



Elk Monitoring in Mount Rainier and Olympic National Parks

2008 – 2017 Synthesis Report

Natural Resource Report NPS/NCCN/NRR—2021/2284





ON THIS PAGE

Elk, *Cervus elaphus*, in Mount Rainier National Park, WA.

Photograph by: Muckleshoot Indian Tribe.

ON THE COVER

Elk in Olympic National Park, August 2012. Inset, view of observer counting same group from inside the helicopter.

Photograph by: NPS I&M program.

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Executive Summary

In 2008, the U.S. Geological Survey (USGS) began collaborating with the National Park Service (NPS)-North Coast and Cascades Network (NCCN), the Muckleshoot Indian Tribe (MIT), Puyallup Tribe of Indians (PTOI), and Washington Department of Fish and Wildlife (WDFW) to develop a standard survey protocol for monitoring long-term changes in the abundance, distribution, and population composition of elk on key summer ranges within Mount Rainier National Park (MORA) and Olympic National Park (OLYM). In MORA, surveys were conducted in two trend count areas (TCAs) that correspond with primary summer ranges used by the North Rainier Herd, which winters outside the park to the North, and the South Rainier Herd, which winters outside the park primarily to the South. In OLYM, we defined five TCAs including an Olympic Core TCA (hereafter, Core TCA) that encompasses summer ranges on the flanks of Mount Olympus, and four TCAs that encompass other primary summer ranges throughout the park.

The standard protocol allows for estimating aerial survey detection biases and adjusting raw survey counts to account for elk that were likely present but not seen during surveys. Previously, we developed a suite of aerial-bias-correction models for use in estimating aerial detection biases and adjusting raw counts of elk in MORA based on sighting conditions related to elk group size, vegetation density, lighting conditions, elk movement, as well as combinations of these and other factors. The models were based on independent sighting records of elk groups by front-seat and back-seat observer pairs in a helicopter, including detection records of some radio-collared elk groups.

Here, we analyze results of the first 10 years of elk monitoring in MORA (2008-2017) and 8 years in OLYM (2008-2015). In a previous report covering surveys conducted from 2008-2011, data were not sufficient to model detection biases of aerial surveys conducted in OLYM; hence, analyses of elk population trends were based on counts adjusted for detection biases in MORA, whereas trends in OLYM were based on raw, unadjusted counts (Griffin et al. 2013, Jenkins et al. 2015).

Our objectives for the current summary were to:

- (1) incorporate additional data to update aerial-bias-correction models previously developed for use in MORA to include corrections for aerial detection bias in both MORA and OLYM,
- (2) examine trends in elk abundance, distribution, and population composition estimates for subalpine summer ranges within MORA and OLYM, and
- (3) estimate effects of seasonal variation and weather on elk abundance and population composition estimates for subalpine summer ranges in both parks.

We updated previously developed aerial-bias-correction models based on 148 simultaneous double-observer sightability (DO-S) trials associated with elk groups containing radio-collared elk (45 in OLYM and 103 in MORA) and 1,653 simultaneous double-observer (DO) trials based on groups without radio-collared elk (288 in OLYM and 1,365 in MORA) acquired from 2008 to 2015. Aerial sightability varied among years, between parks, and in relation to individual sighting conditions,

particularly elk group size and movement, vegetation cover, and lighting conditions. We estimated elk abundance and population composition by model-averaging individual estimates derived from 16 different bias-correction models, each including a variety of single variable and interactive effects.

We conducted 13 surveys of North Rainier TCA and 15 of South Rainier TCA from 2008-2017. We estimated a mean of 359 (SE=34.6) elk present in North Rainier TCA and 477 (SE=50.2) elk in South Rainier TCA during surveys, which corresponds with mean densities of 3.5 and 5.3 elk/km² in North (103.1 km²) and South Rainier (89.3 km²) TCAs, respectively.

Elk abundance in North Rainier TCA increased at an estimated instantaneous annual rate (r_o) of 0.039 (SE=0.028; 95% confidence interval [CI]=-0.02, 0.09) during the 10-year span, although the trend was not statistically significant. Multi-model comparisons indicated that statistical support for population growth over time was small compared to support for competing models that related population changes to weather variability, notably an increasing trend in maximum temperatures measured on survey days.

Replicated surveys of South Rainier TCA revealed a curvilinear (quadratic) trend in elk abundance in South Rainier TCA from 2008-2017. Estimated abundance increased initially from 2008-2011, but subsequently declined resulting in no significant net change over the 10-year period (r_o =-0.021; SE=0.031; 95% CI=-0.12, 0.08). Although abundance appeared to be negatively influenced by increasing summer heat index (SHI) from 2008-2017 in South Rainier TCA, evidence for the observed quadratic trend in elk abundance outweighed that of combined weather effects.

Calf ratios remained approximately constant at about 42 and 36 calves:100 adult females (AF) in North and South Rainier TCAs, respectively. There was a mean total of 41 males:100 AF in both North and South Rainier TCAs. The ratio of males:100 AF tended to increase during the middle years of the time series in South Rainier TCA but remained nearly constant in the later years. The ratio of mature males:100 AF increased in a linear fashion over time in South TCA.

In OLYM, we surveyed Core TCA six times from 2008-2015, and we completed one or two surveys each in Elwha, Northwest, Southeast, and Quinault TCAs from 2011-2014. We estimated a mean of 236 (SE=17.8) elk present during surveys of Core TCA or 2.3 elk/km². Mean elk densities in less-surveyed TCAs ranged from 0.2-2.9 elk/km², with highest densities recorded in Quinault TCA.

Elk abundance estimated in Core TCA appeared to decline steeply over the 8-years sampled in OLYM (r_o =-0.157; 95% CI=-0.32, -0.03); however, statistical support for this trend was weak due to the small number of estimates and considerable unexplained year-to-year variability in estimates. A comparison of statistical support among the 16 models examined indicated there was strongest statistical support for no change in elk abundance. To the extent there was support for declining abundance, it was most closely associated (negatively) with annual variation in SHI.

Elk population composition remained constant from 2008-2015 in OLYM's Core TCA. The weighted mean calf ratio was 36:100 AF (SE=1.6) in Core TCA, whereas the weighted mean ratio of all male classes combined was 60:100 AF (SE=7.5) and the weighted mean ratio of mature males

was 48:100 AF (SE=28.9) in the remaining TCAs. The weighted mean ratio of mature males was 49:100 AF (SE=7.2) in Core TCA.

There was considerable variation in densities of elk among subsample units within each TCA in both parks. Elk densities ranged from <1 to nearly 20 elk/km² in North Rainier TCA, with highest densities recorded in count units on the northern and eastern portions of the TCA. Similarly, elk densities ranged from <1 to approximately 10 elk/km² in South Rainier TCA, with lowest densities in the southeastern 1/3 of the TCA. In OLYM, mean elk densities ranged from 0-15.6 elk/km², reaching greatest densities in the upper Quinault (Quinault TCA) and Hoh Valleys (Northwest TCA). Relative elk densities generally remained constant over time among subsample units within TCAs.

Annual variations in weather, measured during surveys (i.e., daily maximum temperature on the survey day) or cumulatively during summer leading up to surveys (SHI), confounded interpretation of abundance trends within TCAs. The last four years of surveys were increasingly warmer and drier than average, whereas the first four years were cooler and moister than average. Hence, it was not possible to discriminate between declining population trends versus shifts in population distribution (outside TCA boundaries) in response to vegetation phenological changes in the subalpine zone related to drying conditions. Estimated elk abundance in both South Rainier and OLYM's Core TCAs were appreciably lower during 2015—a year noteworthy for having one of the lowest snowpacks on record and marked by early disappearance of snow and hot, dry conditions (Marlier et al. 2017). We postulated that decreased use of South Rainier and OLYM's Core TCAs likely reflected a shift in elk distribution to lower elevations during hot dry summers (hence outside the TCA) rather than decline in actual abundance, although a combination of factors cannot be ruled out.

In contrast, elk populations tended to increase in North Rainier TCA in association with increased temperatures recorded during surveys. We cannot explain the positive association of elk abundance with ambient temperatures at the time of surveys because counts were generally depressed during hot dry weather in other survey units. Consequently, we speculated that the estimated 4% per annum increase in elk populations may be a statistical artifact; but to the extent it was not, it more likely reflected population increase over time despite the warming temperatures, rather than a positive increase in the proportion of elk using the TCA during hot survey conditions. Independent surveys of elk on late-winter ranges outside MORA support the hypothesized growth in North Herd.

The future of elk monitoring within NCCN parks is at a crossroads. The NCCN withdrew funding support for elk monitoring in 2015 in deference to other monitoring priorities and flat funding levels. Washington Department of Fish and Wildlife contributors also withdrew support to refocus limited funding on developing more comprehensive surveys of the entire North and South Rainier Herds, not just the migratory component residing within MORA during summer. Although interpretations of abundance trends reported here are ambiguous, perhaps justifying those decisions, other findings from this analysis are not ambiguous. The ratios of males:100 AF exceeded statewide objectives for hunted elk herds in Washington State, and ratios in OLYM were among the highest ever reported for other protected elk populations. High ratios of males indicated that healthy numbers of breeding males were found across both parks

Moreover, importance of elk as keystone species affecting park ecosystems and cultural significance of elk to multiple user groups is not in question, and perturbations to future elk populations due to changing climate, predator regimes, and diseases are likely imminent. Although funding support, logistical constraints, and analytical challenges all present obstacles to continuing existing elk survey methods, promising new tools for estimating elk abundance are being developed continuously, and each of the partners contributing to the current elk monitoring program share common interests in understanding elk population trends at varying scales. We conclude that a group reexamination of future options for elk monitoring in and around National Parks in NCCN would help to clarify new monitoring directions and potential areas of interest for continued collaboration around both parks.

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List of Terms

Aerial detection bias: Estimation error inherent in aerial surveys resulting from failure of observers to detect all animals present during a survey, or from potentially recording some animals more than once if they move undetected during the survey.

Aerial-bias-correction model: A general term for statistical models used to estimate probability of aerial survey crews sighting groups of animals, which in turn is used to correct raw counts for aerial detection bias. Different models can be developed from observational trials of various types elaborated below.

Sightability trials/data: In sightability trials a single aerial observer (or multiple observers working as a team) attempts to detect animal groups known to be present (either through radio-telemetry or independent observation) under varying environmental, habitat, or survey-specific conditions that are recorded as covariates.

