa-Bianchet and Cote 2008) and is impacted most by population density and winter conditions (Adams and Bailey 1982, Stevens 1983). Males experience greater mortality than females for all but their first year of life (Festa-Bianchet and Cote 2008, Pelletier et al. 2009), with less than 10% of yearling males in the Caw Ridge population surviving to 10 years (Festa-Bianchet and Cote 2008). This may be a result of the substantial reduction in time spent foraging during the breeding season combined with high energy expenditures associated with competition for mating (Mainguy et al. 2008, Pelletier et al. 2009). As a consequence of these factors, males likely start the winter in relatively poor body condition and may experience higher rates of mortality as a result (Pelletier et al 2009). Another contributing factor may be the habitat use patterns displayed by males (Festa-Bianchet and Cote 2008). In contrast to females in nursery groups, males make limited, predictable daily movements, travel in small groups, and utilize forest habitat with regularity, likely making them more vulnerable to predation. Adult female survival is greater than adult male survival (over 50% of yearling females survived to 10 years in the Caw Ridge population), and similar to other ungulates, is relatively high and stable throughout their prime-aged (two to seven or eight) years (Gaillard et al. 1998, Festa-Bianchet and Cote 2008).

When establishing mortality parameters in CDPOP, I used the Caw Ridge survival data (Festa-Bianchet and Cote 2008) for both males and females ranging from two to eight years old (Table A-1) due to the strength of the dataset and its relative agreement with findings from other studies. Survival of adults four to nine years old was 95.2% in the Caw Ridge population (Côté and Festa-Bianchet 2003). Smith (1986) observed 99% survival in adults two to eight years in three subpopulations in Alaska. Hayden (1984) reported a survival rate of 93% for adults over two years in an introduced population of mountain goats in Idaho. When parameterizing models informed by their own literature review, Naylor (1988) used an adult survival rate of 95% and Rice and Gay (2010) used a rate of 92.5% for adults three to eight years old. While direct comparison of these rates is complicated by the differences in adult age-class boundaries, it is evident that the data from Caw Ridge is representative of other populations.

The data from Festa-Bianchet and Cote (2008) used for survival parameters extended to 11 years for males and 16 years for females. While the oldest documented male and female mountain goats were 15 and 18 years old respectively, few survive past 12 years (Chadwick 1977, Festa-Bianchet and Cote 2008). I utilized the 11-year constraint applied by the Cote and Festa-Bianchet dataset to determine the maximum age for males in the simulation. Experimental model runs extending lifespan for males to the actual, observed maximum lifespan showed no appreciable difference in total population size because of the extremely small number of goats surviving to this maximum expectancy. I based the maximum age for females on data from Stevens' (1983) work in the Olympics. At the cessation of that study, one 12-year-old female represented the oldest documented goat in the range, supporting the fact that few survive past 12 years while also suggesting that some may live until at least 13. As such, I set maximum age for females in the model at 13 years.

With the lifespan of both sexes shortened relative to the Caw Ridge data, age-specific survival for individuals nearing the end of life needed to be adjusted accordingly. The mean survival rates for males and females nine years and older in the Caw Ridge population are 71% and 84% respectively. Data on age-specific survival rates for older goats in introduced populations is sparse. Smith (1986) evaluated the rates and causes of mortality within three expanding subpopulations of mountain goats near Ketchikan, Alaska. The annual survival rate for goats over 8 years was 68%. Based on the male to female ratio for each stage from Hamel et al (2006), Rice and Gay (2010) partitioned this pooled survival rate by sex. They calculated a survival rate for animals nine years and older of 71% for females and 58% for males. I calculated the mean survival rate for goats nine years and older using the Caw Ridge and the partitioned Ketchikan data, then reduced survival by one percent for both sexes to slightly bias this rate toward the expanding population values. This resulted in annual survival rates of 76.5% and 63.5% for females and males nine years and older in the modeled population.

For many species of ungulates, adult survival varies minimally between established and expanding populations while juvenile survival is much more sensitive to density effects (Gaillard et al. 1998). I calculated mean kid and yearling survival rates specific to expanding and established populations (70.5% and 66% respectively) using values reported in the literature (Table A-3). I decreased the calculated annual mean kid survival rate for expanding populations by 1 to account for the potential influence of the Klahhane Ridge subpopulation. As described previously, it was determined that this subpopulation had reached ecological carrying capacity. In 1981 there were an estimated 229 goats at Klahhane Ridge (Houston et al. 1994), representing at least one-fifth of the total population at that time. If kid survivorship in the Klahhane subpopulation followed trends of established populations observed elsewhere, then the influence of this sizeable subpopulation would slightly reduce mean kid survivorship for the entire range. There has been no significant difference noted between the survival rates of male and female kids (Stevens 1983, Festa-Bianchet and Cote 2008) so I applied the 69.5% survival rate to both sexes. The calculated mean yearling survival rate for expanding populations was 79% when pooled across sexes. Male and female survival rates for this age class within the Caw Ridge population are representative of this pooled value and as such were retained. CDPOP functions by removing a user-input percent of individuals rather than retaining them, essentially applying mortality to the population. In order to operate within this framework, I subtracted every age- and sex-specific survival rate from 100 to convert the percent of individuals surviving to the percent experiencing mortality.

4.2.2 Female Reproductive Rate

Mountain goats mate during a rutting period that lasts from mid-November until early December (Smith 1976, Festa-Bianchet and Cote 2008, Mainguy et al. 2008). During this period females are in estrous for approximately two days and are constantly courted by a male (Mainguy et al. 2008). While it has been documented that both males and females can have multiple mates, this is a much more common behavior for males (Mainguy et al 2008). Female goats likely need to attain a threshold body weight before becoming sexually mature (Houston et al. 1989, Festa-Bianchet and Cote 2008). In introduced and captive populations, where ample forage is present, females may reach sexual maturity as yearlings. Within these populations, primiparity (giving birth for the first time) has been observed as early as 2 years of age with most females reproducing by 3 years (Stevens 1983, Houston et al. 1989, Bailey 1991). In most native populations however, primiparity does not occur until 3 years and the majority of females will be four or five before first giving birth (Chadwick 1974, Smith 1976, Festa-Bianchet and Cote 2008). Males can become sexually mature as yearlings (Henderson and O'Gara 1978, Houston et al. 1989) but the timing of their participation in the rut varies (Chadwick 1974, Johnson 1983). Males most actively participate in the rut when they have attained their peak mass, which occurs at around six to eight years in native populations (Mainguy and Côté 2008) but can occur earlier in newly introduced and captive populations (Houston et al. 1989). During a study of the native Caw Ridge population, no males three years or younger were observed to take a mate (Mainguy et al. 2008) while in a captive herd all males bred as yearlings (Houston et al. 1989).

Female reproductive rate varies considerably and is likely related to winter conditions endured either during or one year prior to gestation (Brandborg 1955, Stevens 1983, Bailey 1991). Density and time since establishment can also influence reproduction within a population, likely due to differences in resource availability (Smith and Fowler 1981, Johnson 1983, Gaillard et al. 1998, Côté and Festa-Bianchet 2003, Lemke 2004). Colonizing herds as well as populations in areas where the density has been substantially reduced often exhibit higher reproductive rates than native or high-density populations (Caughley 1970, Johnson 1983, Swenson 1986, Bailey 1991, Dane 2002). After the initial increase, female reproductive rate continues to remain relatively high until approximately 13 years of age at which point it declines slightly (Festa-Bianchet and Cote 2008). This reproductive senescence likely has a minimal impact on population dynamics because few females actually survive to this age and the majority of those that do continue to produce kids (Festa-Bianchet and Cote 2008). Females generally give birth to a single kid (Adams and Bailey 1982, Johnson 1983, Cote and Festa-Bianchet 2001), but incidences of twinning also occur with rates varying between established and introduced populations (Table A-4).

I based female reproductive rates on a compilation of data from colonizing herds and the Caw Ridge study. Again, the latter, 16-year study provided the most comprehensive, age-specific dataset. Because early primiparity is characteristic of colonizing populations but was not observed in the native Caw Ridge population, I used the mean reproductive rates for two, three, and four year olds in three introduced populations to supplement the Caw Ridge data (Table A-2). These mean values were reduced by 3 to reflect the lower reproductive rates documented within the subpopulation on Klahhane Ridge. Reproductive rates for females five years and older were based on the Caw Ridge dataset. After several iterative model runs, I set the twinning rate at 5.7%, the mean rate observed by Stevens (1983) for expanding subpopulations across the range. Restrictions within the model limited polygamy to males exclusively rather than both sexes. Mainguy et al (2008) documented half the females in one rutting season out of the three observed taking multiple mates. This suggests polygamy by females may be atypical and as such warrants the imposed restriction.

Table 4-1. Model parameters: annual survival (S) and reproductive rate (RR) by sex (F/M) and age class. Parameters were established using data from Caw Ridge in Alberta, Canada (Festa-Bianchet and Cote 2008) as the baseline. Adjustments were made to survival rates for both sexes at age classes 0 and 9+, and to reproductive rate for age classes 2-4 to reflect demographics for expanding populations.

Years	*0*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*
S F	69.5	84.7	90	90	97.5	95	95	96	91.5	76.5	76.5	76.5	76.5	76.5	0
S M	69.5	73.5	74	75	92	78.5	92	86	70	63.5	63.5	63.5	0	0	0
RR F	0	0	13.4	61.8	70.8	67.2	73.8	73	78.6	84	81.4	81.8	78.3	72.2	0

4.2.3 Movement

CDPOP simulates two types of movement across the landscape: mate movement and natal dispersal. Mate movement occurs every year that an individual is considered sexually mature. Distance travelled for this movement is determined using a probability function constrained by a maximum threshold cost distance, both of which are specified by the user. From each female, the distance to every male on the landscape can be quantified on the basis of a particular cost distance value. This value is converted to a probability value with all cells outside of the user specified threshold becoming a probability of zero. The mating male is chosen using a weighted random draw from the specified probability distribution. This process is then repeated with the next female in an order determined by random draw and continuing through every female. Because male polygamy has been specified, an individual male may be chosen to mate multiple times. Natal dispersal occurs only once during the individual's first year and involves moving from the mother's space to a unique location. Distance of this dispersal is determined in the same manner as mate movement but, unlike the latter, can be specified by sex.

Mate Movement

Throughout the rut, males will expend considerable amounts of energy moving from ridge to ridge as they travel between area subpopulations in search of receptive females (Geist 1964, Smith 1976, Chadwick 1977, Smith and Raedeke 1982, Fox et al. 1989). The actual distance traveled depends on the topography of a particular area and the distance between neighboring groups (Côté and Festa-Bianchet 2003). This rut movement often represents the greatest distance travelled by a male (Smith and Raedeke 1982, Fox et al. 1989). Females, in contrast, predominantly stay within their home range (Geist 1964, Chadwick 1977, Smith and Raedeke 1982, Fox et al. 1989). Smith and Raedeke (1982) present data for the movement of two radio-collared males during the rutting season in 1980 and 1981, a third individual male during the 1981 rut. This study was conducted in a region climatically similar to the Olympic Mountains with similar spatial distribution of goat habitat. Movement distances were extrapolated (Figure 4 in Smith and Raedeke 1982) and ranged from two to 25 kilometers with a mean distance travelled of 6.5 kilometers (standard deviation: 5.5 kilometers). Each movement distance represented kilometers travelled between different subpopulations, with multiple visits recorded for a single male during each rutting season, rather than a total distance for the entire period.

In order to convert Euclidean distances reported in the literature to cost distances for the model, I created a Euclidean-distance matrix using the same process described for the cost distance matrix. I then estimated the approximate relationship between every value in the Euclidean-distance matrix and the corresponding value in the cost distance matrix using simple linear regression (adj. $r^2 = 0.9964$; $p<0.0001$): $ED = 0.89*CD + 133$.

I specified mate movement using a Gaussian probability function with a mean cost distance of 7217 and a standard deviation of 6099 (Euclidean distance mean: 6.5 kilometers; SD: 5.5 kilometers). The maximum cost distance threshold was 27900 (Euclidean distance of 25 kilometers).

Natal Dispersal

Mountain goats typically inhabit summer and winter ranges, migrating seasonally to avoid the deepest snowpack and to access forage (Rideout 1977, Stevens 1983, Fox et al. 1989, Varley 1996, Rice 2008). Females in nursery groups often travel extensively across summer ranges while males utilize areas on the peripheral of this range, spending a greater amount of time in forested areas and moving substantially smaller distances (Festa-Bianchet and Cote 2008). The extent of movement within and between seasonal ranges is largely influenced by topography (Johnson 1983, Festa-Bianchet and Cote 2008). Fidelity to home range is exhibited for both sexes, with females tending to remain within natal ranges and males often dispersing to an independent range that is used habitually once established (Chadwick 1977, Hutchins 1984). Natal dispersal, as defined by Greenwood (1980), involves the movement of an individual from its birthplace to a new location. While natal dispersal is significantly more common for males, it has been noted for females in several populations as well (Hutchins and Stevens 1981, Johnson 1983, Stevens 1983, Festa-Bianchet and Cote 2008). Dispersers of both sexes are predominantly younger, generally between one to three years of age (Stevens 1983, Festa-Bianchet and Cote 2008).

Stevens (1983) conducted a detailed study of mountain goat dispersal in the Olympic Range and defined five categories of long distance (travelling greater than 15 kilometers) movement (migrators, probers, permanent, wanderers, and undefined). Two females, categorized as migrators because their movement was seasonal and repeated annually, each moved 16 kilometers. All other long distance movements were 19 kilometers or greater for either sex. Permanent movements, those resulting in an individual taking up residence in a new area for at least 2 years, resulted in the greatest distances travelled for both sexes. Four females and eight males made permanent movements, with mean distances of 51.8 and 35.5 kilometers travelled respectively (range of 22 to 54 kilometers and a mean of 40.9 kilometers for both sexes combined). From the subpopulation on Klahhane Ridge, the only subpopulation within the Olympic Range considered to have reached carrying capacity, 19.6% of all males and 5.5% of all females emigrated (10% of the total population). Emigration from other subpopulations within the Olympic range was much lower, with 9% of males and no females observed leaving their natal range; however, this figure is based on a sample size that is quite small in comparison to the Klahhane Ridge population. Across all subpopulations in the Olympics, females dispersed significantly farther than males. Festa-Bianchet and Cote (2008) saw 59% of two- and three-year old males disappearing from Caw Ridge during July and August. (Note that the percent dispersing reported for Klahhane Ridge was based on *all* males or females within the subpopulation rather than just two- and three-year-olds as reported here.) While a portion of this disappearance could be explained by mortality, the authors hypothesize that most of these young males emigrated to a new population. Two females, one yearling and one two year old, were known to have emigrated from Caw Ridge.

Based on the observations of Stevens (1983), I defined natal dispersal as movement greater than or equal to 17 kilometers from an individual’s birthplace. Movement below this threshold is likely movement within the natal range, including annual migration. I used a negative exponential function to determine probability of dispersal for both sexes and manipulated the parameters until I achieved approximately 14% of total males (49% of male kids) and 2% of total females (12% of female kids) dispersing (moving a distance greater than or equal to 17 kilometers). These figures are similar to the range of values reported by Festa-Bianchet and Cote (2008) as well as Stevens (1983). I used a maximum distance threshold of 54 kilometers (CD = 60,322) for females and 48 kilometers (CD = 53,614) for males. A summary of modeled parameters is included in the appendix A (Table A-5).

4.3 Sensitivity Analyses

After parameterizing the model, I assessed relative sensitivity of the modeled population to changes in annual reproductive rate, juvenile (kids and yearlings) mortality, and male and female mortality (all age classes for each sex). Using the "12 founder" scenario to initialize the model, I individually increased each parameter by 10% then subsequently decreased each parameter by 10% and simulated population growth over time. To asses variability in population growth, I performed 10 replicate runs for each parameter.

4.4 Model Validation 1990 - 2030

I used the single "12 Founder" simulation run most closely representing the mean of the 10 replicate runs at simulated year 55 to initialize model validation. I reduced this modeled 1983 population to the observed population estimate of 389 (95% CI 181 - 597) goats observed during the aerial survey in 1990. This reduction was intended to incorporate the effect of the animals removed through translocation and harvest activity between 1981-89, the loss of kids orphaned by these actions, and possible increased mortality due to relatively harsh winters toward the end of this period. I then simulated population growth from 1990 to 2030 using the parameters previously outlined. Four sex-based removal scenarios were evaluated: one simulated a completely randomized removal and three simulated removals biased toward females with 70%, 75% and 80% of those removed being female. To asses variability in population growth, I performed 10 replicate runs for each removal scenario.

5.0 Results

5.1 Model Calibration

I used the 1983 aerial survey population estimate of 1,175 plus an additional 213 goats as the population reference value for model calibration. Prior to the 1983 survey, 151 goats were removed from Klahhane Ridge (Houston et al. 1994). I assumed random removal which would result in at least 62% of those removed being female. Based on data from the 1985 – 1989 removals (Houston et al. 1994), I also assumed that 66% of these females were lactating resulting in 62 associated kid deaths. Actual removals prior to 1983 combined with associated kid deaths (213 total mountain goats) were not accounted for in the model and were therefore added to the 1,175 population estimate producing a new, population reference value of 1,388 (95% CI 1,053 – 1,723).

At year 55 none of the confidence intervals for the three modeled scenarios overlap, indicating significant difference between them all (Figure 5-1). The “12 Founder” population model most closely matched the observed population estimate +213, with a modeled mean total population of 1,449 (95% CI 1,328 – 1,570), only 4.4% above the reference value. The "11 Founder" scenario produced a modeled mean population of 1,162 (95% CI 1,030 – 1,294), which is 16.3% below the reference value. While this scenario does not represent the 1983 population estimate as well as the "12 Founder" scenario, the modeled mean of the "11 Founder" scenario is still within the 95% confidence limits of the 1983 population estimate (1,053 – 1,723). "Caw Parameters" resulted in a modeled mean population of 346 (95% CI: 323 - 369), well below the 95% confidence limits of the 1983 population estimate at 75% lower than observed.

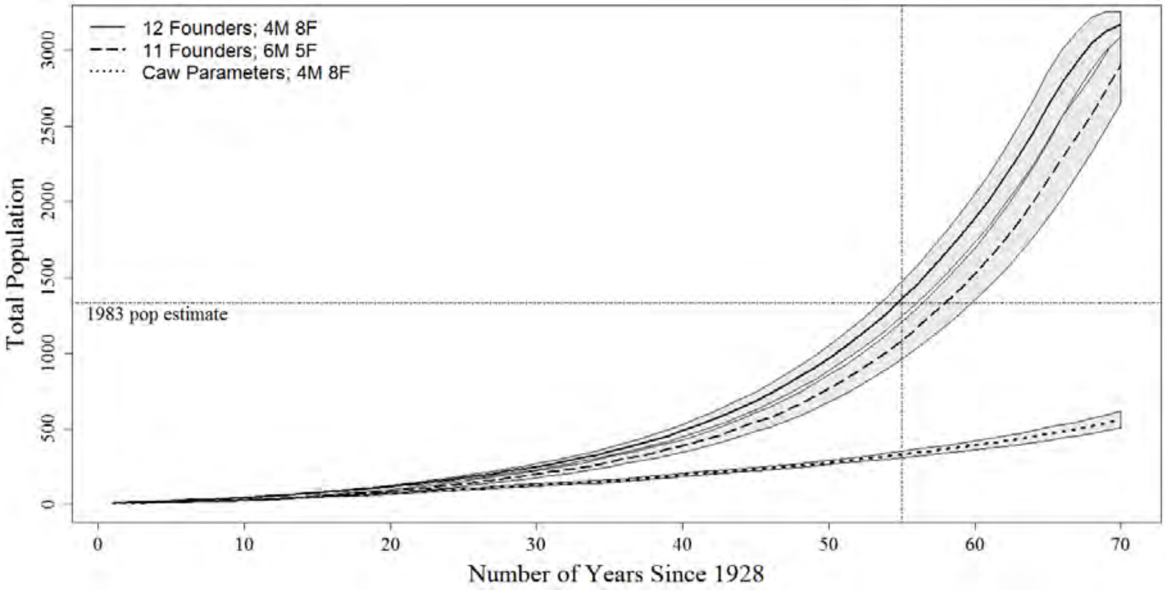


Figure 5-1. Modeled mean population of mountain goats. The vertical dotted line at 55 years since 1928 corresponds to the year 1983 with the horizontal line indicating the actual population estimate of 1175 with 213 individuals added to account for removals prior to 1983 and presumed, associated kid deaths not included in the model. Two modeled scenarios used parameter estimates for expanding populations and represented the most realistic extremes based on anecdotal accounts ("12 Founders" and "11 Founders"). The third scenario used parameter estimates for the established population at Caw Ridge ("Caw Parameters"). Shaded areas correspond to 95% confidence limits for each modeled scenario.

The two modeled expanding population scenarios produced similar male to female ratios: 0.625 (95% CI 0.607 – 0.643) for the "11 Founders" scenario and 0.628 (95% CI

0.622 – 0.635) for “12 Founders” (Figure 5-2). The modeled established population (“Caw parameters”) consistently had fewer males to every one female than either of the modeled expanding populations (“11 Founders” or “12 Founders”). At year 55 the model using Caw Ridge parameter estimates had a male to female ratio of 0.546 (95% CI 0.524 – 0.569).

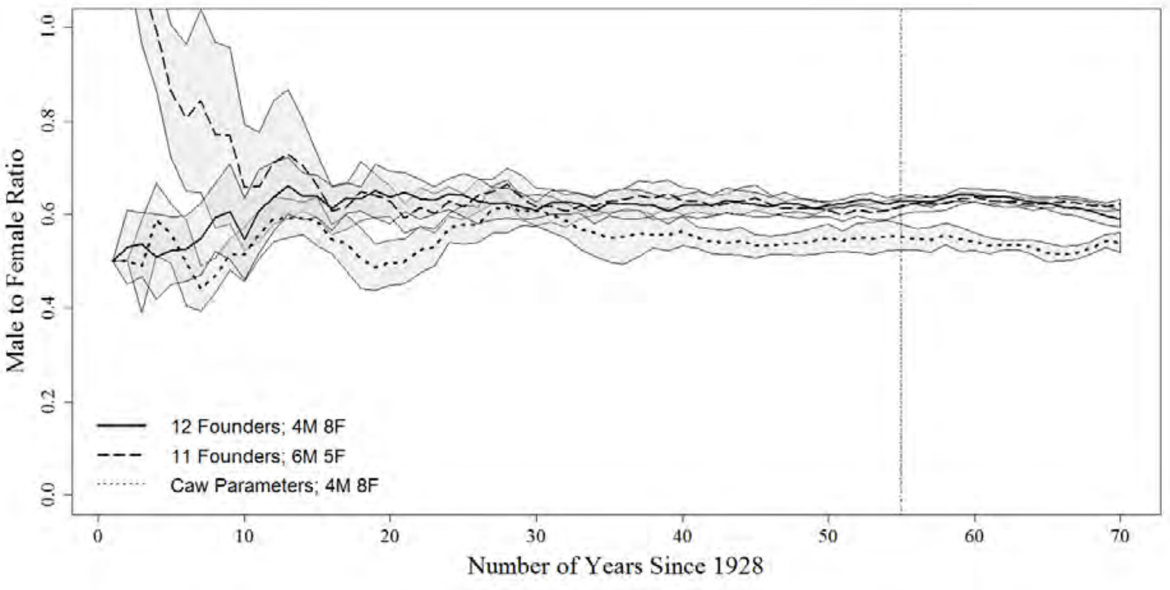


Figure 5-2. Modeled male to female ratio. Two modeled scenarios used parameter estimates for expanding populations and represented the most realistic extremes based on anecdotal accounts (“12 Founders” and “11 Founders”). The third scenario used parameter estimates for the established population at Caw Ridge (“Caw Parameters”). Shaded areas correspond to 95% confidence limits for each modeled scenario. Modeled expanding populations had a greater number of males to every one female than the modeled established population. The vertical dotted line at 55 years since 1928 corresponds to the year 1983.

Modeled observed heterozygosity (H_o) was similar for all scenarios with substantial overlap between confidence limits (Figure 5-3). The “Caw Parameters” scenario exhibited the highest H_o at the start of the simulated period but ended with the lowest, falling below the “11 Founder” scenario at year 20 and the “12 Founder” scenario at year 51. The “11 Founder” scenario exhibited the greatest H_o throughout the majority of the period. At year 55, H_o for the “11 Founder”, “12 Founder” and “Caw Parameter” scenarios were 0.535 (95%

CI 0.524 – 0.546), 0.518 (95% CI 0.501 – 0.535) and 0.515 (95% CI 0.488 – 0.542) respectively. At year 55, all modeled scenarios exhibited much higher H_o than observed by Shirk (2009) in ONP and H_o values below those reported for Caw Ridge (Mainguy et al. 2005).

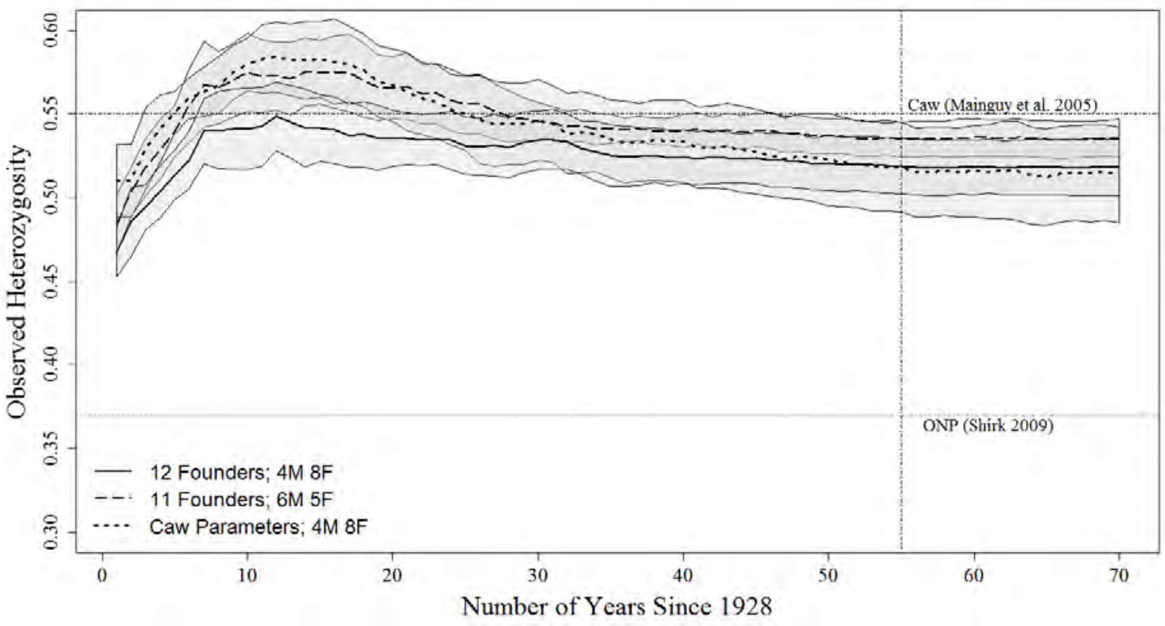


Figure 5-3. Modeled observed heterozygosity. Horizontal dotted lines show actual observed heterozygosity for Caw Ridge (top) and Olympic National Park (bottom). The vertical dotted line at 55 years since 1928 corresponds to the year 1983. Two modeled scenarios used parameter estimates for expanding populations and represented the most realistic extremes based on anecdotal accounts ("12 Founders" and "11 Founders"). The third scenario used parameter estimates for the established population at Caw Ridge ("Caw Parameters"). Shaded areas correspond to 95% confidence limits for each modeled scenario with substantial overlap exhibited between all scenarios.

From the "12 Founder" simulation, I selected the model run that most closely represented the population mean of all runs at year 55 to evaluate natal dispersal. This run simulated a population of 1,469 which is approximately 20 goats greater than the mean for all model runs and 81 greater than the observed 1983 population estimate +213 goats. Modeled dispersal occurred in a predominantly southern and slightly eastward direction. Males dispersed in greater numbers than females with both sexes appearing to disperse similar distances. Consistent with observations, modeled dispersal in 1938 shows goats inhabiting Mount Appleton and Klahhane Ridge (Figure 5-4). Both sexes are present at these sites, which contradicts early records that did not document nannies with kids-at-heel until 25 – 30 years later. The model indicates that Mount Olympus and the central interior portion of the range contain individuals of both sexes. In reality, these areas were last to be populated. One male and one female reached the eastern border of Olympic National Park and several goats are approximately eight kilometers from Mount Constance where anecdotal records document the first sighting in 1935.