Simultaneous double-observer (DO) trials/data: DO trials are attempts made by front- and back-seat observer pairs in an aircraft to independently detect animal groups that do not contain any radio-collared animals. These groups are conditionally present in the data set only if they were detected by at least one observer. Although detection history is always collected, sometimes exclusively, it is more common to also record corresponding covariate data that may help explain sighting probability variation among groups to reduce bias due to lack of independence among groups.

Simultaneous double-observer sightability (DO-S) trials/data: DO-S trials are a combination of both DO and sightability trials. DO-S trials are attempts by front- and back-seat observer pairs to observe animal groups known to be present within the survey area and that contained at least one radio-collared animal. DO-S trials allow for unconditional estimation of detection probability because inclusion of DO-S trials in the data set is not contingent on any circumstance other than that the group was present in the surveyed area. DO-S trials of groups containing collared animals are assumed to be a random sample of all groups, with respect to recorded covariates.

Introduction

In 2007, the North Coast and Cascades Network (NCCN) of the National Park Service (NPS) began developing and implementing a program for monitoring trends in abundance, sex and age composition, and distribution of elk (*Cervus elaphus*) populations within Mount Rainier National Park (MORA) and Olympic National Park (OLYM). Elk populations were selected as one of 12 ‘vital signs’ within NCCN—each intended to represent overall condition of park resources, effects of environmental stressors, or specific natural resources of important human value (NPS, <https://www.nps.gov/im/vital-signs.htm>, Accessed 18 May 2020). Because elk populations have such extraordinary value to several agencies and sovereign Native American Tribes, monitoring protocols were developed collaboratively with NPS, Muckleshoot Indian Tribe (MIT), Puyallup Tribe of Indians (PTOI), and Washington Department of Fish and Wildlife (WDFW). This is the only monitoring program within NCCN that was developed collaboratively with several agencies and that is supported by funding and personnel from each collaborating agency and Tribe. We completed and published the peer reviewed elk monitoring protocol in 2012 (Griffin et al. 2012) and synthesized results of the first four years of monitoring in both parks (2008-2011) in 2015 (Jenkins et al. 2015). Here, we build on the previous synthesis by adding four to six years to the data set (depending on park) and reexamining trends in elk abundance, distribution and population composition on high-elevation summer ranges in both parks throughout the 8-10-yr monitoring period.

Elk as a Vital Sign

As key components of lowland and mountain ecosystems in the Pacific Northwest, elk are tightly woven into ecological, historical, and cultural fabrics of MORA and OLYM. Historically, Roosevelt elk (*Cervus elaphus roosevelti*), the Pacific coastal subspecies of elk, were abundant in floodplains and riparian forests along most major river systems in western Washington (Raedeke and Taber 1982). During summer, many herds migrated to subalpine meadows in adjoining mountains (Schwartz and Mitchell 1945, Starkey et al. 1982). Although ethnographic records clearly indicate that elk are indigenous to both Olympic Mountains and Cascades Ranges, elk had become rare or absent around Mount Rainier prior to Euro-American settlement in the mid-1800s (Gustafson 1983, Schullery 1983). By the start of the 20th century, unregulated elk hunting for meat, antlers, and trophy ‘ivory’ teeth had widely decimated elk populations throughout accessible and settled areas of Oregon and Washington (Harper and colleagues 1985, Murie 1951). A notable exception occurred on Washington’s Olympic Peninsula where a largely inaccessible wilderness helped protect a remnant stronghold of native Roosevelt elk (Schwartz and Mitchell 1945).

Mount Rainier National Park was created in 1899 to preserve sights and ecosystems associated with Mount Rainier, including its fish, wildlife, and renowned subalpine meadows. The area that would become OLYM was set aside first as Mount Olympus National Monument in 1909 when elk populations in the Pacific Northwest may have been at their nadir. The monument was established explicitly to protect the last stronghold of Roosevelt elk and its native forested habitat. Concurrently, elk were protected from hunting throughout Washington in the early 1900s and an active campaign was waged to eradicate wolves (*Canis lupus*) and reduce other predator populations, notably cougar (*Puma concolor*), to restore elk populations throughout Washington. Rocky Mountain elk (*Cervus*

elaphus nelsoni) were reestablished in the Cascades Range in and around MORA through several translocations of elk from Yellowstone and Grand Teton National Parks from 1912-15 and 1932-33 (Bradley 1982).

Elk Numbers increased in both parks during the early 20th century in response to coordinated enhancement efforts. In Mount Olympus National Monument, over-browsing was reported in western rainforest valleys as early as 1915, and large numbers of elk were reported dying during severe winters beginning in 1918 (Schwartz 1939). During the 1930s, biologists reported abundant elk populations and concerns about overgrazing on several key wintering areas of what is now OLYM (Murie 1935a, Murie 1935b, Sumner 1938, Schwartz 1939). Elk were observed in MORA in 1915, and by the 1930s elk inhabited the primary summer ranges used by elk today (Bradley 1982). During the 1950s to 1970s, widespread logging of elk winter and spring ranges adjoining MORA improved winter and spring forage conditions and stimulated population growth of migratory elk herds wintering adjacent to and summering within the park (Raedeke and Lehmkuhl 1985, Jenkins and Starkey 1996). As elk populations continued to grow adjacent to MORA during the 1970s, increasing signs of trailing, trampling, and grazing impacts led to questions of whether elk herds using the park during summer were adversely affecting ecological conditions in subalpine meadows (Bradley 1982, Ripple et al. 1988).

Elk were chosen as a vital sign in both MORA and OLYM in large measure because of their strong ecological interactions with vegetation communities and history of concerns over adverse effects of elk on signature resources of each park. There has been nearly a century of concern and debate over potential impacts of naturally regulated elk populations and high levels of herbivory in low-elevation temperate rainforests in OLYM. Recent research has demonstrated the ongoing significant ecological role of elk and deer herbivory in shaping both structure and composition of the park's renowned rainforest communities (Happe 1993, Woodward et al. 1994, Schreiner et al. 1996). The ongoing debate over negative impacts of elk on ecosystem properties in OLYM currently focuses on whether excessive elk populations have impaired riparian vegetation communities and altered river channel characteristics (Beschta and Ripple 2008, East et al. 2017). Concerns over ecological effects of elk on subalpine communities in MORA have abated during the last two decades, but renewed population growth would likely reignite concerns over elk grazing and trampling effects on subalpine ecosystems.

There are complex processes and interactions at play with potential to influence elk populations in both MORA and OLYM in the future. Changing land uses, hunting, disease, climate, and predator management programs on lands adjacent to these parks all have potential to influence elk population trends and ecosystem dynamics within. There have been recent proposals to reintroduce wolves to OLYM (Ratti et al. 2004) and natural wolf recolonization in Washington is occurring, with wolves from Canada and Idaho now reproducing in Washington (Wiles et al. 2011). Wolf packs have established territories north and east of MORA and WDFW has begun installing camera stations to better track wolf colonization in response to a growing number of wolf reports in and around MORA (M. Tirhi, Wildlife Biologist, WDFW, personal communication). The colonization of wolves in the region would likely affect both elk abundance and distribution (Fieberg and Jenkins 2005). Further,

as climate continues to change in the Pacific Northwest, elk populations may be influenced by shifts in temperature, precipitation and snowpack (Salathé et al. 2009); forest disturbance regime (Dale et al. 2001, Westerling et al. 2006); and vegetation (Zolbrod and Peterson 1999). Nationally, increased prevalence and proliferation of diseases (e.g., chronic wasting disease, paratuberculosis, and brucellosis) is a growing concern for wildlife managers (Daszak et al. 2000, Angers et al. 2006). In Washington State, recent emergence and spread of Treponeme Associated Hoof Disease (TAHD) in elk presents a very real concern for managers of elk populations throughout western Washington (<https://wdfw.wa.gov/species-habitats/diseases/elk-hoof>, Accessed 9 January 2020).

None of these issues is simple, and all have implications for policy and management. Obtaining reliable information on elk population trends is a critical first step in discussing and addressing elk conservation and management across agency and Tribal jurisdictions. Over time, elk monitoring results may be used to help the parks evaluate effects of climate change, external impacts, and other stressors that may influence elk populations across park boundaries. These same results are useful to Tribes and agencies in the Mount Rainier area in meeting their population management objectives. Further, improved understanding of elk population trends is needed to interpret effects of NPS policies on natural regulation of ungulate populations and associated ecosystem effects and to communicate these trends to a diverse and interested public.

History of Elk Monitoring in Mount Rainier and Olympic National Parks

For over 30 years, the MIT, PTOI, NPS, and WDFW have worked together to monitor trends in abundance and composition of elk herds that migrate into MORA during summer. Historically, MIT, PTOI, NPS, and WDFW surveyed elk nearly annually in subalpine summer ranges of MORA from either fixed wing airplanes or helicopters during evenings in late summer and early fall. Survey crews recorded numbers of elk seen within survey units defined by Bradley (1982). Bradley (1982) recommended an index of abundance, ‘E4’, multiplied by two, as a standard metric for comparison of elk abundance over time. The index ‘E4’ was the mean of three different *ad hoc* indices, which are described fully in the previous synthesis report (Jenkins et al. 2015). The multiplier was intended to account for aerial detection biases (i.e., elk present but not seen by aerial survey crews) and was based on comparisons of aerial survey counts with densities of elk computed from pellet group surveys in Cedar River Watershed (Schoen 1977). Abundant research has shown, however, that aerial detection biases are influenced by variations in vegetation density, elk behavior and other factors that are not likely to be constant among areas or over time (Samuel et al. 1987, McCorquodale et al. 2013, Griffin et al. 2013)

Olympic National Park does not have the same history of surveying elk on summer ranges as MORA. Rather, early focus for elk monitoring in OLYM was on winter and spring ranges in western valleys of the park in response to historical concerns about elk-vegetation dynamics on heavily utilized winter ranges as well as other management concerns near park boundaries (Houston et al. 1987, Jenkins et al. 2015). Elk were surveyed on key wintering areas on the west side of OLYM annually from 1985-91, and as funding permitted from 1992-2010. These early-spring surveys were discontinued in 2010 due to funding and logistical constraints, not due to lack of park interest in gaining a better understanding of elk population trends. In 2008, OLYM began conducting surveys of

elk in high-elevation subalpine habitats using the same methods as MORA to yield comparable survey results in both parks.