Modeled dispersal in 1947 (Figure B-1) shows increasing populations in the central interior range, which contradicts observations. Modeled goats continued to move south with several having reached Mount Anderson within a time period similar to that observed. The ridges surrounding the headwaters of Gray Wolf River and its two largest tributaries, Cameron Creek and Grand Creek, are sparsely populated. By 1959, one goat had dispersed as far south as Sawtooth Ridge (Figure B-2), approximately 5 kilometers from the southern National Park boundary. Historical reports noted the first goat on Sawtooth Ridge in 1957 and past the southern border in 1960. Modeled dispersal progress in 1968 (Figure B-3) shows the greatest density of goats near Mount Olympus and Mount Ferry. A sizeable population of goats exists outside the eastern National Park boundary. One modeled female goat is approximately 69 kilometers from the release site and represents the greatest dispersal distance for that time period.

Modeled dispersal in 1983, the year corresponding to the first aerial survey, shows colonization across the Olympic Range (Figure 5-5). Pockets of densely distributed goats occur at Klahhane Ridge, Mount Appleton, Mount Olympus, Mount Ferry, and Mount Dana. The ridges around Gray Wolf River and its tributaries are well populated. While most of the goats occur within ONP, a sizeable population inhabits terrain outside the eastern park boundary and non-park lands to the south and southwest are occupied by several smaller groups. The greatest distance between release site and an individual goat is approximately 70 kilometers.

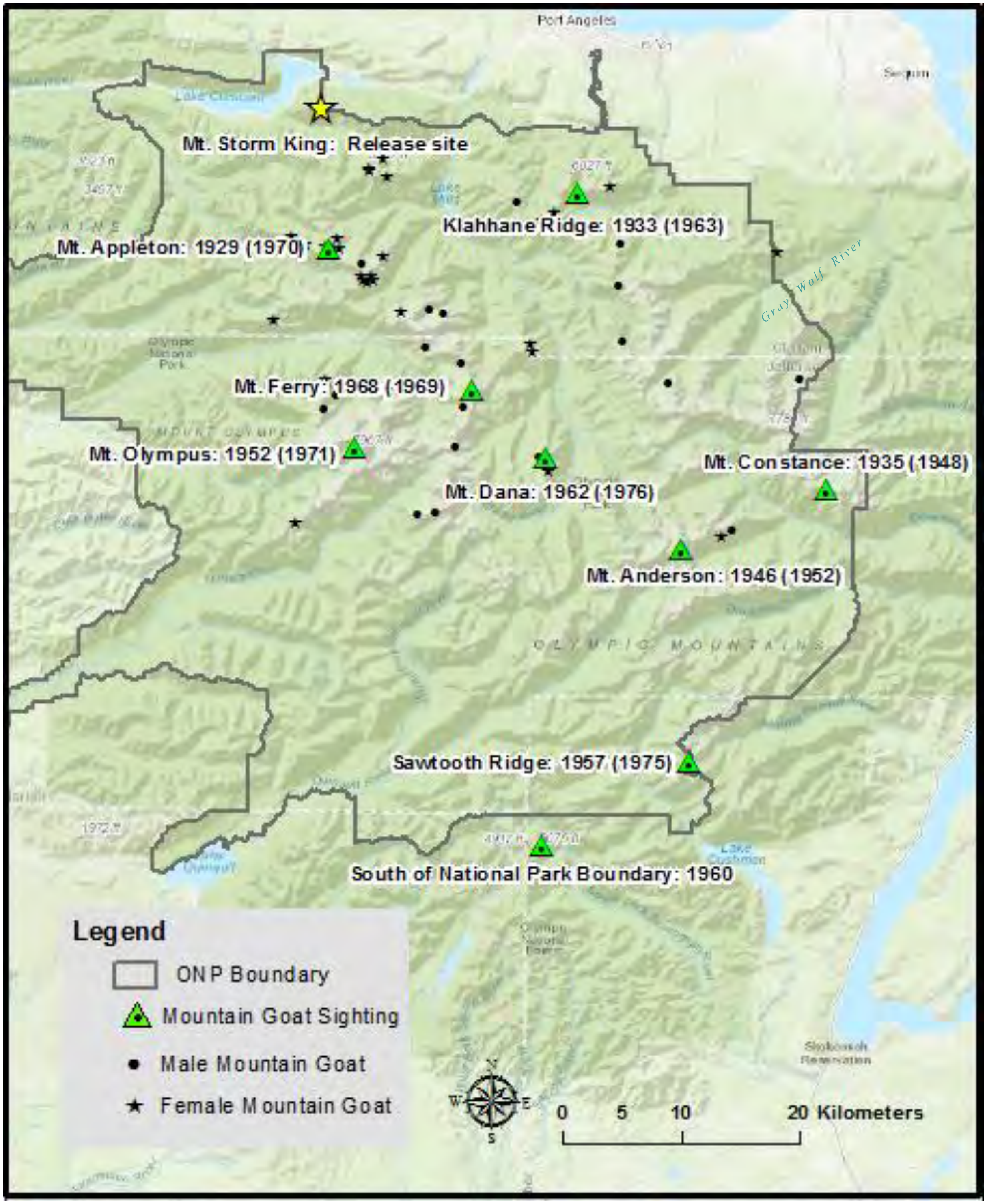


Figure 5-4. Modeled dispersal by sex for 1938. Male mountain goats are symbolized by closed circles and females are symbolized by filled stars. Year of actual first mountain goat sightings at sites specified by green triangles shown followed by year of first nanny with kid at-heel sightings (parentheses). Modeled dispersal in 1938 shows goats present at Mount Appleton and Klahhane Ridge, which is consistent with observations.

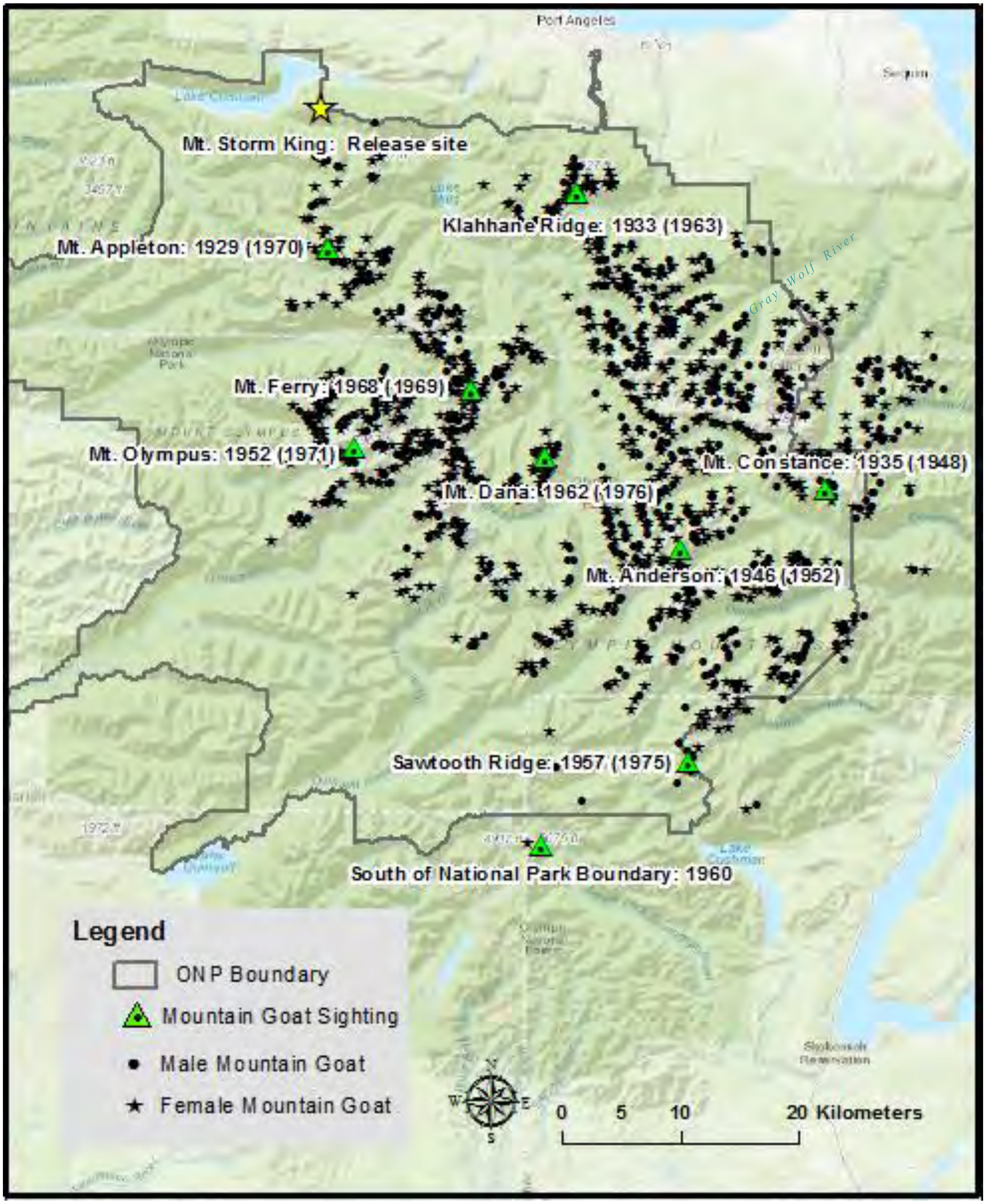


Figure 5-5. Modeled dispersal by sex for 1983.Male mountain goats are symbolized by open circles and females are symbolized by filled stars. Year of actual first mountain goat sightings at sites specified by green triangles shown followed by year of first nanny with kid-at-heel sightings (parentheses). Modeled dispersal in 1983 shows colonization of the entire range, which is consistent with observed.

5.2 Sensitivity Analyses

Adult (2+ years) mortality sensitivity analyses revealed striking differences between sexes. Both a 10% increase and a 10% decrease in male mortality produced modeled mean population estimates that varied little from the "12 Founder" scenario (1,404 and 1,445, respectively; Figure 5-6). Ninety-five percent confidence intervals on each sensitivity parameter broadly overlapped, with both encompassing the confidence intervals of the "12 Founder" scenario as well.

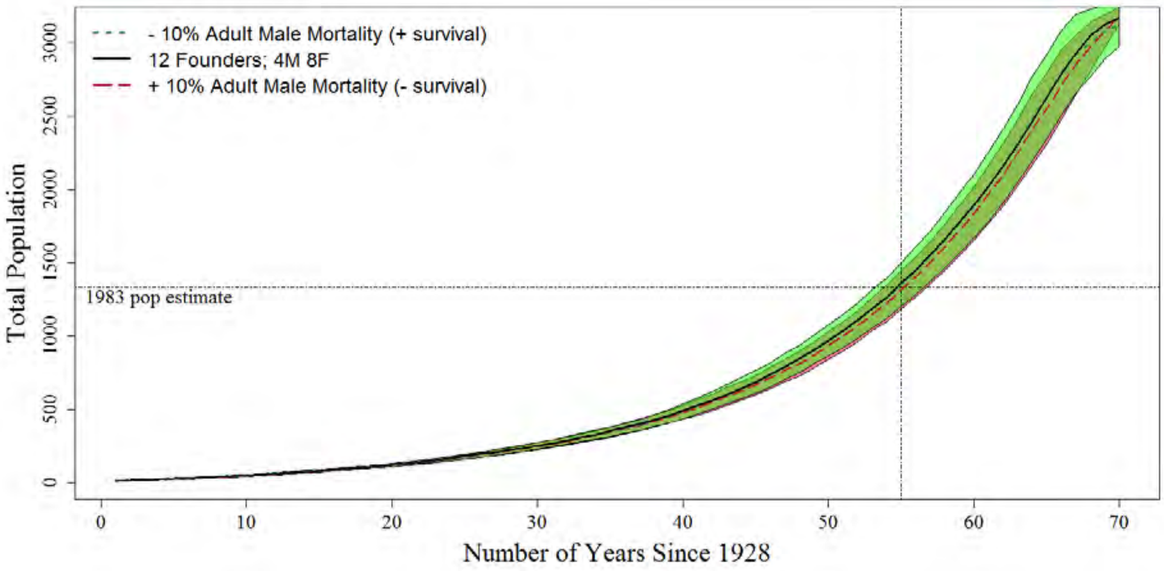


Figure 5-6. Adult male (2+ years) mortality sensitivity analysis. The intersection of the vertical and horizontal lines marks the 1983 population estimate +213 for removals prior to 1983 and related kid mortality. The green dotted line represents a 10% decrease in mortality (increase in survival) for adult males, while the red dashed line shows a 10% increase in mortality (decrease in survival). The difference between the two is virtually indiscernible indicating population growth has limited sensitivity to adult male mortality. The "12 Founder" scenario is represented by the solid black line. Envelopes around each line show 95% confidence limits.

Modeled population growth was much more sensitive to changes in adult female mortality than adult male. A 10% decrease in mortality (increase in survival) for females two years and older resulted in a modeled mean population of 2,007 (95% CI 1,850 – 2,164) at year 55, representing a 39% increase from the "12 Founder" modeled mean population the same year (Figure 5-7). A 10% increase in mortality (decrease in survival) for adult females produced a modeled population mean 27% lower than the "12 Founder" scenario (1,061 95% CI 980 – 1,141). Both the positive and negative adjustments to adult female mortality produced modeled mean population estimates significantly different from the "12 Founder" scenario. Additionally, female mortality sensitivity analyses were statistically different from male and represented a significantly greater impact on modeled population growth.

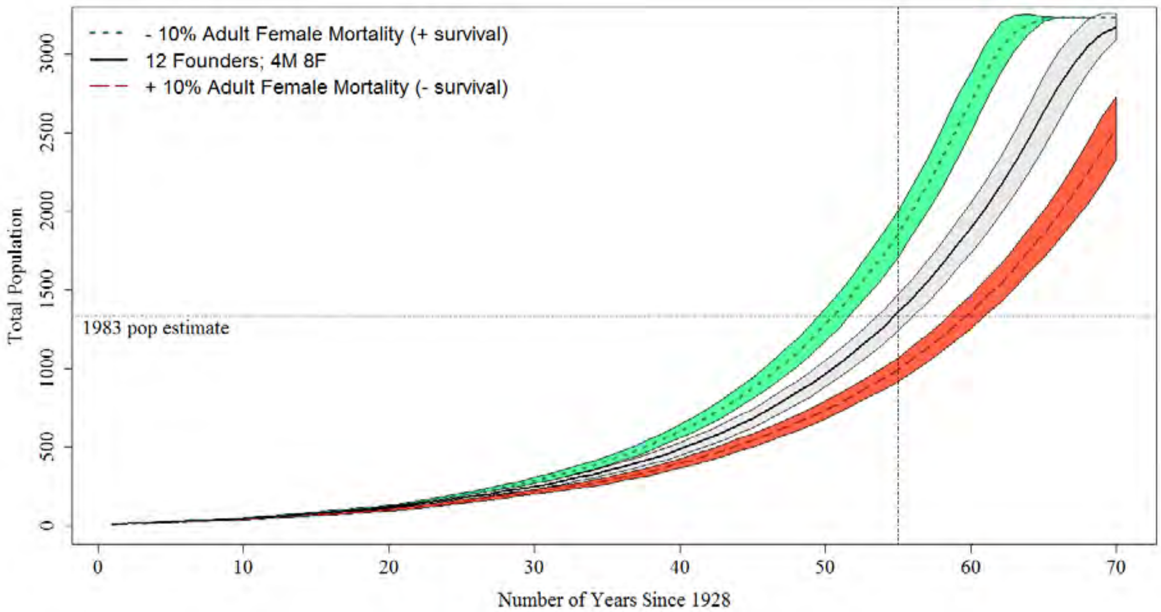


Figure 5-7. Adult (2+ years) female mortality sensitivity analysis. The intersection of the vertical and horizontal lines marks the 1983 population estimate +213 for removals prior to 1983 and related kid mortality. The green dotted line represents a 10% decrease in mortality (increase in survival) for adult females, while the red dashed line shows a 10% increase in mortality (decrease in survival). The "12 Founder" scenario is represented by the solid black line. Envelopes around each line show 95% confidence limits. Adult female mortality had a much greater impact on population growth than adult male.

Modeled population growth was more sensitive to changes in both juvenile mortality (kids and yearlings) and annual reproduction, than changes in adult mortality. A 10% decrease in juvenile mortality (increase in survivorship) resulted in a population mean of 2,253 at year 55 (95% CI 2,071 – 2,434) which is significantly different from the "12 Founder" mean and represents a change of approximately 55% (Figure 5-8). A 10% increase in juvenile mortality (decrease in survivorship) produced a population of 847 at year 55 (95% CI 778 – 915), a negative change of approximately 42%, which is significantly different from both the "12 Founder" scenario and the 10% decrease in juvenile mortality (increase in survivorship).

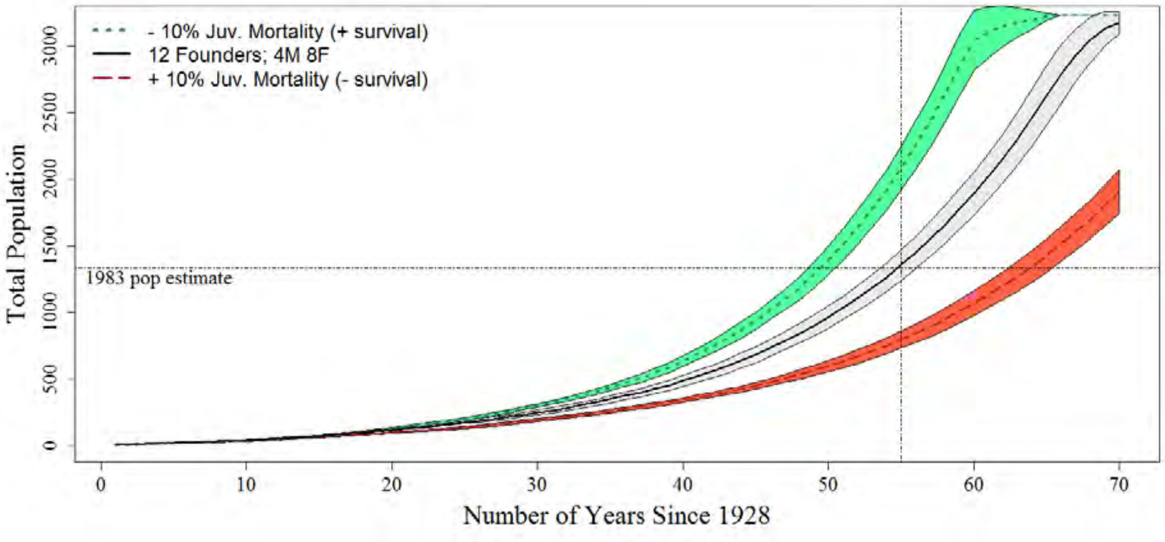


Figure 5-8. Juvenile mortality sensitivity analysis. The intersection of the vertical and horizontal lines marks the 1983 population estimate +213 for removals prior to 1983 and related kid mortality. The green dotted line represents a 10% decrease in mortality (increase in survival) for one and two year olds of both sexes, while the red dashed line shows a 10% increase in mortality (decrease in survival). The "12 Founder" scenario is represented by the solid black line. Envelopes around each line show 95% confidence limits.

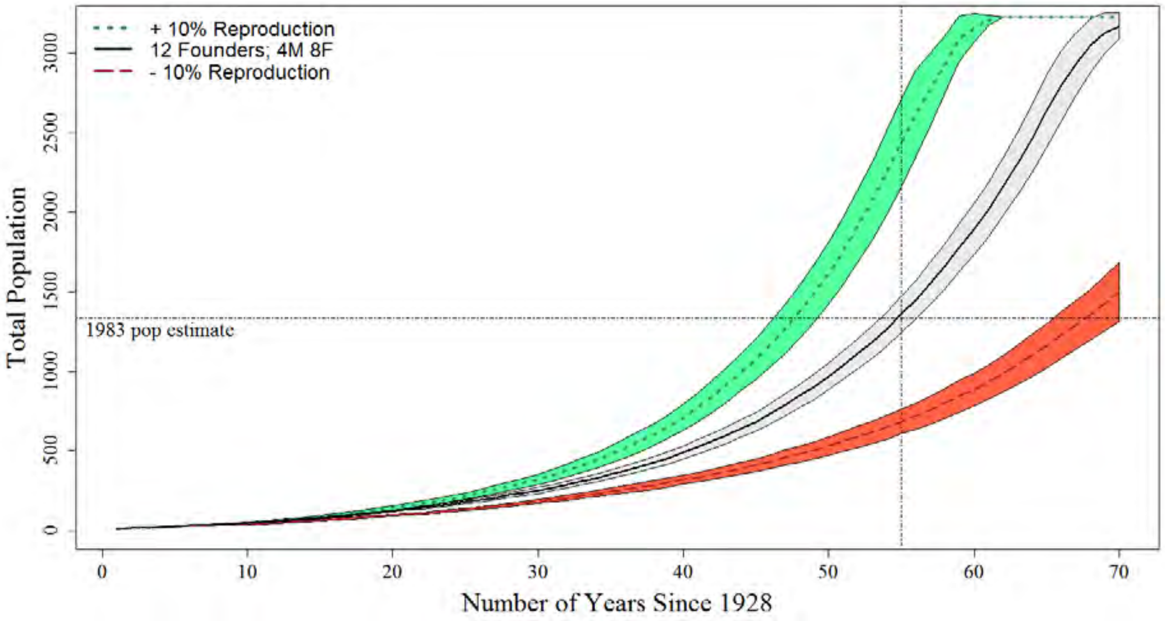


Figure 5-9. Annual reproduction sensitivity analysis. The intersection of the vertical and horizontal lines marks the 1983 population estimate +213 for removals prior to 1983 and related kid mortality. The green dotted line represents a 10% increase in the percent of females reproducing annually (ages 2+), while the red dashed line shows a 10% decrease. The "12 Founder" scenario is represented by the solid black line. Envelopes around each line show 95% confidence limits.

When evaluating the sensitivity of annual reproduction, I observed a similar trend with both the increase and decrease in reproduction producing significantly different population means at year 55 (2,620 95% CI 2,345 – 2,892 and 719 95% CI 634 – 803 respectively). Manipulating annual reproduction by +/- 10% for each age class produced a greater percent change than the +/- 10% manipulation to juvenile mortality. However, there is slight overlap in the 95% confidence intervals of both the positive and negative manipulation of these parameters indicating the difference in sensitivity between annual reproduction and juvenile mortality may not be significant. Modeled population growth was significantly more sensitive to changes in annual reproduction than to adult female mortality.

5.3 Model Validation: 1990 - 2030

I selected the model run that most closely represented the population mean of all runs at year 55 to initialize model validation. This run simulated a population of 1,469 which is approximately 20 goats greater than the mean for all model runs and 81 greater than the observed population estimate +213. I removed 1,080 individual goats, using four removal scenarios, in order to initialize the model validation run with the 389 goats estimated for the 1990 aerial survey.

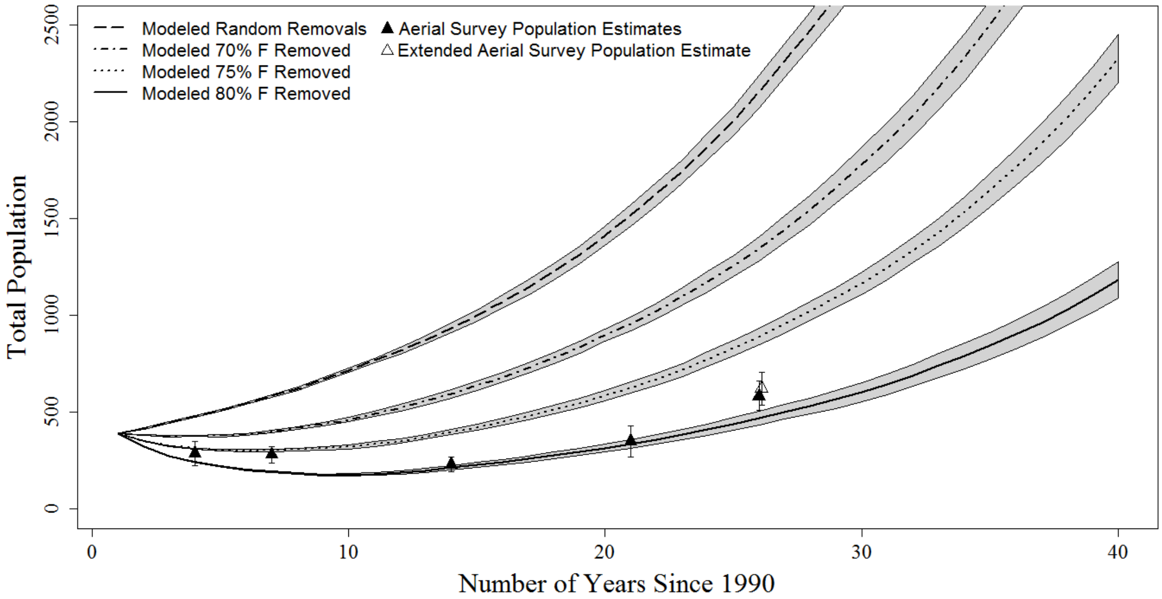


Figure 5-10. Modeled population growth from 1990 – 2030. Four removal scenarios were evaluated: 1) random removals (dashed line), 2) 70% females removed (dashed/dotted line), 3) 75% females removed (dotted line), and 4) 80% females removed. Shaded area around each line shows 95% confidence limits. Aerial survey (>1,540 meters) population estimates for 1994, 1997, 2004, 2011, and 2016 are represented with closed triangles. Error bars show 95% confidence limits on each estimate. The open triangle represents the 2016 population estimate for an expanded survey area (>1,450 meters).

The four modeled removal scenarios produced significantly different population means for every year from 1990 to 2030 (Figure 5-10). When randomly removing individual goats to attain the 1990 population estimate of 389, approximately 62% of the individuals removed were female. This removal scenario resulted in immediate and sustained population growth. When 70% of the individual goats removed were female, the population slightly declined before surpassing the initializing population size at year six with a modeled population of 400. When 75% of the removals were female the modeled population declined until year six and surpassed the initializing population size in year 13. Year four and year seven modeled population means were within the 95% confidence limits of the observed population estimates for the corresponding years (1994 and 1997 respectively; Table 5-1). When 80% of the removals were female the modeled population declined for almost a decade, reaching a low of 176 animals at year 8 and surpassing the initial starting population at year 23. The modeled population means at years 14 and 21 were within the 95% confidence limits of the observed estimates for the corresponding years (2004 and 2011 respectively). At year 26 there is slight overlap between the 95% confidence limits of the modeled population mean and the observed population estimate, however the modeled mean is just outside the confidence limits of the estimate.

Table 5-1. Modeled population growth by removal scenario. Four removal scenarios were modeled with model output at years corresponding to observed population estimates shown here, along with 95% confidence limits for each value (LCI = Lower Confidence Interval; UCI = Upper Confidence Interval). Values closest to those observed are shown in bold.

	Modeled Removal Scenario				**Observed**
	Random	*70% F*	*75% F*	*80% F*	**Pop. Estimate**
Year 4	511	378	**305**	221	288
LCI	507	373	299	217	225
UCI	514	384	310	224	351
Year 7	623	419	**307**	183	281
LCI	615	410	299	178	238
UCI	632	427	315	188	324
Year 14	999	638	423	**229**	230
LCI	968	612	407	216	193
UCI	1030	664	439	242	267
Year 21	1629	1025	671	**360**	350
LCI	1568	985	638	336	270
UCI	1690	1065	704	385	430
Year 26	2314	1444	955	**502**	584
LCI	2227	1376	909	463	508
UCI	2401	1513	1001	540	660

Using the two removal scenarios demonstrating population growth trends that most closely matched observed (75% and 80% females removed), I evaluated male to female ratio and observed heterozygosity over the modeled 40-year period. As one would expect, the number of males to one female at the start of the modeled period was higher for the 80% female removal scenario than for the 75% scenario (7.28 and 2.85 respectively). Both modeled removal scenarios reached the male to female ratio observed for the “11 and 12 Founder” scenarios during model calibration runs (~0.6) in approximately 12 years. This ratio was maintained for the remainder of the modeled period.

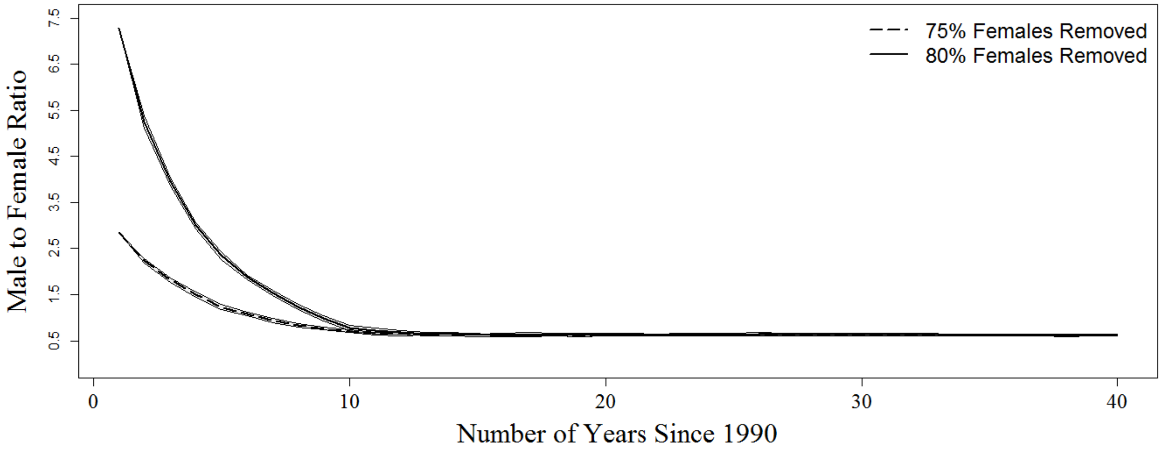


Figure 5-11. Modeled male to female ratio from 1990 – 2030. Two of four removal scenarios are shown: 1) 75% females removed and 2) 80% females removed. After year 11 the male to female ratio maintains at approximately 0.6, the same value from the "11 Founder" and "12 Founder" model calibration scenarios.