Monitoring and Reporting Objectives

The goal of elk monitoring in MORA and OLYM is to detect changes in abundance, spatial distribution, and herd composition of elk that use selected summer range areas when elk are seasonally concentrated and highly visible in both parks. Here, we report trends in each of these measures on selected Trend Count Areas (TCA) corresponding with key summer range areas for elk in each park. Estimates are based on surveys conducted from 2008-2015 in OLYM and 2008-2017 in MORA.

Objectives of this 10-year reporting interval are to:

- (1) incorporate new data to update aerial-bias-correction models previously developed for use in MORA to include corrections for aerial detection bias in both MORA and OLYM;
- (2) examine trends in estimated elk abundance, distribution, and population composition on subalpine summer ranges within MORA and OLYM; and
- (3) estimate effects of seasonal variation and weather on elk abundance and population composition on subalpine summer ranges in both parks.

Elk Populations and Study Areas

Mount Rainier National Park

We monitored trends in two migratory elk herds that summer in MORA—a North and a South Herd. These herds refer collectively to elk that congregate on summer ranges within northeastern and southeastern quadrants of MORA, respectively, and that migrate to fall-winter-spring ranges largely outside park boundaries to the north and south (Figure 1).

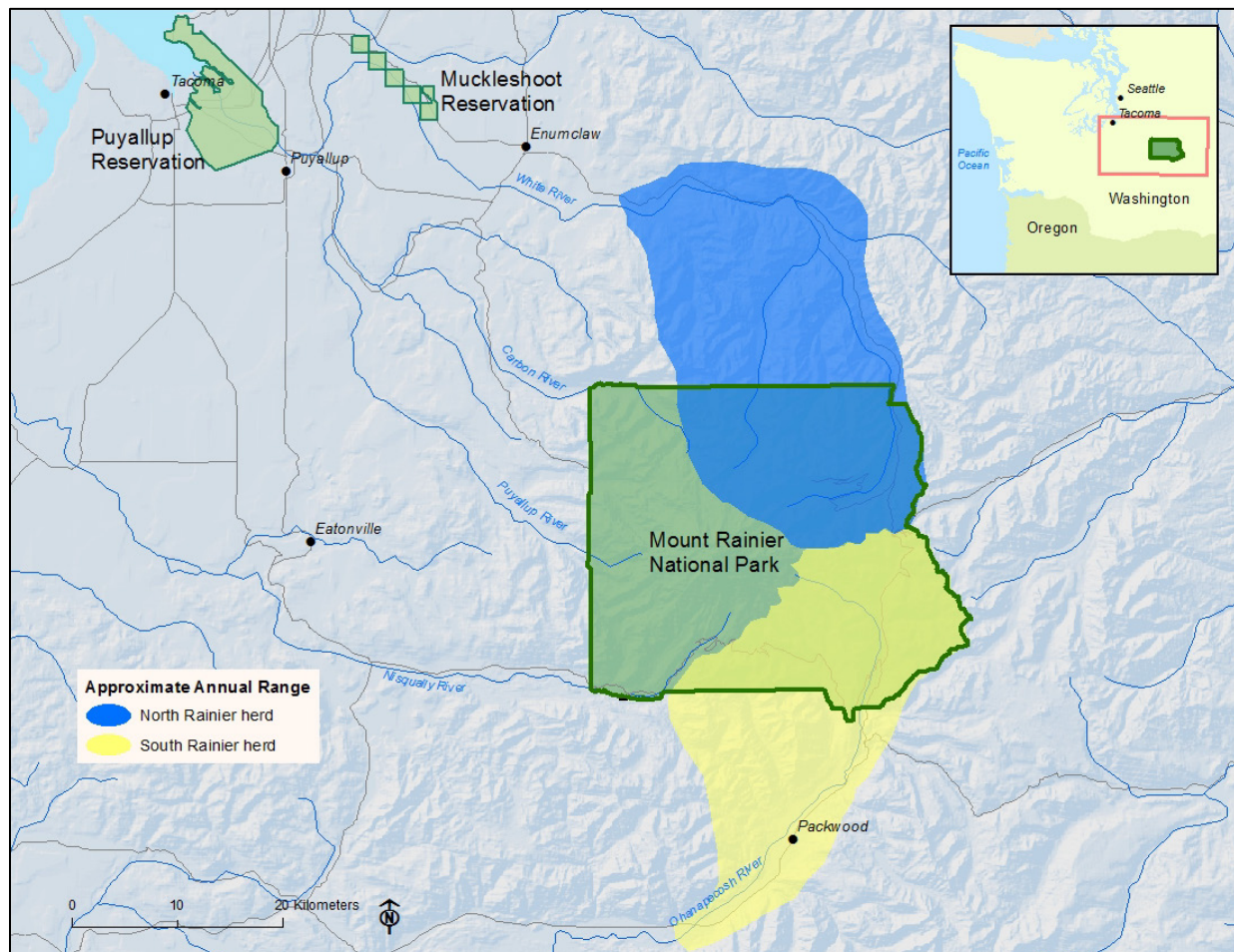


Figure 1. Approximate annual ranges of migratory components of North Rainier (blue) and South Rainier (yellow) elk herds that use MORA during summer. These elk migrate from MORA to lower elevations outside the park during winter. Winter ranges may also be used by nonmigratory elk and elk from other adjacent high-elevation summer ranges.

The migratory herds of MORA are subsets of Washington’s North and South Rainier Herds that are managed by WDFW and Native American Tribes. The ‘greater’ North Rainier Herd inhabits primarily the Snoqualmie, Green, and White River Valleys in Pierce and King Counties (WDFW 2020). The portion of North Rainier Herd that summers in MORA, the focus of this study, is recognized by WDFW and MIT as the White River sub-herd. Approximately 50% of the White River

sub-herd migrates annually into MORA during summer (MIT, unpublished data). This population segment migrates to lower elevations in the White River valley for winter (Figure 1), where it mixes with elk from other migratory subpopulations as well as a resident population component that stays year-around at low elevations.

The ‘greater’ South Rainier Herd inhabits primarily the Cowlitz Valley in Thurston and Lewis Counties (Huang et al. 2002, Moeller 2010). The portion of the South Rainier Herd monitored in MORA migrates to winter range near the city of Packwood where it mixes with elk from other migratory herds and elk that reside year-round at low elevations (Moeller 2010). The exact proportion of the Packwood sub-herd that migrates to MORA is not known, but approximately 46% of this sub-herd migrates north of Packwood onto summer ranges in and near the Park boundary (Moeller 2010). A small number of the adjacent Yakima Elk Herd have also been identified using summer ranges in and near Mount Rainier during summer (Moeller 2010). Consequently, elk from the Yakima Herd may be represented occasionally in our counts.

We monitored elk in two Trend Count Areas (TCAs) corresponding with the summer ranges of the North and South herds in MORA (Figure 2). The TCAs corresponded closely with herd units first defined by Bradley (1982) and used historically as the framework for all subsequent surveys (Figure 2). The North Rainier TCA (103 km²) is between 1,500 and 2,100 m elevation. The South Rainier TCA (89 km²) is between 1,350 and 2,100 m elevation, except on some southwest-facing slopes where past landslides and wildfires maintained open parklands down to 1,200 m. Within these defined survey areas, we referred to satellite-derived estimates of vegetation cover and type (Pacific Meridian Resources 1996) and excluded areas of continuously dense forest canopy, rock, or permanent snow from the study area (Griffin et al. 2012). The TCAs encompassed primarily subalpine woodlands and meadows consisting of mosaics of subalpine parkland forests dominated by subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*), subalpine meadows, and low shrublands (Franklin et al. 1988). The tallest trees in subalpine parklands were generally <20 m tall. Canopy closure was highly variable but tended not to be dense near tree line.

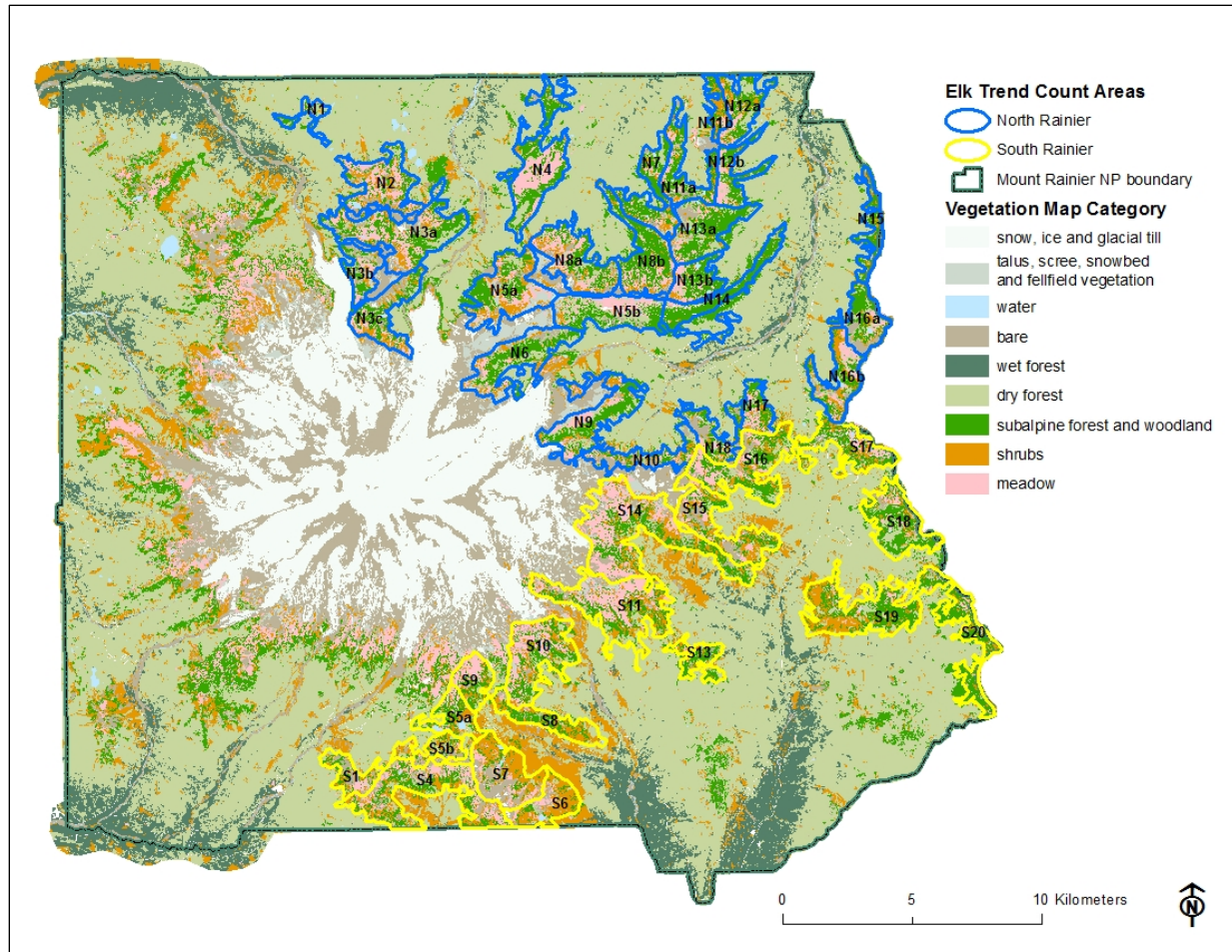


Figure 2. Summer trend count areas (TCA) in MORA, including North Rainier TCA (103 km²; survey units in blue) and South Rainier TCA (89 km²; survey units in yellow).