Modeled mean observed heterozygosity was slightly higher for the scenario with 75% females removed than with 80% but there was substantial overlap in the 95% confidence limits for each scenario suggesting this difference is not likely significant. At the start of the period, modeled mean observed heterozygosity for both scenarios was approximately 0.55 matching that recorded by Mainguy et al. (2005) for the established population at Caw Ridge. Modeled observed heterozygosity increased slightly for both scenarios then decreased to values similar to those at year 0. Modeled mean observed heterozygosity for both reduction scenarios was substantially greater than the H_o recorded by Shirk (2009) for ONP animals. Due to this large discrepancy, I performed a second evaluation of modeled H_o to assess whether the low diversity observed by Shirk was an error in measurement resulting from the effect of small sample size (n = 12). Using the 80% females removed scenario, I sampled 12 individual goats from each of the 10 model runs. Shirk possessed coordinates for 10 of his 12 ONP genetic samples. I selected the 10 modeled goats nearest these coordinates from each of the 10 replicate runs, as well as two additional, randomly generated points to obtain a modeled sample size equal to Shirk. Mean modeled H_o for this smaller sample size across all replicate runs was 0.57.

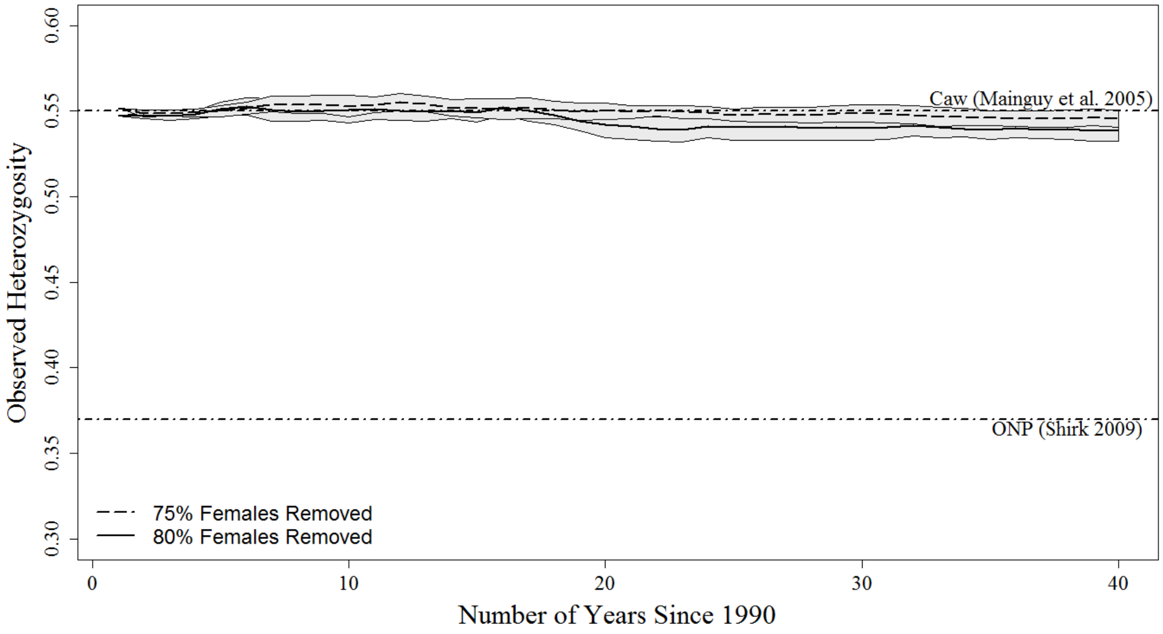


Figure 5-12. Modeled mean observed heterozygosity from 1990 – 2030. H_o for the 75% removal scenario (dashed line) and 80% removal scenario (solid line) was similar to the H_o recorded for the Caw Ridge population (top horizonal line). The lower horizontal line shows recorded H_o for goats in ONP.

6.0 Discussion

6.1 Model Calibration

My research objective was to parameterize an existing model for use with mountain goats in the Olympic Range, with calibration utilizing the period from introduction to the first aerial survey in 1983 and validation through simulation of the period from 1990 to present. Model calibration was successful with both the "11 Founder" and "12 Founder" scenarios producing modeled mean populations within the 95% confidence limits of the 1983 observed population estimate (adjusted to account for removals prior to that date). The “12 Founder” scenario was more closely representative of the Olympic population with the reference population value (1983 estimate plus 213) included within the 95% confidence limits of the modeled population mean. In comparison, the scenario using parameters from the established population at Caw Ridge was an extremely poor fit for the observed population growth trend. These results suggest that goats within the Olympic Range exhibited population dynamics similar to those applied in both the “11 Founder” and “12 Founder” scenarios of the model.

As theorized by Stevens (1983), the difference in modeled population growth between the scenario using parameters from the established population at Caw Ridge and the two scenarios using parameters from expanding populations (including those in the Olympics), demonstrates that mountain goats in the Olympic Range were displaying population dynamics associated with rapid growth. Eruptive fluctuations have been documented in established populations (Smith 1986, Dane 2002) and in populations recently introduced into new habitat (Lentfer 1955, Caughley 1970, Hayden 1984). Riney (1964) proposed a four-phased population growth model for eruptive fluctuations of ungulates resulting from introduction or a major shift in resources. The first phase is a period of population growth, characterized by high rates of survival and early primiparity, as animals capitalize on plentiful forage found in the new habitat. The greater the suitability of the habitat the more rapid this growth. During the second phase, animals have surpassed carrying capacity and resource depletion leads to plateaued growth and a decline in fitness, survival and reproduction. Eventually the population plummets as resource limitation results in vulnerability to disease and winter starvation, and adult fecundity rates decrease. Relative population stability occurs during the final phase as ecological equilibrium is attained. Further eruptive oscillations can occur if this equilibrium is disturbed.

Parameter estimates used in the model were lower than those observed in newly introduced populations in Montana and Idaho (Lentfer 1955, Hayden 1984), and higher than those observed by Stevens (1983) in Olympic populations other than Klahhane Ridge shortly before the first aerial survey. These estimates were applied consistently throughout the modeled period. In order to achieve the growth observed and to display vital rates documented by Stevens, it is likely the Olympic population first exhibited dynamics similar to those in Montana and Idaho, and as time progressed dynamics driving growth began to lower. The population at Klahhane Ridge was characterized by vital rates indicative of the plateau encountered during Riney's second phase. This was the only subpopulation displaying this trend during Stevens' research. Considering the vast expanse of suitable habitat available to mountain goats in the Olympics and the comparatively low density of the many other subpopulations throughout the range, it is likely that rapid growth rates outside of Klahhane Ridge would have persisted for some time were they not disrupted by removals.

6.1.1 Natal Dispersal

Mountain goat distribution and density within the Olympic Range varies both spatially and temporally. At the time of the first aerial survey in 1983, substantial subpopulations inhabited areas around Chimney Rock, Mount Dana, Mount Ferry, Buckhorn Mountain, Mount Appleton, Mount Claywood, Klahhane Ridge, Royal Basin, Mount Washington, and Mount Constance. The 2016 survey revealed similar subpopulation concentrations around Chimney Rock, Mount Washington, and Klahhane Ridge. Large subpopulations had established in new areas around Mount Olympus, the northern and southern ends of the Bailey Range (near Mount Carrie and Bear Pass, respectively), and in the Sawtooth range on the southeastern park boundary. The subpopulation near Mount Appleton appears substantially reduced and the area around Mount Dana produced a survey count of zero compared to 45 during the 1983 survey. While census units in the eastern portion of the range do not all directly align between survey years, it is apparent that several areas have experienced dramatic declines, including Buckhorn Mountain, Mount Constance, Royal Basin, and Mount Claywood. Several areas were not surveyed during both years and could not be used for direct comparison including Mount Ferry, which was not surveyed in 2016, and Mount Anderson, Muncaster Mountain, and The Brothers, all of which were not surveyed in 1983. However, Mount Ferry was included in the 2011 survey (count of 0 in the equivalent census area) and Mount Anderson and Muncaster Mountain were included in the 1990 survey (each with a count of 4 in the equivalent census area), providing evidence of substantial subpopulation decline in the former and increase in the latter two.

Modeled dispersal distribution and density at year 55 was relatively consistent with observed patterns in 1983 with the most striking incongruency being the sizeable subpopulation inhabiting Mount Olympus. The model shows a high density of goats in this area, which was not consistent with reports at the time, but is more representative of observed distribution patterns in 2016. As mentioned previously, deep and persistent snowpack may have limited mountain goat access to the western portion of the Olympic Mountains. Not only are these areas characterized by exceptionally high amounts of snowfall, they also contain the range’s largest glaciers. However, these conditions have begun to change due to climate change. In 1982 there were 266 glaciers in the Olympic

Mountains (Spicer 1986). This number decreased to 184 by 2009, a combined glacier area loss of 34%, with glaciers facing south or in the eastern portion of the range experiencing the greatest loss (Riedel et al. 2015). Glaciers on Mount Olympus lost 12% to 61% of their total area during this period. This glacial recession is indicative of a correlated loss of snowpack in general. While newly exposed areas once covered by glaciers will remain barren of vegetation for decades, it is likely the reduction in snowpack exposed new habitat options in areas once only marginally accessible. The glacier on Mount Carrie (Carrie) and two on Mount Anderson (Eel and Anderson) have also exhibited dramatic recession (total area losses of 37%, 23%, and 77% respectively) and represent areas with little to no inhabitation during the first or second aerial surveys with greater numbers noted in 2016, perhaps also the consequence of newly exposed habitat. Due to lack of sufficient data, I did not incorporate snowpack and glaciation into the model so this was not a feature influencing modeled dispersal patterns. As such, density and distribution trends noted during any one of the aerial surveys should be considered when evaluating modeled dispersal. Application of this new consideration may explain the previously mentioned incongruency noted around Mount Olympus.

I noted two additional differences when comparing subpopulation aggregation patterns of the model and aerial surveys. For every survey year, counts for the ridges surrounding Gray Wolf River, Cameron Creek, and Grand Creek were meager to nonexistent while the model showed colonization of this area. It is apparent that habitat features unique to that area and unrelated to elevation discourage goat presence. The second difference was noted at Mount Washington, just over the southeastern park boundary. Modeled dispersal at year 55 shows fewer goats inhabiting the area than counted during aerial survey in 1983.

Mount Washington is situated at the far edge of suitable mountain goat habitat and is surrounded on three sides by river valleys and lakes, leaving only one entry point that does not involve navigation of landscape features highly resistant to movement. It is possible that this relative inaccessibility, combined with Mount Washington's location at the far edge of the range, may have limited modeled dispersal to this area. Additionally, I only considered dispersal distribution for one of the ten total modeled runs and other modeled runs potentially may have shown greater inhabitation of this area.

Anecdotal reports of dispersal progress after introduction cite the year a mountain goat was first reported in an area as well as the year the first nanny with kid-at-heel was reported. For most sites, the difference between these events is five to 15 years (Moorhead and Stevens 1982). At Mount Appleton and Klahhane Ridge, the difference was substantially greater at 41 and 30 years respectively. Modeled dispersal progress did not follow this same trend. It seems unlikely that goats of both sexes would pass through these areas to colonize other portions of the range unless these areas were characterized by less than ideal habitat features. However, the subsequent return to these areas and relatively high densities found in both during the 1983 aerial survey suggest that this was not the case. Based on this, I would assume that anecdotal records did not reflect the actual year of first presence but rather simply the year of first report. These records were not the result of any systematic or consistent surveys and failed to reflect the earlier occupancy of each site.

6.2 Sensitivity Analyses

Sensitivity analyses revealed that population growth was not sensitive to 10% changes in adult male mortality and was quite sensitive to the same changes in adult female mortality.

Increases in adult female mortality have been found by many others to have a strong negative impact on population growth rate (Gaillard et al. 1998, Langvatn and Loison 1999, Gaillard et al. 2000) and this fact has been embraced by game managers who utilize restricted harvest on productive females to help maintain stable population sizes.

Modeled population growth was more sensitive to changes in reproductive rate than to either juvenile or adult female mortality. These findings appears contrary to several other studies of mountain goats and ungulates in general where it was found that adult female survival produced the greatest change in population growth (Escos et al. 1994, Walsh et al. 1995, Hamel et al. 2006). However, it is impossible to make a direct comparison due to several factors, most significantly, those pertaining to mortality rate sensitivity. As previously described, CDPOP applies mortality rates to the population rather than survival rates. As such, in contrast to previous studies, I adjusted mortality by 10% rather than survival. Because mortality rate values are lower than survival rate values, a +/- 10% adjustment based on these lower values would be smaller than one based on the larger values, thereby producing a smaller effect overall. These studies also classified adults as at least three years and older while I classified them as two years and older due to the earlier primiparity in this population and their contribution to recruitment. This difference changes the number of individuals in the population impacted by each parameter manipulation. Furthermore, the earlier primiparity of the modeled population no doubt increased the influence reproductive rate has on population growth.

It is generally true that juvenile survival rates are naturally more variable than reproductive rates, which are in turn more variable than adult survival rates. This means that functionally, adult survival, though found to have a high impact on population growth, does not necessarily have a greater influence on this growth than recruitment or juvenile survival since the latter of the two shows considerably greater natural variation resulting in the potential for stronger influence. In terms of my modeled population, reproductive rates, which have moderately high natural variation, are also shown to have the greatest influence on population growth meaning that natural variation in this vital rate could have a sizeable impact on population viability.

6.3 Model Validation

I successfully validated the model for removal scenarios where 75% to 80% of the animals removed were female. While there are no records indicating the sex of captured animals, it is reasonable to assume that adult females may have been captured at a disproportionately greater rate than adult males due to relative ease of capture. At Caw Ridge in British Columbia nannies traveled in nursery groups averaging 11.9 individuals while males were three times more likely to be observed alone and had a group size averaging 2.6 (Festa-Bianchet and Cote 2008), making adult females and their cohorts much easier to spot during ground or aerial survey and capture efforts. Adult males also spent approximately half their time in forested areas while nursery groups were almost always observed in open spaces (Festa-Bianchet and Cote 2008), thereby further increasing their sightability. Two capture reports for collaring efforts in Alaska (Nichols 1980) and Washington (Jenkins et al. 2011*a*) documented a greater proportion of captured females. In Alaska, the sex ratio of captured goats three years and under was equivalent while 75% of the adults captured were female (9 out of 12). Seventy four percent (17/23) of the total captures in Washington were female.

This disruption of the sex ratio in favor of males caused by disproportionate removal was evidently of considerable detriment to population growth.

Biased capture, along with additional kid deaths likely resulting from the removal of associated nannies, would easily explain the population decline of greater magnitude than the removals and the continued decline and stasis the following decade. Between 1985 and 1989, 66% of the adult females captured during the removal efforts in the Olympics were lactating. Records from the aforementioned captures in Alaska and Washington documented similar statistics. In Alaska, 78% of the captured adult females had kids (Nichols 1980). While capture records for Washington were incomplete (lactation status was not documented for three females), at least 64% of the females captured were lactating (Jenkins et al. 2011). Age class estimates were not recorded for these captured animals so it is unknown whether the two captured females identified as non-lactating were adults, which makes direct comparison to the percentages from ONP and Alaska difficult but does grant confirmation that the 66% observation from the Olympic captures is reasonable and perhaps even modest.

Between 1981 and 1989 there were 407 goats removed from Olympic National Park by the National Park Service (NPS), an additional 111 legally harvested outside park boundaries, and another three harvested illegally within park boundaries. Prior to this time, 40 goats had also been removed from Klahhane Ridge by NPS personnel. Assuming a 75% female bias for removals (335 females) and a 66% lactation rate for captured adult females, approximately 221 kids would have suffered mortality related to the 447 removals conducted by park officials. According to mountain goat harvest records for the state of Washington from 1948 – 1981, approximately 49% of animals harvested annually were male (Johnson 1983). Assuming half of the 114 animals harvested were female, 38 kids would have suffered related mortality. In summary, there is strong likelihood that a total of approximately 820 goats were removed, either directly or indirectly, from the Olympic Range between 1972 and 1989, including 259 kids and 392 females. While not all of these animals were removed between the 1983 and 1990 surveys, the disruption of natural sex and age ratios would have lasting impacts. A high number of reproducing females were removed along with a large portion of the future reproducing population, with both factors likely driving the observed population decline. Sex ratios were restored after twelve years for modeled populations which is similar to the time that observed populations began to increase again.

6.4 Observed Heterozygosity

Modeled observed heterozygosity was strikingly different from that documented by Shirk (2009) for mountain goats in the Olympic Range. While I anticipated observed heterozygosity to be high during the modeled period from introduction until 1983 due to the intermixing of two very distinct source populations, I was surprised the subsequent population reduction did not produce a dramatic decline in H_o. This discrepancy between modeled and observed H_o could result from a number of causes. First, the Shirk 2009 sample size was small (n=12) and possibly did not capture the true H_o of the Olympic Range. Error in measurements due to sampling effects is a known but ongoing area of research in population genetics (Landguth et al. 2012*b*, Oyler-McCance et al. 2013). However, my spatially selective sampling trial largely discredits this possibility. Second, introduction conditions related to sex and genetics were unknown so the discrepancy could also result if the true H_o of the founding goats was different from what I applied in the model. Genotypes for individual founding goats were randomly created for each run based on allele frequencies calculated from samples collected between 2004 and 2009 near the originating translocation sites. H_o values may have been considerably different eighty years prior when the founding goats were actually retrieved but it is impossible to predict this difference due to the complexity of population dynamics. Additionally, modeled genotypes were generated assuming a low degree of genetic relatedness. The genotypes of the founders in my simulations were based on a random draw from large source populations with high genetic diversity. In reality it is likely that the goats captured for translocation were closely related due to the composition of nursery groups. This relatedness would reduce overall genetic diversity of the founding population far below that used in my simulations. Finally, the small size of each group brought from BC and Alaska (group sizes of 4, 2, and 5 or 6) makes the potential for genetic admixing highly vulnerable to sex composition and mortality. If there was at least one male from each of the three originating locations and these males survived to reproduce with females from different locations, genetic admixing would be high. However, if males were not captured at every location or there was not a male surviving to reproduce from every location, then admixing would be reduced as females are not as likely as males to take more than one mate. Furthermore, if every member of one of the groups died this would completely eliminate genetic influence from that particular area, reducing H_o considerably.

A third and final factor contributing to the discrepancy between the H_o observed by Shirk and modeled H_o relates to the deterministic nature of the CDPOP model. The founding mountain goat population in the Olympic range was derived from a small number of founding individuals. As a result, alleles possessed by the founding individuals will be frequent in the founding population as well. Genetic drift accompanying this founder event, and accentuated by the new population's small size, is known as a founder effect (Hartl 2000, Templeton 2006). Genetic drift results in a reduction in genetic variability (Halliburton 2004, Templeton 2006). For the first few decades after introduction, the founding population would have experienced periods of decline and growth in response to natural stochasticity in vital rates and environmental conditions. This variability was not reflected in the model. Genetic drift during periods when the population was at a relatively small size would have a significant and deleterious impact on diversity that would persist as the population entered the subsequent period of growth, a phenomenon known at a bottleneck effect (Halliburton 2004, Templeton 2006). Small, isolated populations are additionally vulnerable to inbreeding which decreases the frequency of heterozygous genotypes (Hartl 2000). Continuous growth simulated by the model would have omitted stochastic population fluctuations, most importantly population declines, thereby lessening genetic drift and inbreeding depression, and producing artificially higher observed heterozygosity.

6.5 Model Limitations

I recognize that this model, as with all models, inherently possesses limitations. When estimating model parameters, it is impossible to know precise vital rates for a given population at any moment in time. I made my estimates based on thorough review of the literature but variation exists between individuals and environments, and across landscapes and time. Additionally, the extent of mountain goat research is limited, especially in relation to expanding populations, so while my review was thorough, the data informing many parameters were few. My model does not account for environmental stochasticity, including fluctuations in climate, predation, or nutrient availability that are certain to have a dramatic impact on population viability. Furthermore, the model prohibited the application of standard deviations to most vital rates. While adult survivorship for mountain goats is known to be fairly stable (Festa-Bianchet et al. 2003), juvenile survival, especially that of kids, can vary widely (Chadwick 1977, Stevens 1983). At Caw Ridge, year-to-year kid survival varied from 38 to 92% (Festa-Bianchet and Cote 2008). The stochasticity of population dynamics is apparent in the variation between observed population estimates the first decade after removal. Variations such as this were not reflected by the model and instead were represented by mean values intending to capture the general trends of an age class over time. This produced a population-growth-trend curve rather than the undulating line characteristic of true populations, likely impacting H_o as discussed above.

While no ecological model can ever be entirely accurate due to the complexity and dynamics of related processes, some models can be extremely useful for attempting to understand and predict complex phenomena. This particular model has been successfully calibrated and validated using empirical data, confirming its potential to further our understanding of mountain goat population dynamics and to inform management decisions related to removal and augmentation. This model is the first spatially explicit, individual-based introduction model for mountain goats and represents a novel contribution to the field of wildlife management.

7.0 Management Implications

My model clearly demonstrates the negative impact a reduction in the number of females will have on population viability. If the goal in ONP is to drastically reduce or eliminate mountain goats from the Olympic Range, removal efforts should be highly biased toward females, with minimal effort invested in locating and capturing adult males. Furthermore, female dominated nursery groups have greater sightability which facilitates ease of capture, reducing risk to capture crews. Primarily removing females has the greatest likelihood of slowing and even preventing additional population growth over the next decade. Initiating a period of negative growth would alleviate considerable time pressure from land managers as additional population control measures were enacted. Conversely, augmenting North Cascade populations with high numbers of females has the greatest chance of improving population viability. Adherence to capture protocol focused entirely on nursery groups satisfies objectives of land managers for both ranges, ensuring the greatest probability of success in each case, thereby maximizing time and monetary resources invested in each project.

The current model could additionally be applied to estimate the number of removals necessary to push the Olympic population into an extinction vortex (Gilpin and Soule 1986). This information would provide invaluable feedback to NPS personnel as final population management decisions are assessed. With some manipulation of parameter estimates, this model could also be used to evaluate augmentation scenarios in the North Cascades.

8.0 Bibliography

Adams, L. G., and J. A. Bailey. 1982. Population dynamics of mountain goats in the Sawatch Range, Colorado. The Journal of Wildlife Management 46:1003–1009.

Anunsen, C. S., and R. Anunsen. 1993. Response to Scheffer. Conservation Biology 7:954–957.

Ayotte, J. B., K. L. Parker, J. M. Arocena, and M. P. Gillingham. 2006. Chemical composition of lick soils: functions of soil ingestion by four ungulate species. Journal of Mammalogy 87:878–888.

Bailey, J. A. 1991. Reproductive success in female mountain goats. Canadian Journal of Zoology 69:2956–2961.

Brandborg, S. M. 1955. Life History and Management of the Mountain Goat in Idaho. Wildlife bulletin no. 2, State of Idaho Department of Fish and Game, Boise, ID.

Castillo, J. A., C. W. Epps, A. R. Davis, and S. A. Cushman. 2014. Landscape effects on gene flow for a climate-sensitive montane species, the American pika. Molecular Ecology 23:843–856.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology 51:53–72.

Chadwick, D. H. 1974. Mountain goat ecology: logging relationships in the Bunker Creek drainage of western Montana. Thesis, University of Montana.

Chadwick, D. H. 1977. Ecology of the Rocky Mountain goat in Glacier National Park and the Swan Mountains, Montana. Final report, Glacier National Park, West Glacier, Montana.

Cooke, G. M., E. L. Landguth, and L. B. Beheregaray. 2014. Riverscape genetics identifies replicated ecological divergence across an amazonian ecotone. Evolution 68:1947–1960.

Cote, S. D., and M. Festa-Bianchet. 2001. Reproductive success in female mountain goats: the influence of age and social rank. Amimal Behavior 62:173–181.

Côté, S. D., and M. Festa-Bianchet. 2003. Mountain goat. Chapter 49. G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild Mammals of North America, Biology, Management, and Conservation. Second edition. The Johns Hopkins University Press, Baltimore, Maryland.

Cushman, S., K. McKelvey, J. Hayden, and M. Schwartz. 2006. Gene flow in complex landscapes: testing multiple hypothesis with causal modeling. The American Naturalist 168:486–499.

Dane, B. 2002. Retention of offspring in a wild population of ungulates. Behaviour 139:1–21.

Dijkstra, E. W. 1959. A note on two problems in connexion with graphs. Numerische Mathematik 1:269–271.

DiLeo, M. F., J. D. Rouse, J. A. Dávila, and S. C. Lougheed. 2013. The influence of landscape on gene flow in the eastern massasauga rattlesnake (*Sistrurus c. catenatus*): insight from computer simulations. Molecular Ecology 22:4483–4498.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169.

Escos, J., C. L. Alados, and J. M. Emlen. 1994. Application of the stage-projection model with density-dependent fecundity to the population dynamics of Spanish ibex. Canadian Journal of Zoology 72:731–737.

Festa-Bianchet, M., and S. D. Cote. 2008. Mountain Goats: Ecology, Behavior, and Conservation of an Alpine Ungulate. Island Press, Washington, DC, USA.

Festa-Bianchet, M., J.-M. Gaillard, and S. D. Côté. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. Journal of animal ecology 72:640–649.

Festa-Bianchet, M., M. Urquhart, and K. G. Smith. 1994. Mountain Goat Recruitment: Kid Production and Survival to Breeding Age. Canadian Journal of Zoology 72:22–27.

Fox, J. L., C. A. Smith, and J. W. Schoen. 1989. Relation between mountain goats and their habitat in southeastern Alaska. General technical report PNW-GTR-246, U.S. Forest Service.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of ecology and Systematics 31:367–393.

Geist, V. 1964. On the rutting behavior of mountain goat. Journal of Mammalogy 45:551–568.

Gillespie, J. H. 2004. Population Genetics: A Concise Guide. Second. Johns Hopkins University Press, Baltimore, Maryland.

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: processes of species extinction. Pages 19–34 *in*. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 1140–1162.

Halliburton, R. 2004. Introduction to Population Genetics. Pearson Prentice Hall, Upper Saddle River, NJ.

Hamel, S., S. D. Côté, K. G. Smith, and M. Festa-Bianchet. 2006. Population dynamics and harvest potential of mountain goat herds in Alberta. Journal of Wildlife Management 70:1044–1053.

Happe, P. J. 2011. Mountain Goat Action Plan. National Park Service. <https://www.nps.gov/olym/learn/management/upload/Mountain-Goat-ACTION-PLAN_2011_Final.pdf>. Accessed 15 Dec 2016.

Hartl, D. L. 2000. A Primer of Population Genetics. Sinauer Associates, Inc., Sunderland, Massachusetts.

Hayden, J. A. 1984. Introduced mountain goats in the Snake River Range, Idaho: characteristics of vigorous population growth. Biennial Symposium of the Northern Wild Sheep and Goat Council 4:94–119.

Henderson, R. E., and B. W. O'Gara. 1978. Testicular development of the mountain goat. The Journal of Wildlife Management 42:921–922.

Houston, D. B., B. B. Moorhead, and R. W. Olson. 1986. An aerial census of mountain goats in the Olympic Mountain Range, Washington. Northwest Science 60:131–136.

Houston, D. B., B. B. Moorhead, and R. W. Olson. 1991. Mountain goat population trends in the Olympic Mountain Range, Washington. Northwest Science 65:212–216.

Houston, D. B., C. T. Robbins, and V. Stevens. 1989. Growth in wild and captive mountain goats. Journal of Mammalogy 70:412–416.

Houston, D. B., E. G. Schreiner, and B. B. Moorhead. 1994. Mountain Goats in Olympic National Park: Biology and Management of an Introduced Species. National Park Service, Scientific Monograph NPS/NROLYM/NRSM-94/25.

Houston, D. B., E. G. Schreiner, B. B. Moorhead, and R. W. Olson. 1991. Mountain goat management in Olympic National Park: a progress report. Natural Areas Journal 11:87–92.

Houston, D. B., and V. Stevens. 1988. Resource Limitation in Mountain Goats: a Test by Experimental Cropping. Canadian Journal of Zoology 66:228–238.

Hutchins, M. 1984. The mother-offspring relationship in mountain goats. Dissertation, University of Washington, Seattle, WA.