Olympic National Park

Spanning elevations from sea level to over 2,400 m, OLYM encompasses summer ranges and many winter ranges used by migratory elk herds on the Olympic Peninsula, particularly in western drainages. Additionally, there are low-elevation resident herds in western and northern valleys that remain at low to middle elevations throughout the year (Figure 3).

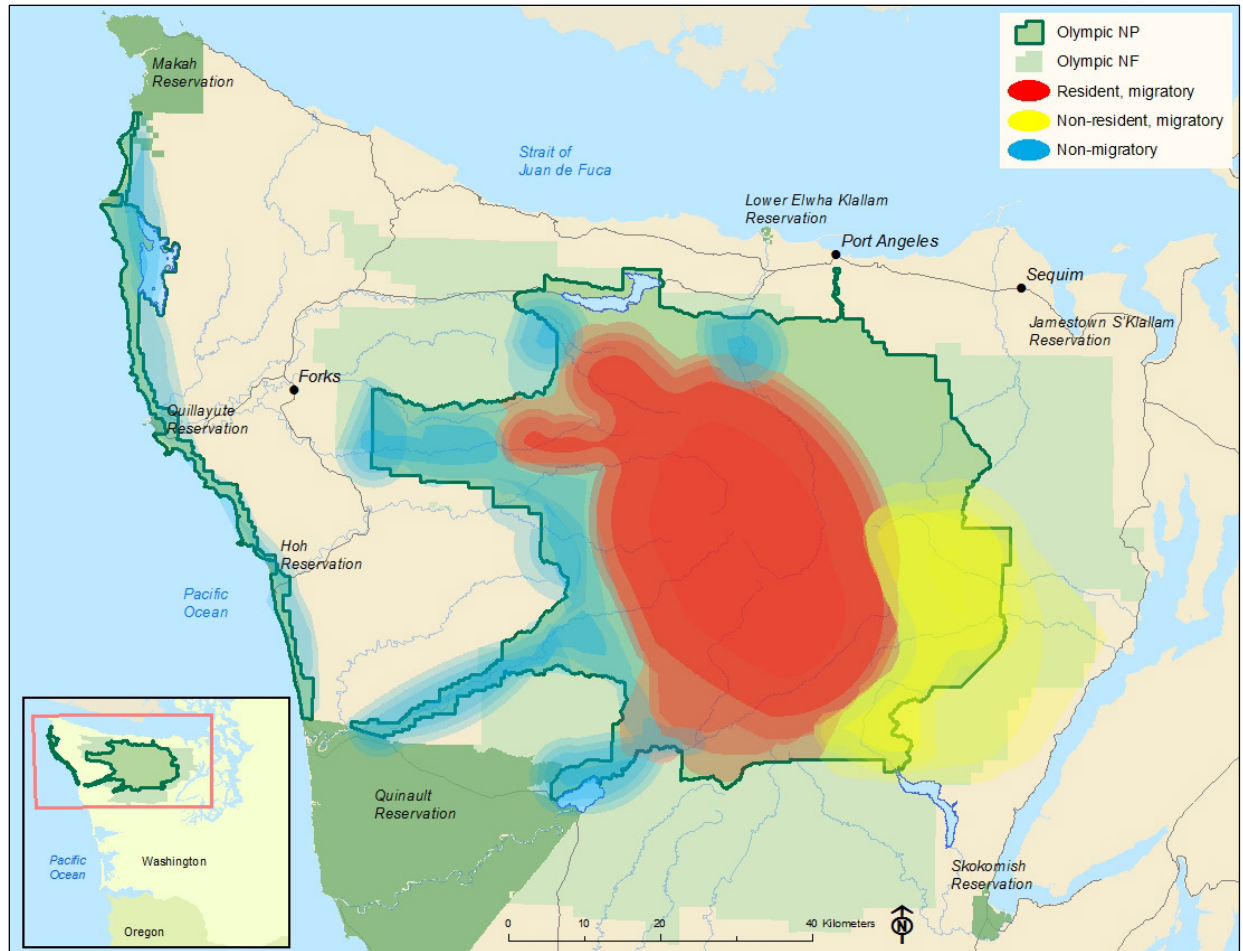


Figure 3. Map of OLYM and surrounding areas of the Olympic Peninsula, showing the approximate distributions of elk that use OLYM during all or part of the year. Red shading indicates approximate combined summer and winter range areas occupied by migratory elk herds that reside in the park throughout the year. Yellow indicates approximate areas used by migratory herds that summer in the park and winter outside the park (non-resident migratory). Blue indicates area occupied by non-migratory elk herds. The shaded tones of red, blue and yellow on the periphery of each distribution indicate they are approximations lacking identifiable boundaries. The annual ranges of many herds overlap; this map does not show ranges of all elk herds on the Olympic Peninsula.

We surveyed elk in five TCAs that encompassed most summer ranges used by migratory elk herds in OLYM (Figure 4). Subalpine habitats extend to lower elevations in OLYM than in MORA; consequently, we defined summer TCAs as ranging between 1,200 m and 1,650 m elevation. This elevation range was confirmed by data collected from GPS-collared elk (NPS, unpublished data). As in MORA, the TCAs in OLYM comprised a mosaic of subalpine fir and mountain hemlock forests, and a diversity of high elevation meadow and shrub communities (Fonda and Bliss 1969, Kuromoto and Bliss 1970).

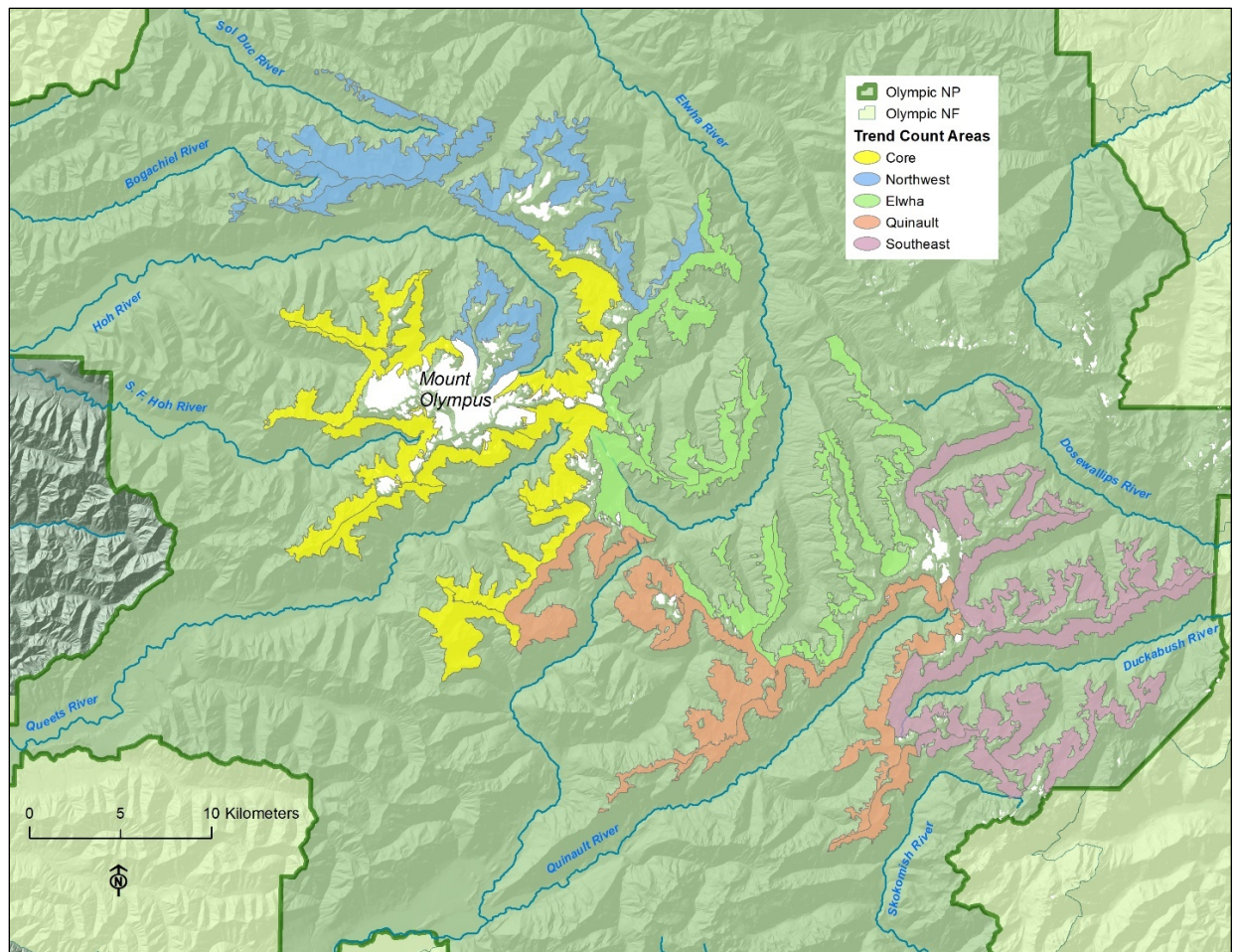


Figure 4. Trend count areas in OLYM, including Core TCA (surveyed annually) and four alternate TCAs surveyed once every fourth year. Core, Northwest, Elwha, Quinault, and Southeast TCAs are approximately 100, 81, 73, 79, and 86 km², respectively.