Hutchins, M. 1995. Olympic mountain goat controversy continues. Conservation Biology 9:1324–1326.

Hutchins, M., and V. Geist. 1987. Behavioural considerations in the management of mountain-dwelling ungulates. Mountain Research and Development 7:135–144.

Hutchins, M., and V. Stevens. 1981. Olympic mountain goats. Natural History 90:58–69.

Jenkins, K., K. Beirne, P. Happe, R. Hoffman, C. Rice, and J. Schaberl. 2011*a*. Seasonal distribution and aerial surveys of mountain goats in Mount Rainier, North Cascades, and

Olympic National Park. Open-file report 2011-1107, US Geological Survey, Reston, Virginia.

Jenkins, K., P. Happe, P. C. Griffin, K. Beirne, R. Hoffman, and W. Baccus. 2011*b*. Mountain goat abundance and population trends in the Olympic Mountains, Washington, 2011. Open-File Report 2011-1313, Report, Reston, VA.

Jenkins, K. J., P. J. Happe, K. F. Beirne, and W. T. Baccus. 2016. Mountain goat abundance and population trends in the Olympic Mountains, northwestern Washington, 2016. Open-file report 2016-1185, U.S. Geological Survey.

Jenkins, K. J., and E. E. Starkey. 1984. Habitat use by Roosevelt Elk in unmanaged forests of the Hoh Valley, Washington. The Journal of Wildlife Management 48:642–646.

Johnson, R. L. 1983. Mountain goats and mountain sheep of Washington. Biological bulletin no. 18, Washington Department of Game.

Kitchen, J., and R. Allaby. 2013. Systems Modeling at Multiple Levels of Regulation: Linking Systems and Genetic Networks to Spatially Explicit Plant Populations. Plants 2:16–49.

Landguth, E. L., and S. A. Cushman. 2010. CDPOP: a spatially explicit cost distance population genetics program. Molecular Ecology Resources 10:156–161.

Landguth, E. L., B. C. Fedy, S. Oyler-McCance, A. L. Garey, S. L. Emel, M. Mumma, H. H. Wagner, M.-J. Fortin, and S. A. Cushman. 2012*a*. Effects of sample size, number of markers, and allelic richness on the detection of spatial genetic pattern. Molecular Ecology Resources 12:276–284.

Landguth, E. L., B. C. Fedy, S. J. OYLER-McCANCE, A. L. Garey, S. L. Emel, M. Mumma, H. H. Wagner, M.-J. Fortin, and S. A. Cushman. 2012*b*. Effects of sample size, number of markers, and allelic richness on the detection of spatial genetic pattern: STUDY DESIGN IN LANDSCAPE GENETICS. Molecular Ecology Resources 12:276–284.

Langvatn, R., and A. Loison. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer Cervus elaphus in Central Norway. Wildlife Biology 5:213–223.

Lemke, T. O. 2004. Origin, expansion, and status of mountain goats in Yellowstone National Park. Wildlife Society Bulletin 32:532–541.

Lentfer, J. W. 1955. A two-year study of the Rocky Mountain goat in the Crazy Mountains, Montana. The Journal of Wildlife Management 19:417–429.

Lyman, R. L. 1994. The Olympic mountain goat controversy: a different perspective. Conservation Biology 8:898–901.

Mainguy, J., and S. D. Côté. 2008. Age- and state-dependent reproductive effort in male mountain goats, Oreamnos americanus. Behavioral Ecology and Sociobiology 62:935–943.

Mainguy, J., S. D. Côté, E. Cardinal, and M. Houle. 2008. Mating tactics and mate choice in relation to age and social rank in male mountain goats. Journal of Mammalogy 89:626–635.

Mainguy, J., A. S. Llewellyn, K. Worley, S. D. Cote, and D. W. Coltman. 2005. Characterization of 29 polymorphic artiodactyl microsatellite markers for the mountain goat (Oreamnos americanus). Molecular Ecology Notes 5:809–811.

Mateo-Sánchez, M. C., N. Balkenhol, S. Cushman, T. Pérez, A. Domínguez, and S. Saura. 2015. A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? Landscape Ecology 30:1405–1420.

Moorhead, B. B., and V. Stevens. 1982. Introduction and dispersal of mountain goats in Olympic National Park. Pages 46–50 *in*. Ecological Research in National Parks of the Pacific Norhtwest. Oregon State University Forest Research Laboratory, Corvallis, Oregon.

National Park Service. 2017. Draft mountain goat management plan/environmental impact statement. <https://parkplanning.nps.gov/document.cfm?parkID=329&projectID=49246&documentID=77644>. Accessed 23 Jul 2017.

Naylor, K. S. 1988. Distribution, habitat use and population characteristics of introduced mountain goats at Pend Oreille Lake, Idaho. Thesis, University of Idaho.

Nichols, L. 1980. Mountain goat movement study. Federal Aid in Wildlife Restoration, Project W-21-1, job no. 12.5R, State of Alaska Department of Fish and Game.

Oyler-McCance, S. J., B. C. Fedy, and E. L. Landguth. 2013. Sample design effects in landscape genetics. Conservation Genetics 14:275–285.

Parks, L. C. 2013. Mountain goat genetic diversity and population connectivity in Washington and southern British Columbia. Thesis, Western Washington University.

Parks, L. C., D. O. Wallin, S. A. Cushman, and B. H. McRae. 2015. Landscape-level analysis of mountain goat population connectivity in Washington and southern British Columbia. Conservation Genetics 16:1195–1207.

Pelletier, F., J. Mainguy, and S. D. Côté. 2009. Rut-induced hypophagia in male bighorn sheep and mountain goats: foraging under time budget constraints. Ethology 115:141–151.

Pfitsch, W. A., and L. C. Bliss. 1985. Seasonal forage availability and potential vegetation limitations to a mountain goat population, Olympic National Park. American Midland Naturalist 113:109–121.

Pojar, T. M. 1981. A management perspective of population modeling. Pages 241–262 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of Large Mammal Populations. John Wiley & Sons, Inc., New York.

Poole, K. G., K. D. Bachmann, and I. E. Teske. 2010. Mineral lick use by GPS radio-collared mountain goats in southeastern British Columbia. Western North American Naturalist 70:208–217.

PRISM Climage Group. n.d. Oregon State University. <http://www.prism.oregonstate.edu>. Accessed 13 Dec 2017.

Prunier, J. G., B. Kaufmann, J.-P. Léna, S. Fenet, F. Pompanon, and P. Joly. 2014. A 40-year-old divided highway does not prevent gene flow in the alpine newt Ichthyosaura alpestris. Conservation Genetics 15:453–468.

Rice, C. G. 2008. Seasonal altitudinal movements of mountain goats. The Journal of Wildlife Management 72:1706–1716.

Rice, C. G. 2010. Mineral lick visitation by mountain goats, Oreamnos americanus. The Canadian Field-Naturalist 124:225–237.

Rice, C. G., and D. Gay. 2010. Effects of mountain goat harvest on historic and contemporary populations. Northwestern Naturalist 91:40–57.

Rice, C. G., K. J. Jenkins, and W.-Y. Chang. 2009. A sightability model for mountain goats. The Journal of Wildlife Management 73:468–478.

Rideout, C. B. 1977. Mountain goat home ranges in the Sapphire Mountains of Montana. Pages 201–225 *in* W. Samuel and W. G. Macgregor, editors. Proceedings of the First International Mountain Goat Symposium. Ministry of Recreation and Conservation, Fish and Wildlife Branch, Victoria, BC.

Rideout, C. B., and R. S. Hoffmann. 1975. Oreamnos americanus. American Society of Mammologists 63:1–6.

Riedel, J. L., S. Wilson, W. Baccus, M. Larrabee, T. J. Fudge, and A. Fountain. 2015. Glacier status and contribution to streamflow in the Olympic Mountains, Washington, USA. Journal of Glaciology 61:8–16.

Riney, T. 1964. The impact of introductions of large herbivores on the tropical environment. Pages 261–273 *in*. The Ecology of Man in the Tropical Environment. Volume 4. International Union for the Conservation of Nature, Morges, Switzerland.

Row, J. R., P. J. Wilson, C. Gomez, E. L. Koen, J. Bowman, D. Thornton, and D. L. Murray. 2014. The subtle role of climate change on population genetic structure in Canada lynx. Global Change Biology 20:2076–2086.

Scheffer, V. B. 1949. Mammals of the Olympic National Park and Vicinity. Northwest Fauna Occasional Monographs on Vertebrate Natural History Number 2. Society for Northestern Vertebrate Biology, Olympia, WA.

Scheffer, V. B. 1993. The Olympic goat controversy: a perspective. Conservation Biology 7:916–919.

Schreiner, E., and A. Woodward. 1994. Study documents mountain goat impacts at Olympic National Park. Park Science 14:23.25.

Shafer, A. B. A., S. D. Côté, and D. W. Coltman. 2011. Hot spots of genetic diversity descended from multiple pleistocene refugia in an alpine ungulate. Evolution 65:125–138.

Shafer, A. B., J. Poissant, S. D. Côté, and D. W. Coltman. 2011. Does reduced heterozygosity influence dispersal? A test using spatially structured populations in an alpine ungulate. Biology letters rsbl20101119.

Shirk, A. J. 2009. Mountain goat genetic structure, molecular diversity, and gene flow in the Cascade Range, Washington. Thesis, Western Washington University.

Shirk, A. J., D. O. Wallin, S. A. Cushman, C. G. Rice, and K. I. Warheit. 2010. Inferring landscape effects on gene flow: a new model selection framework. Molecular Ecology 19:3603–3619.

Singer, F. J. 1978. Behavior of mountain goats in relation to US Highway 2, Glacier National Park, Montana. The Journal of Wildlife Management 42:591–597.

Slabach, B. L., T. B. Corey, J. R. Aprille, P. T. Starks, and B. Dane. 2015. Geophagic behavior in the mountain goat (*Oreamnos americanus*): support for meeting metabolic demands. Canadian Journal of Zoology 93:599–604.

Smith, B. L. 1976. Ecology of Rocky Mountain goats in the Bitterroot Mountains of Montana. Thesis, University of Montana.

Smith, C. A. 1986. Rates and causes of mortality in mountain goats in southeast Alaska. The Journal of wildlife management 50:743–746.

Smith, C. A., and K. J. Raedeke. 1982. Group size and movements of a dispersed, low density goat population with comments on inbreeding and human impact. Biennial Symposium of the Northern Wild Sheep and Goat Council 3:54–67.

Smith, T. D., and C. W. Fowler. 1981. An overview of the study of the population dynamics of large mammals. Pages 1–18 *in*. Dynamics of Large Mammal Populations. John Wiley & Sons, Inc., New York.

Spear, S. F., N. Balkenhol, M.-J. Fortin, B. H. Mcrae, and K. Scribner. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis: Molecular Ecology 19:3576–3591.

Spicer, R. C. 1986. Glaciers in the Olympic Mountains, Washington: present distribution and recent variations. Thesis, University of Washington, Seattle, WA.

Stevens, V. 1983. The dynamics of dispersal in an introduced mountain goat population. Dissertation, University of Washington, Seattle, WA.

Swenson, J. E. 1986. Reproductive response of the Absaroka mountain goat population to an experimental reduction. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 5.

Tabor, R. W. 1987. Geology of Olympic National Park. Pacific Northwest National Parks and Forests Association, Seattle, Washington.

Templeton, A. R. 2006. Population Genetics and Microevolutionary Theory. John Wiley & Sons, Inc., Hoboken, New Jersey.

Varley, N. C. L. 1996. Ecology of mountain goats in the Absaroka Range, south-central Montana. Thesis, Montana State University, Bozeman, Montana.

Walsh, N. E., B. Griffith, and T. R. McCabe. 1995. Evaluating growth of the porcupine caribou herd using a stochastic model. The Journal of Wildlife Management 59:262–272.

Webster, E. B. 1932. Status of mountain goats introduced into the Olympic Mountains, Washington. The Murrelet 13:25.

Wright, K. 1996. Getting the goats: a national park struggles to rid itself of a charismatic ungulate. Scientific American 22–26.

Appendices

Appendix A. Parameter estimation supplemental information

Table A-1. Caw Ridge survival and reproductive rates compared to parameter estimates used in the “12 Founder” and “11 Founder” scenarios. Juvenile (0-1) and >9 years survivorship, and reproductive rates of 2-4 year old females were adjusted based on data from expanding populations.

	Female Survival		**Male Survival**		**Female Reproductive Rate**	
Age Class	*Caw Ridge*	*Model*	*Caw Ridge*	*Model*	*Caw Ridge*	*Model*
0	64	69.5	64	69.5	0	0
1	84.7	84.7	73.5	73.5	0	0
2	90	90	74	74	0	13.4
3	90	90	75	75	3.9	61.8
4	97.5	97.5	92	92	49	70.8
5	95	95	78.5	78.5	67.2	67.2
6	95	95	92	92	73.8	73.8
7	96	96	86	86	73	73
8	91.5	91.5	70	70	78.6	78.6
9	100	76.5	72.5	63.5	84	84
10	85	76.5	57	63.5	81.4	81.4
11	80	76.5	67	63.5	81.8	81.8
12	88	76.5	0	0	78.3	78.3
13	45	76.5	0	0	72.2	72.2
14	56	0	0	0	64	0

Table A-2. Female reproductive rates for age classes 0-4 from three introduced populations. The means of these rates were used to inform model parameter estimates.

Age Class	**Stevens 1983**	**Bailey 1991**	**Smith 1984**	**Mean**
0	0	0	0	0
1	0	0	0	0
2	11.11	0	38	16.37
3	78.39	52	64	64.80
4	92.97	66	60	72.99

Table A-3. Juvenile survivorship (%) for expanding and established populations. Multiple survival rates were listed when authors provided separate rates for each year of their study rather than means. Overall means were used to inform model parameter estimates.

Percent Kid Survival

Expanding Populations		*Established Populations*	
57	Adams & Bailey 1982	67, 71	Smith 1976
70	Stevens 1983	59, 73	Chadwick 1977
88	Hayden 1984	62	Dane 2002
67	Dane 2002	64	Festa-Bianchet & Cote 2008
70.5	mean	66	mean

Percent Yearling Survival

Expanding Populations		*Established Populations*	
72	Dane 2002	70	Dane 2002
71	Smith 1986	100, 67	Smith 1976
95	Hayden 1984	56, 85	Chadwick 1977
79.3	mean	75.6	mean

Table A-4. Twinning rates (%) for expanding and established populations. Two rates are listed for the same author when study results were presented by year rather than mean for all years.