Methods

Survey Design

In MORA, our initial goal was to complete two replicate aerial surveys in both North and South TCAs annually. Due to funding and logistical constraints, however, we did not always complete replicated surveys of both TCAs. As a cost-saving measure, in 2011, we adopted a reduced sampling goal of completing two replicate surveys of each TCA on alternating years and one survey in intervening years (Griffin et al. 2012).

We devised a different sampling schedule in OLYM to ensure complete coverage of important summer ranges over several survey years. Each survey year, we attempted to survey the Olympic Core TCA (hereafter, Core TCA) plus one of four non-core TCAs, thereby completing surveys in all TCAs over a 4-year span. A longer sampling interval was required in OLYM than in MORA to survey the larger summer range area on a fixed budget. The sampling design at OLYM summer TCAs achieves widespread sampling over OLYM summer ranges and documents changes in abundance in Core TCA in each year of survey.

Survey Methods

Aerial Surveys

We surveyed elk in each TCA by helicopter (Bell 206BIII, Bell Helicopter, Hurst, TX; or Hughes 500D, MacDonnell-Douglas Helicopters, Inc., Mesa, AZ) from 13 August–19 September 2008–2017. In MORA, all survey flights were conducted during evenings, beginning as early as four hours before sunset and ending as late as 30 minutes after sunset, when elk tend to be most visible during evening feeding bouts. The goal was to survey an entire TCA on a single evening using two helicopters and survey crews operating simultaneously in complementary halves of a TCA, but logistical issues sometimes required surveying over multiple days. In OLYM, due to larger areas covered and use of a single helicopter, surveys were conducted during evenings (same prescriptions as in MORA) and mornings (30 minutes before to four hours after local sunrise) often over multiple days. In both parks, elk were surveyed from approximately 100–150 m above ground level along flight lines approximately 250–500 m apart. Flight speed was approximately 85 km/hr with a search intensity of approximately 0.35 km²/min. Each TCA was subdivided into smaller survey units to facilitate communication between two helicopters operating simultaneously, ensure complete survey coverage, and to allow examination of spatial patterns of elk use within TCAs (Figures 2 and 4).

Although it is desirable to retain consistent crews for all surveys, due to logistic constraints it was often necessary in MORA to substitute one or more observers between surveys. As a result, there were numerous observers with insufficient sample size to estimate sighting probability differences among individual observers. This limitation, requiring reliance on sighting probabilities averaged over observers, likely increased the overall estimated measurement error rate.

Survey crews consisted of a pilot and three experienced observers, one seated beside the pilot in a front seat, and two in the rear seats. The pilot and front-seat observer had views to the front, sides, and below the flight path. Each back-seat observer had a view to one side of the flight path. Although

the pilots' attention was focused always on flying safely, pilots also detected elk. While searching for elk, observers recorded elk groups that were detected up to 300 m outside survey unit boundaries. This allowed for more careful determination later of whether observed groups near TCA boundaries were inside or out of count areas based on GPS coordinates. Abundance estimates were based on elk locations confirmed within TCA boundaries, but we included elk groups up to 300 m from TCA boundaries in estimating population composition.

In-flight procedures required each observer to search independently for elk but to collaborate in determining group size, composition, and covariates of detected groups. Individual survey team members recorded elk observations independently. This was accomplished by each observer maintaining separate records of their elk sightings without communicating with one another until the helicopter had flown sufficiently past an observed elk group to ensure that each observer in the helicopter had a chance to spot it independently. We noted rare occasions when observations were not independent between front- and back-seat observer pairs (i.e., through inadvertent communications); we omitted non-independent observations from the data set used for model fitting but retained them for abundance estimation.

We determined and recorded whether each observed elk group was seen by a front-seat observer, back-seat observer, or both, and whether there were radio-collared elk in the group. We recorded locations of each group using a GPS unit. We classified each elk in the group as an adult female, young of the year (i.e., calves), yearling male, subadult male, or adult male based on antler characteristics and body size (Griffin et al. 2012). If a motion-stabilizing camera was available, we photographed groups containing ≥ 20 individuals to reduce bias in group size estimation and sex-age determinations (Cogan and Diefenbach 1998, Schoenecker et al. 2006). We recorded the following covariates associated with each observed elk group: group size and composition, percent concealing vegetation within 10 m of any elk in the group (V; using five interval classes: 0, 1–25, 26–50, 51–75, or 76–100%), whether the group was standing on herbaceous vegetation (H; yes or no), whether the group was in forest vegetation (F; yes or no), lighting conditions (L; flat or high contrast), and group activity when first detected (M; moving or not). We noted whether each elk group was detected to the left, right, or both sides of the helicopter's flight path. We noted when an elk group was directly below the helicopter's flight path and not visible to back-seat observers (C; centerline yes or no). A separate covariate denoted whether the elk group was on the same side of the helicopter as the pilot (P; yes, if group on same side as a pilot-observer). After completing the count of a survey unit, we used radio-telemetry to identify and locate any radio-collared elk that were missed during the surveys. We recorded the same covariates for missed groups as for groups detected during the survey.

Data Management

The Project Lead entered field survey data into the project's relational database and reviewed and verified the data. Database records were verified for complete and accurate transcription by retrieving and visually comparing entered data against the original forms. Aerial photographs of elk groups were examined and, if necessary, composition classifications of groups were amended. Once data for the season were entered and verified, we identified and corrected inconsistencies in the data

(i.e., missing or out-of-range values) by running a set of pre-built validation queries. We used a structured procedure to impute missing covariate values based on modal or median values recorded for each covariate. For observations with missing data for group size or activity, we substituted the median group size computed from all groups that contained ≥ 1 adult female and were detected in the same category of percent concealing vegetation. For observations with no percent concealing vegetation recorded, we used median group size and vegetation cover score based on all observed groups with ≥ 1 adult female. For observations missing a value for light level, we used the same light level as recorded in the preceding and subsequent observations. We used audio recordings of cockpit conversation and global positioning system (GPS) records of the survey flight path to determine on which side of the helicopter an elk group was located when that information was not recorded on paper in flight. To enhance accuracy in model development we did not use observations with imputed covariate values in model fitting, unless those observed groups contained at least one radio-collared elk. We included observations with imputed covariate values for radio-collared groups to bolster sample size of DO-S trials used in modeling. We used all elk groups observed during surveys in computing abundance estimates regardless of whether covariate values were imputed so as not to unnecessarily bias estimates by excluding observed groups with missing covariates.

Project spatial data were stored in a geodatabase (ESRI, Redlands, California) that contained several feature datasets, each of which contained sets of point, polygon, or line feature classes. The main feature datasets were for navigation, survey area boundaries, records of survey flight paths, records of animal observations, and spatial analyses. Spatial features in the geodatabase were linked with the projects relational database records via primary key relationships maintained in the relational database.

We processed spatial data collected in the field as soon as possible after a survey. At the end of a field season, final coordinate data for group observations were derived from matching GPS flight line time stamps with time stamps recorded in the field and making any necessary final adjustments by matching available photographs with digital orthorectified aerial photography. These final coordinates were then stored in the relational database. The relational database is the long-term repository for observation coordinates where additional processing and quality assurance procedures are documented.

Data Analysis

Introduction to Aerial-Bias-Correction Models

A large array of methods exists for modeling aerial survey detection biases. To understand our choice of methods, it is useful to review some key modeling approaches and their relative strengths and limitations. The reader is referred to the list of terms on Page 1 for additional definitions of data collection methods used in developing aerial-bias-correction models.

Sightability model (M_S):

A statistical model (commonly based on logistic regression) that is fit to data from DO-S trials and used to estimate the probability of sighting a group of animals as a function of covariates that affect detection bias, which is then used to correct raw observations for aerial-detection-bias. Sightability

models are calibrated using DO-S trials, but then are typically applied to similar surveys in which no known groups are available, and the pre-calibrated model is assumed to apply without further validation for the current survey time, place, conditions, and observers.

Simultaneous double-observer models (M_D):

A statistical model (commonly based on logistic regression) fitted to data from DO trials that estimates the probability of sighting a group of animals as a function of covariates that affect detection bias. These models are structured identically to M_S models, however, due to the conditional inclusion of observations, they are more likely to be biased. However, unlike M_S models, M_D models use data collected at the same time and place for which abundance estimates are produced, thereby reducing bias due to changing conditions over time and space. Furthermore, without the need for known groups, the data set is typically much larger, leading to higher precision.

Simultaneous double-observer sightability model containing heterogeneity correction (M_{DSH}):

A special class of sightability model developed from DO-S and DO trials combined for estimating populations with radio-collared animals. M_{DSH} models include a heterogeneity parameter that accounts for conditional probability that an observer pair detects animal groups not containing radio collars. The heterogeneity parameter is determined based on DO-S trials, in which there are animals known to be present from radio-telemetry. Typically, data from DO trials are also included for model fitting, which adds to sample size for estimating all model parameters except the heterogeneity bias correction term. This hybrid method helps mitigate the different sources of biases inherent in M_S and M_D models by drawing on the strengths of each method to overcome the limitations of the other.

Development of M_{DSH} Models

We chose M_{DSH} models for this analysis because they combine the strengths of bias correction obtained from DO-S trials with data from DO trials collected during the current survey (not just in a prior calibration phase). In addition to providing data on the current time, place, and conditions, the DO data substantially increases the sample size for model fitting leading to more precise estimates (Griffin et al. 2012). The DO data enables the model to correct for bias due to measured covariates, while the DO-S data adds an additional correction for bias caused by heterogeneity among groups that was not fully accounted for by the measured covariates.

Our M_{DSH} models were based on detection histories of two independent observer pairs in a helicopter (i.e., DO data) and on telemetry-based detections of collared elk groups (DO-S data). The DO trials provided estimates of conditional detection probabilities because estimated probabilities were conditional upon one or both observers seeing the elk groups. The DO-S trials provided independent data used to estimate implicit residual heterogeneity bias that would not be quantifiable from DO observations alone, thus producing unconditional estimates of detection probabilities. The models were structured to include effects of specified covariates on unconditional probability that each pair of observers in the helicopter (front-seat pair or back-seat pair) detected a given elk group. For additional details on the M_{DSH} modeling approach and analytical methods, the reader is referred to the original publications that described both the M_{DSH} modeling concepts, model development, and previous applications (Model M_H in Griffin et al. 2012, 2013; Jenkins et al. 2015).

Previously, we developed a suite of M_{DSH} models for estimating detection biases associated with aerial helicopter surveys of elk conducted in MORA from 2008-2011 (Griffin et al. 2012, 2013; Jenkins et al. 2015). Here, we update previous models using additional data acquired from these and additional surveys conducted in MORA and OLYM from 2008-2015. Based on high support from previous models and in the literature (Anderson et al. 1998, McIntosh et al. 2009, McCorquodale et al. 2013, Griffin et al. 2013), we considered 10 potential main-effect covariates collected during surveys that could influence sighting probability (Table 1). In discussing these main effects, we refer to annual or “year” effect as a single main effect, even though it is seven parameters, one parameter for each of 7 survey years (2009-2015) following the first year (2008). There were also potentially $10 \times 9/2 = 45$ two-way interactions of these main effects or 55 potential predictor variables that could be considered (including interactions and 10 main effects). We used our prior experience (Griffin et al. 2013, Lubow et al. 2016) and *a priori* reasoning about the sighting process based on experience of field observers to consider effects of a subset of 12 potential two-way interactions and a single three-way interaction on sighting probabilities (Table 1). Considering all potential interactions, aside from being prohibitively time consuming, would almost certainly lead to finding spurious support for a few interactions based on chance alone. Additional rationale used to winnow the potential field of covariates is provided in Lubow et al. (2016). We reasoned that the data set size and complexity justified including selected interaction terms.

We considered 16 alternative models of covariate effects on sighting probabilities. The global model contained an intercept, 10 main effects, 12 two-way interactions and one three-way interaction mentioned above. In each of 13 additional models, one interaction term was excluded to evaluate its importance. A fifteenth model considered covariate $M:F$ (movement x forest vegetation interaction) as a substitute for $M:V$ (movement x vegetation cover interaction), which were highly correlated with each other. In the 16th model, the main effect of year (seven parameters) was excluded to assess the importance of this effect because estimating it for each year poses a substantial added cost for analysis and because we introduced this effect for the first time in the current analysis. We used Akaike’s Information Criterion for small sample size (AIC_c) to evaluate model support among 16 candidate models (Burnham and Anderson, 2002). We evaluated importance of each tested variable by examining evidence ratios (ER) of AIC_c model weights for the global model (containing all parameters) to weights of models excluding the parameter of interest. If the global model had stronger support ($ER > 1$), that implied support for including the parameter. In the one model where $M:V$ was substituted for $M:F$ we examined the ratio of support for the model with $M:F$ (or default case) to support for the model with $M:V$.

Table 1. Model components, their interpretation, and rationale used to model detection probabilities during aerial elk surveys in Mount Rainier and Olympic National Park, 2008-2017. Model components included 10 main effects, 12 two-way interactions, and one three-way interaction.

Effect Type	Effect	Component	Interpretation	Rationale for Inclusion
Main	1	OLYM (<i>O</i>)	Additional effect of OLYM (relative to MORA) on detection probability (added to Intercept)	Detection probabilities may differ between parks due to factors that are not captured by individual covariates (e.g., different crews, pilot, etc.).
	2	Hetero (<i>U</i>)	Common effect of heterogeneity biases in all models of both front-seat and back-seat observers in MORA and OLYM	Observer pairs viewing from the same platform are not completely independent; there are some elk groups with identical values for all measured covariates that may be more or less difficult for both observers to detect.
	3	Logarithm of Group Size $\ln(N)$	Natural logarithm of group size. Additional effect for larger groups	Natural logarithm of group size is expected to influence detection probabilities for both back- and front-seat observer pairs.
	4	Moving (<i>M</i>)	Common additional effect of movement (compared to the reference of no movement, either bedded or standing)	Movement might improve detection probabilities if elk have not had a chance to move from the helicopter in response to disturbance before they are sighted, or movement might reduce detection probabilities if movement precedes detection causing elk to move to greater distances or seek cover where they are harder to detect.
	5	Forest (<i>F</i>)	A potential effect on detection probability of an elk being in forest versus shrub or herbaceous vegetation, independent of percent cover effect	Forest vegetation may have a different effect on detection probabilities (separate from vegetation cover) because trees may obscure more than shrubs of lower stature or causing differences in shading.
	6	% Veg Cover (<i>V</i>)	Common effect of vegetation cover on detection probability	Elk are less easily seen in greater obscuring vegetation cover >2 m tall.
	7	Flat Light (<i>L</i>)	Common effect of flat lighting on detection probabilities	Elk may be more difficult to see in bright light because of contrasting shadows and window glare.
	8	Group on Pilot's Side (<i>P</i>)	An effect on front-seat observers of an elk group being on the pilot's side of the aircraft	The primary job of pilots is to fly safely and navigate, so they are less attentive to observations of elk and primary observers have less visibility on the pilot's side.
	9	Back Seat (<i>R</i>)	Effect of an observer being in the back seat on detection efficiency	Even after accounting for inability to see elk on the centerline, the view of back-seat observers is less than that of front-seat observers because of smaller windows and restricted viewing angles.

Table 1 (continued). Model components, their interpretation, and rationale used to model detection probabilities during aerial elk surveys in Mount Rainier and Olympic National Park, 2008-2017. Model components included 10 main effects, 12 two-way interactions, and one three-way interaction.

Effect Type	Effect	Component	Interpretation	Rationale for Inclusion
Main (continued)	10	Year (Y)	An effect of an individual survey year on detection efficiency	A year effect may pick up differences in detection efficiencies that are not related to other covariates, for example, yearly changes in crew, pilots, aircraft, etc.
Two-way interactions	1	<i>O:U</i>	An additional heterogeneity effect on detection probability at OLYM (added to Hetero)	Parks may have different observation conditions in the two parks that are not accommodated equally by existing model variables.
	2	<i>O:M</i>	Additional effect of movement on detection efficiency in OLYM (added to the effect of M)	Movement may have a different effect on detection probabilities in OLYM because of more recent and disturbing helicopter capture operations and potentially different movement responses of elk from the helicopter. Elk may move farther from helicopter before the helicopter is in position to view them (i.e., there may be an unintended consequence of not measuring distance as a sighting covariate).
	3	<i>O:V</i>	Additional effect of % vegetation cover on detection efficiency in OLYM (added to the effect of V)	Different types of vegetation provide denser cover in OLYM than in MORA. For example, OLYM has more dense shrub fields in avalanche chutes and headwater basins.
	4	$\ln(N):M$	Additional effect of group size in groups that are moving compared to those that are still. This is added to the group size effect for still groups	Movement may have a different effect on detection probabilities for large groups; equivalently, group size may have a different effect when groups are moving.
	5	$\ln(N):V$	Additional effect of large groups in dense vegetation	Because of the way we coded vegetation cover (around the entire group) larger groups may be more detectable in comparable cover than smaller groups.
	6	<i>M:F or M:V</i>	Additional effect of movement in forest or more heavily vegetated environment	Movement may draw attention more readily in forested or vegetated environment than in open or shrub cover. <i>M:F</i> and <i>M:V</i> are closely related, so only one of these should be included.

Table 1 (continued). Model components, their interpretation, and rationale used to model detection probabilities during aerial elk surveys in Mount Rainier and Olympic National Park, 2008-2017. Model components included 10 main effects, 12 two-way interactions, and one three-way interaction.

Effect Type	Effect	Component	Interpretation	Rationale for Inclusion
Two-way interactions (continued)	7	$M:R$	Additional effect on back-seat observer detection probability when elk are moving (added to effect M for back-seat observers)	If elk are moving in response to the helicopter, rear-seat observer detection probabilities may differ relative to front-seat observers due to differences in viewing angles, and if elk change behaviors as the helicopter passes, movement response may elicit a positive effect on rear-seat observers; or if elk have moved greater distances from the helicopter, may elicit a negative effect on rear-seat observers.
	8	$F:V$	Additional effect of vegetation cover in forest environment (added effect of F on V)	% obstructing vegetation may have a greater effect in tall vertical structure than in relatively shallow shrub cover.
	9	$F:L$	Additional effect of lighting in forest environment (added effect of F on L)	Lighting is expected to affect elk sightability differently in different vegetation, with negative effects of bright lighting and resulting shadows likely to be greatest in forest cover.
	10	$V:L$	Additional effect of lighting in dense vegetative cover	Same rationale as for $F:L$: Lighting is expected to affect elk sightability differently in different vegetation, with negative effects of bright lighting and resulting shadows likely to be greatest in dense vegetation.
	11	$U:R$	Addition effect of heterogeneity for rear-seat observers	Different models accounting for sighting probabilities may explain differing amounts of variation for front and rear observers leaving different residual bias due to unmodeled heterogeneity.
	12	$O:P$	Additive effect of groups on the pilot's side in OLYM	Different pilots and flying conditions in the two parks could result in different effects.
Three-way interactions	1	$M*O*Y_{14-15}$	Additive effect of movement in OLYM that varies between the years 2008-13 versus 2014-15	The different movement effect in OLYM may diminish after helicopter captures were completed.

Estimation of Elk Abundance and Population Composition

We estimated elk abundance in each surveyed unit and TCA by weighting raw counts of elk in each observed group by the inverse of group-specific unconditional detection probabilities estimated from the suite of MDSH models. For each of k MDSH models, we computed specific correction factors, $\hat{\theta}_{j,k}$, for each elk group, j , as $1/\hat{p}_{U,j,k}^*$ (Griffin et al. 2013). This application of Horvitz-Thompson correction factors for estimating detection biases in aerial surveys is well established (Steinhorst and Samuel 1989, Borchers et al. 1998). Group-specific correction factors derived from $\hat{p}_{U,j,k}^*$ can be thought of as the per-observed-elk contribution to the overall estimate of abundance, according to model k . We computed a model-averaged estimate of abundance, $\bar{N}_{a,t}$, for TCA a and survey t (Equation 1):

$$\bar{N}_{a,t} = \sum_{j \in a} \sum_k n_{t,j} \cdot \hat{\theta}_{j,k} \cdot \hat{w}_k. \quad (\text{Equation 1})$$

where $k=16$ models, $n_{t,j}$ is the raw count of elk in the j^{th} group in survey t , and $\hat{w}_k$ is the AIC_c model weight for model k .