Expanding Populations				*Established Populations*	
18	Foster 1985	33*	Hayden 1984	1.4**	Stevens 1983
35*	Lentfer 1955	8.9	Varley 1996	2	Festa-Bianchet et al. 1994
27*	Lentfer 1955	5.8**	Stevens 1983	10	Chadwick 1977
12.4	Houston et al. 1994	9	Bailey 1991		
25*	Hayden 1984				

*Rates for expanding populations observed less than 15 years after introduction.

**Established twinning rate for Klahhane Ridge in the Olympic mountains. The expanding rate is for the other studied subpopulations distributed across the range.

Table A-5. Model parameter description, estimate, and source.

Parameter	**Model Estimate**	**Source/s**
Mean offspring	1	Hutchins and Hansen 1982; Johnson 1983; Festa-Bianchet and Cote 2008
Offspring sex ratio	Equal	Stevens 1983; Festa-Bianchet and Cote 2008
Mate Replacement*	Male Polygamy	Wigal and Coggins 1982; Johnson 1983; Mainguy et al 2008
Mate movement probability function	Gaussian	
Mean	6.5 km	Smith & Raedeke 1982
Standard deviation	5.5 km	Smith & Raedeke 1982
Maximum threshold	25 km	Smith & Raedeke 1982
Female natal dispersal probability function	Negative Exponential	
Equation	$10^{-0.00007*cd}$	
Maximum threshold	54 km	Stevens 1983
Total females	2%	Stevens 1983; Festa-Bianchet and Cote 2008
Total female kids	12%	
Male natal dispersal probability function	Negative Exponential	
Equation	$10^{-0.00001*cd}$	
Maximum threshold	48 km	Stevens 1983
Total males	14%	Stevens 1983; Festa-Bianchet and Cote 2008
Total male kids	49%	Festa-Bianchet and Cote 2008
Twinning	5.7%	Stevens 1983
Philopatry (strict)	No	Stevens 1983; Festa-Bianchet and Cote 2008
Population growth model	Exponential	Stevens 1983; Houston et al 1994
Number of loci	19	Shafer et al 2011
Maximum number of alleles/locus	29	Shafer et al 2011; Mainguy et al 2008

Appendix B. Modeled natal dispersal results

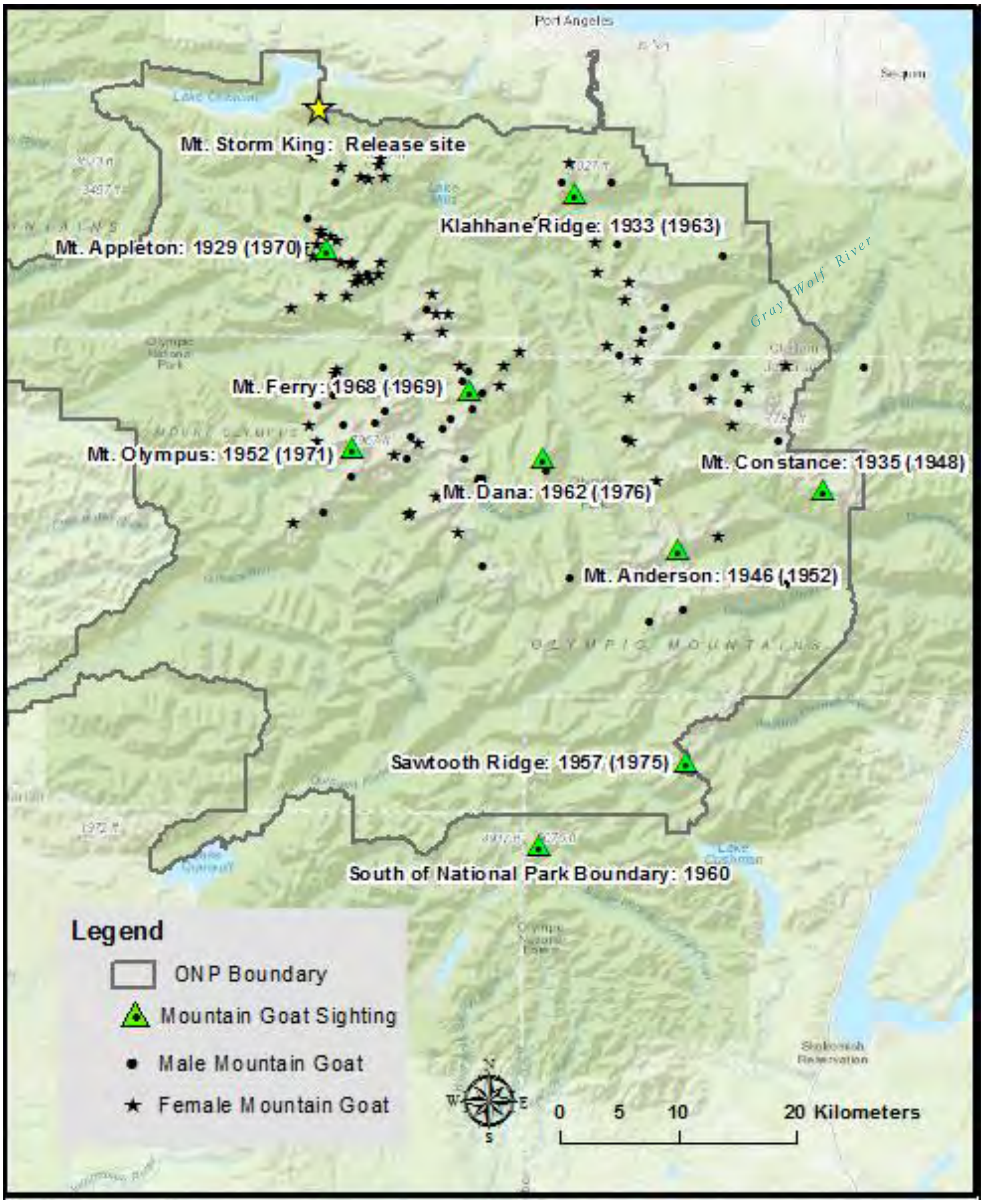


Figure B-1. Modeled dispersal by sex for 1947. Male mountain goats are symbolized by open circles and females are symbolized by filled stars. Year of actual first mountain goat sightings at sites specified by green triangles shown followed by year of first nanny with kid-at-heel sightings (parentheses). Modeled dispersal in 1947 shows goats inhabiting the Mount Olympus and the central range, which was not consistent with observed dispersal. A few goats are seen near Mount Anderson which matches observations at that time.

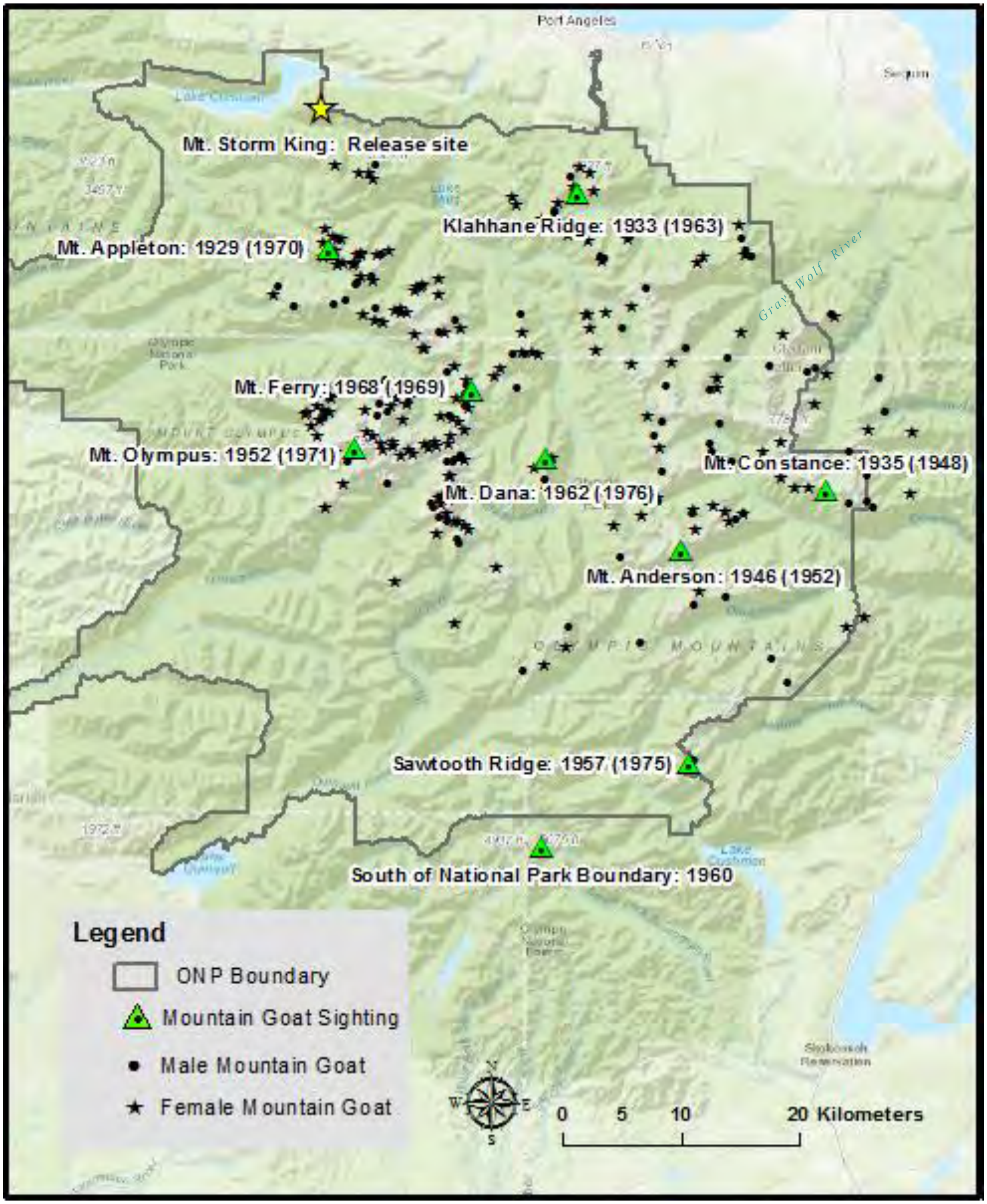


Figure B-2. Modeled dispersal by sex for 1959. Male mountain goats are symbolized by open circles and females are symbolized by filled stars. Year of actual first mountain goat sightings at sites specified by green triangles shown followed by year of first nanny with kid-at-heel sightings (parentheses). Modeled dispersal in 1959 shows goats inhabiting the central range, which was not consistent with observed dispersal.

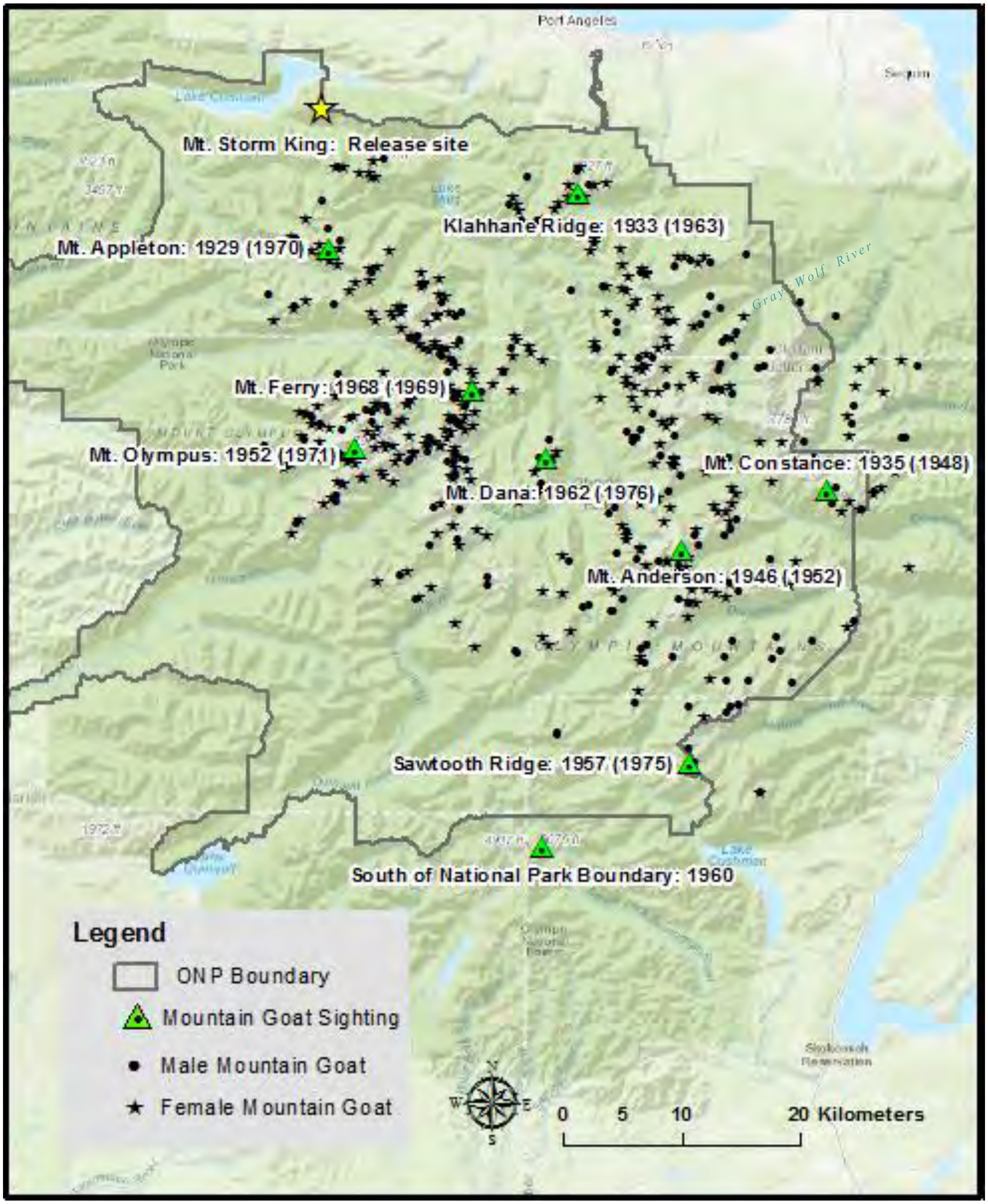


Figure B-3. Modeled dispersal by sex for 1968. Male mountain goats are symbolized by open circles and females are symbolized by filled stars. Year of actual first mountain goat sightings at sites specified by green triangles shown followed by year of first nanny with kid-at-heel sightings (parentheses). Modeled dispersal in 1968 shows sizeable subpopulations inhabiting the ridges near Grey Wolf River and its tributaries.