In cases where one or more survey units were not surveyed in a TCA, we imputed elk abundance estimates for missing survey units to minimize potential underestimation. We imputed missing estimates, $\bar{N}'_{a,t}$, as the mean elk abundance directly estimated for the same survey units in other years (2008-2017). We added imputed abundance estimates from un-surveyed units to direct estimates from surveyed units. The **imputed total abundance** for such survey, $\bar{N}_{a,t}^*$ was the sum of direct and imputed estimates (Equation 2).

$$\bar{N}_{a,t}^* = \bar{N}_{a,t} + \bar{N}'_{a,t} \quad (\text{Equation 2})$$

For survey replicates in which one or more units was not surveyed, we used the imputed total abundance value as point estimates for trend estimation. In most cases after 2008, survey areas where we imputed missing values comprised <4% of total TCA abundance.

We estimated herd composition within each TCA as ratios of calves, yearling males, subadult males, mature males, and total males relative to 100 adult females. We estimated composition ratios from numbers of each sex and age class observed within 300 m of a survey unit boundary. To estimate abundance of each sex and age class of elk within observed groups, we multiplied numbers of calves, adult females and each male size/age class observed in each group of elk, j , by group-specific, model-specific correction factors, $\hat{\theta}_{j,k}$, and by AIC_c model weights, $\hat{w}_k$, (Equation 3):

$$\bar{N}_{c,a,t} = \sum_k \sum_j n_{j,c,a,t} \cdot \hat{\theta}_{j,k} \cdot \hat{w}_k, \quad (\text{Equation 3})$$

where, $\bar{N}_{c,a,t}$ is the estimated total number of elk in age-sex class, c , and $n_{j,c,a,t}$ is the number of elk of age-sex class c seen in group j in TCA a and survey t . We did not impute composition of elk in survey units that were not surveyed. This reflects our assumption that composition ratios are representative of each TCA, even if one or more survey units were not surveyed.

We estimated variance of abundance, $\widehat{\text{Var}}(\widehat{N}_{a,t})$, and composition ratio estimates using a data bootstrapping method (Wong 1996, Griffin et al. 2012 [see Appendix C of that report], Griffin et al. 2013 [Supplemental Material]) to account for variance due to: 1) random detection of animal groups within surveyed areas, 2) variation in M_{DSH} model estimation (Steinhorst and Samuel 1989, Fieberg and Giudice 2008), and 3) model selection uncertainty. Because we had estimates for all areas, there was no variation due to subunit sampling.

For surveys in which one or more units was not surveyed, we estimated variance for each non-surveyed unit, $\widehat{\text{Var}}(\widehat{N}'_{a,t})$ as the variance of mean elk abundance computed from other surveys of the same unit. To find total imputed variance of abundance for surveys with one or more non-surveyed units, $\widehat{\text{Var}}(\widehat{N}^*_{a,t})$, we assumed independence of variances and added $\widehat{\text{Var}}(\widehat{N}'_{a,t})$ for all missing units to variance of $\widehat{\text{Var}}(\widehat{N}_{a,t})$ estimated from bootstrapping.

Trends in Abundance

We examined temporal trends in natural log of model-averaged estimates of elk abundance, $\ln(\widehat{N}^*_{a,t})$, using general linear models programed in SAS 9.4 (SAS Institute 2014). The natural-log transformation of abundance is standard practice for analyzing population change because the resulting regression line slope is a measure of instantaneous annual per-capita rate of population increase or decrease under an exponential growth model (i.e., r_o , *sensu* Caughley and Birch 1971, Ryding et al. 2007). We weighted log-transformed abundance estimates by inverse of their variances following Gerrodette (1991) to ensure that imprecise estimates of abundance carried less weight in trend analysis than precise estimates.

Although our primary interest was trends in abundance (i.e., effect of time [year]), we fit a suite of related models that included both linear and quadratic temporal terms combined with a seasonal effect (Julian date of the survey) or weather variables that we postulated may also influence survey results (Table 2). We structured temporal models around *a priori* hypotheses that number of elk using TCAs may also reflect survey variations in (1): Julian dates of the survey, as well as cumulative heat and soil moisture indices that we hypothesized would influence forage phenology and elk use of subalpine meadows; (2) maximum temperature (MaxT) during survey days, which we hypothesized based on previous survey experience influenced elk activity in the subalpine zone; and (3) lunar illumination due to potential for elk to forage more nocturnally during near-full moon phases. For each model that included a given effect we also had a similarly structured model without that effect for comparison.

Table 2. Descriptions of models fit to estimates of elk abundance in North Rainier and South Rainier TCAs in MORA and Core TCA in OLYM, 2008-2017; where k is the number of model parameters (including model intercept, covariate coefficients, and error sum of squares). Time refers to the year of survey. Summer Heat Index was computed as the deviation between cumulative growing degree-days (above 5° C, measured from the date of snow melt out to the survey date) and the predicted mean for that date. Maximum temperature refers to peak temperature averaged among survey days. Soil moisture deficit was computed as the deviation between cumulative soil moisture deficit (measured from snow melt to the survey date) and the predicted mean for that date. Lunar Illumination refers to the percent of full moon illuminated during the night following the survey.

Model	Description	k
M0	Null	2
M1	Time	3
M2	Time + Time2	4
M3	Julian date	3
M4	Julian date + Time	4
M5	Julian date + Time + Time2	5
M6	Summer heat index	3
M7	Summer heat index + Time	4
M8	Summer heat index + Time + Time2	5
M9	Maximum temperature	3
M10	Maximum temperature + Time	4
M11	Maximum temperature + Time + Time2	5
M12	Soil moisture deficit	3
M13	Soil moisture deficit + Time	4
M14	Soil moisture deficit + Time + Time2	5
M15	Lunar illumination	3
M16	Lunar illumination + Time	4
M17	Lunar illumination + Time + Time2	5

We used Akaike's Information Criterion adjusted for small sample size (AIC_c) and model weights to compare support among competing models of abundance trends. We judged relative support for temporal trend and effects of seasonal and weather covariates based on evidence ratios (ER). For trend analysis, we computed ER as the ratio of AIC_c model weight for each alternative model ($\hat{w}_k$) to the null model ($\hat{w}_{null}$). Values >1 indicate support for alternative models and the effects they contained, whereas values <1 indicated greater support for no effects (constant).

We derived weather variables primarily from Cayuse Pass and Waterhole SNOTEL sites in MORA and OLYM, respectively (<https://www.wcc.nrcs.usda.gov/snow/>; Accessed 18 May 2020). The Cayuse Pass weather station was situated at 1597 m (5240 ft) in altitude near the boundary separating North and South Rainier TCAs in MORA. The Waterhole site was at 1527 m (5010 ft) feet, approximately 20 km northeast of Core TCA in OLYM. We determined maximum temperature for

each survey day, or we averaged daily maximums for surveys spanning >1 day. We computed Summer Heat Index (SHI) as cumulative number of growing degrees summed across days since snow melt out. For each day since melt out, we computed growing degrees as the difference between mean temperature each day and 5° C, a commonly used baseline indicating the temperature for positive plant development in cool-season plants. From these data we computed growing degree-days (GDD) as cumulative number of growing degrees summed among days since snow melt out. Because GDD is positively associated with time since melt out (hence, also Julian date), we computed SHI for each survey date as the difference between measured cumulative GDD and the mean for that date. Daily mean GDDs were derived from a linear regression of cumulative GDD against Julian dates from 14 August and 20 September pooled among 2008-2017.

We derived an index of Soil Moisture Deficit (SMD) from soil moisture measured at 20-40 cm depth at Sunrise weather station in MORA (NPS, unpublished data) and at Waterhole SNOTEL site at OLYM

(https://www.nrcs.usda.gov/wps/portal/nrcs/detail/or/snow/products/?cid=nrcs142p2_046339, Accessed 12 February 2021). We computed a daily SMD as the difference between soil moisture measured each day following snow disappearance and the mean overwinter soil moisture percentage. The mean overwinter soil moisture was derived from readings measured from November 1 each year to the first snow-free day the following spring. As in the case of growing degrees, we summed daily SMD readings from snowmelt until the survey date to reflect soil moisture conditions during the growing season preceding the survey, and to smooth out daily variations resulting from recent rains. We computed SMD indices for each survey as the difference between cumulative SMD readings during surveys to mean SMD calculations derived during the period of study (2008-2017 for MORA and 2008-2015) for OLYM. Daily mean cumulative SMD values were derived from a linear regression of cumulative SMD against Julian dates from 14 August and 20 September pooled among 2008-2017.

Lastly, we recorded percentage of moon illumination during each summer survey. Moon illumination was measured as percentage of full moon illuminated during the night following each survey, ranging from 0 for new moon phases and 100% for full moon phases

(<http://www.astronomyknowhow.com/month-percentage.php>; Accessed 17 December 2019).

We examined temporal trends in elk abundance to discriminate between observed rates of change in elk abundance and temporal changes remaining after controlling for weather effects. First, we computed instantaneous per-capita rate of change in abundance (r_o) using linear regression of $\ln(\hat{N}_{a,t}^*)$ against year. Second, we computed a similar model-averaged predicted abundance for each survey while holding each seasonal and weather variable constant at its mean value. The resulting trends in predicted elk abundances represented effect of time *after* accounting for all variation in seasonal and weather covariates present in the models (i.e., the residual temporal variation if all else had remained constant).

Trends in Spatial Distribution

We assessed changes in elk spatial distributions within each TCA based on changes in relative elk density measured among survey units of a TCA. We computed relative elk density in each survey unit during each survey as estimated density relative to mean density measured across all survey units in a TCA. Relative densities <1 indicated densities less than the TCA mean, whereas relative densities >1 indicated greater than mean TCA density. We tested for statistically significant temporal trends in relative density within individual survey units. For each survey unit we fit a linear regression where all available estimates of relative density for the unit were the response variable, predicted as a function of time, in years. A negative trend indicated relative elk density declined over time, whereas a positive trend indicated a relative increase in local density irrespective of overall abundance trends. Such analyses identified changes in distribution such as may occur in response to changes in human disturbance impacts or long-term habitat changes. We had no *a priori* hypotheses about effects of covariates other than time on spatial distribution in summer survey areas, so this analysis did not include multi-model inference. Rather, we concluded that there was a statistically significant trend in relative density over time if the coefficient of time in the linear regression was statistically significant based on a *z*-test (where $z = \text{coefficient point estimate} / \text{coefficient standard error}$) and assuming a type-I error rate of 0.10.

Trends in Population Composition

We estimated trends in composition of elk groups observed in MORA and OLYM using a weighted linear regression of composition ratios against time. Linear regression on data that must be nonnegative can be problematic (e.g., heteroscedastic variances and predicted negative values); however, our data fit linear models with Gaussian variation adequately. Like the analysis of abundance, we weighted composition estimates by inverse variance to allow for a proportionally greater influence of precise estimates (Gerrodette 1991). However, because there were several near-zero values for ratios of yearling males per 100 adult females, we felt that extraordinarily low variances associated with these estimates would place excessive weights on these values. Therefore, we fit unweighted regression models for analyses of trends in yearling male ratios.

We examined trends in ratios of calves, yearling males, subadult males, mature males, and of all male age classes combined per 100 adult females (:100 AF). We examined several potential models of change in composition ratios: the null model in which ratios did not vary over time and models that incorporated effects of time (i.e., year), Julian date of the survey, SHI, and MaxT recorded on survey days (Table 3). We hypothesized that ratios of adult males observed with the female aggregations would likely increase as the peak breeding season approached toward the end of each annual survey window (i.e., early to mid-September). Further, we hypothesized that SHI or MaxT may affect composition ratios due to potential differences in nutritional requirements or heat tolerances of male and female elk. As with trends in abundance, we used AIC_c and model weights to examine support among competing models of trends in population composition and to examine relative contributions of temporal trend among years compared to trends associated with seasonal and weather effects.

Table 3. Descriptions of models fit to composition ratios of elk in North Rainier and South Rainier TCAs in MORA and Core TCA in OLYM: where: k is the number of model parameters (including model intercept, covariate coefficients, and error sum of squares); Time refers to survey year; Maximum Temperature refers to peak temperature averaged among survey days; Summer Heat Index is the difference between cumulative number of growing degree-days (above 5° C) assessed from the time snow melts out to the survey date and the predicted mean for that date.

Model	Description	k
M0	Null	2
M1	Time	3
M2	Julian date	3
M3	Time + Julian date	4
M4	Summer heat index	3
M5	Time + Summer heat index	4
M6	Maximum temperature	3
M7	Time + Maximum temperature	4

Results

Aerial Surveys

We conducted 28 aerial surveys in MORA from 2008-2017, 13 surveys of North Herd and 15 of South Herd TCAs (Table 4). In 12 surveys we were unable to survey small areas due to time constraints caused by approaching darkness. Survey coverage was most limited in 2008 when considerable time was spent collecting data for M_{DSH} model development. Overall, we completed an average of nearly 97% survey coverage of TCAs, thus requiring minimal imputation of counts from missing survey units. Survey intensity ranged from 0.3-0.5 km²/min, averaging 0.35 (Standard Deviation [SD]=0.06) km²/min.

We conducted six surveys of Core TCA in OLYM from 2008-2015 (Table 5). We surveyed about 93% of Core TCA in 2008 and completed the survey in all remaining years. Survey intensity in Core TCA averaged 0.38 (SD=0.07) km²/min indicating comparable survey intensity to that in MORA and to the overall survey intensity goal of 0.35 km²/min. We completed two surveys in Elwha TCA in 2012 and 2014, and one survey each in Northwest, Southeast, and Quinault TCAs in OLYM from 2011-2014. Survey intensity tended to be higher in Elwha and Southeast TCAs than Core TCA.

M_{DSH} Models

We updated M_{DSH} models developed previously for MORA (Jenkins et al. 2015) using 148 DO-S trials associated with elk groups containing radio-collared elk (45 in OLYM and 103 in MORA) and 1,653 DO trials based on groups without radio-collared elk (288 in OLYM and 1,365 in MORA) acquired from 2008 to 2015. The model set presented here was revised (compared to Jenkins et al. 2015) to include annual effects on detection probability and the addition of several interaction terms that allowed sightability effects to differ among years and between OLYM and MORA, as elaborated below.

Support for individual models of detection bias ranged from $\hat{w}_k = 0.0$ –20.4% of total model weight (Table 6). The model parameters for each of 16 candidate models are shown in Table 6. Of 15 effects tested in the final candidate set, effect of year (annual variation in sighting probability, seven parameters) had by far the most overwhelming support with an evidence ratio (ER= $\hat{w}_{\text{Global}} / \hat{w}_{\text{Alternative}}$) of 5,572. Eight other models had ER>1, indicating greater support for including than excluding specific model parameters. The interaction of $M:F$ had greater support than closely related $M:V$ (ER=1.72).

Table 4. Flight summary statistics for aerial surveys of elk in North and South Rainier trend count areas (TCA) in MORA, 2008-2017. Shown for each replicate survey are: TCA name, year, survey dates, replicate number (Rep), omitted survey units, survey duration in minutes, survey intensity in km²/min, the area surveyed in km², and percentage of TCA surveyed (% of TCA).

TCA	Year	Survey Dates	Rep	Survey Units Omitted	Survey Duration (mins)	Survey Intensity (km²/min)	Area Surveyed (km²)	% of TCA
North	2008	8/22, 8/26	1	N6, N15, N16a, N16b, N17, N18	249	0.34	83.6	81.0
North	2008	9/3, 9/6	2	N3b, N5a, N5b, N9, N10, N14	248	0.30	73.3	71.1
North	2009	8/17	1	none	331	0.31	103.1	100.0
North	2010	8/17	1	none	218	0.47	103.1	100.0
North	2010	8/25	2	none	277	0.37	103.1	100.0
North	2011	8/17	1	N16b	310	0.32	99.2	96.2
North	2011	9/12	2	N11b	289	0.35	100.0	97.0
North	2012	8/27, 8/30, 9/5	1	N9	259	0.38	97.4	94.5
North	2013	8/19	1	none	285	0.36	103.1	100.0
North	2013	9/19	2	none	207	0.50	103.1	100.0
North	2014	8/25	1	N1	256	0.39	100.8	97.8
North	2015	8/13	1	none	272	0.38	103.1	100.0
North	2017	8/16	1	none	297	0.35	103.1	100.0
South	2008	8/26, 9/10	1	none	262	0.34	89.3	100.0
South	2008	9/10, 9/11	2	S5b	229	0.38	87.3	97.7
South	2009	8/18	1	S20	267	0.32	84.6	94.7
South	2009	9/2	2	none	212	0.42	89.3	100.0
South	2010	8/18	1	none	291	0.31	89.3	100.0
South	2010	8/26, 9/1, 9/2	2	none	198	0.45	89.3	100.0
South	2011	9/1, 9/13	1	S5b, S20	282	0.29	82.6	92.5
South	2012	8/14	1	none	265	0.34	89.3	100.0
South	2012	8/28	2	none	272	0.33	89.3	100.0

Table 4 (continued). Flight summary statistics for aerial surveys of elk in North and South Rainier trend count areas (TCA) in MORA, 2008-2017. Shown for each replicate survey are: TCA name, year, survey dates, replicate number (Rep), omitted survey units, survey duration in minutes, survey intensity in km²/min, the area surveyed in km², and percentage of TCA surveyed (% of TCA).

TCA	Year	Survey Dates	Rep	Survey Units Omitted	Survey Duration (mins)	Survey Intensity (km ² /min)	Area Surveyed (km ²)	% of TCA
South	2013	8/21	1	none	306	0.29	89.3	100.0
South	2014	8/21	1	none	300	0.30	89.3	100.0
South	2014	8/27	2	none	292	0.30	87.0	97.4
South	2015	8/11	1	S13	418	0.20	85.1	95.3
South	2015	9/8	2	none	225	0.40	89.3	100.0
South	2017	9/6	1	S17	247	0.35	85.3	95.4

Table 5. Flight summary statistics for aerial surveys of elk in trend count areas (TCA) of OLYM, 2008-2011. We list only surveys that covered ≥75% of a TCA and identifiable TCA units were surveyed. Partial reconnaissance surveys completed in 2008 are not reported. Shown for each replicate survey are: TCA name, year, survey dates, replicate number (Rep), omitted survey units, survey duration in minutes, survey intensity in km²/min, area surveyed in km², and percentage of TCA surveyed (% of TCA).

TCA	Year	Survey Dates	Rep	Survey Units Omitted	Survey Duration (min)	Survey Intensity (km ² /min)	Area surveyed (km ²)	% of TCA
Core	2008	9/2-9/4	1	none	376	0.25	93.6	92.9*
Core	2011	9/7-9/8	1	none	245	0.41	100.7	100.0
Core	2012	8/21-8/25	1	none	257	0.39	100.7	100.0
Core	2013	8/27-8/28	1	none	256	0.39	100.7	100.0
Core	2014	8/18-8/19	1	none	248	0.41	100.7	100.0
Core	2015	8/17-8/19	1	none	234	0.43	100.7	100.0
Northwest	2011	9/6	1	none	159	0.46	72.7	100.0
Elwha	2012	8/20-8/22	1	none	203	0.40	80.8	100.0
Elwha	2014	8/19	1	none	147	0.55	80.8	100.0

Table 5 (continued). Flight summary statistics for aerial surveys of elk in trend count areas (TCA) of OLYM, 2008-2011. We list only surveys that covered $\geq 75\%$ of a TCA and identifiable TCA units were surveyed. Partial reconnaissance surveys completed in 2008 are not reported. Shown for each replicate survey are: TCA name, year, survey dates, replicate number (Rep), omitted survey units, survey duration in minutes, survey intensity in km^2/min , area surveyed in km^2 , and percentage of TCA surveyed (% of TCA).

TCA	Year	Survey Dates	Rep	Survey Units Omitted	Survey Duration (min)	Survey Intensity (km^2/min)	Area surveyed (km^2)	% of TCA
Southeast	2013	8/30/	1	SE4	159	0.54	85.8	93.7
Quinault	2014	8/17-8/18	1	none	208	0.36	74.4	100.0

Table 6. Coefficient estimates and model support statistics for each of 16 contributing MDSH models used in model averaging. Alternative models are titled with the single term that was removed (-) from the global model and the term substituted (+) for the one removed.

Type of Parameter	Parameter ^B	Model ^A															
		-Y ₀₈ -Y ₁₅	-M*O	-P*O	-ln(N)*M	-F*V	-U*R	-V*L	-M*F +M*V	-U*O	-V*O	Global	-F*L	-M*R	-M*F	-M*O*Y ₁₄ -Y ₁₅	-ln(N)*V
Common ^C Main Effect Parameter Estimates	Intercept	0.012	0.442	0.390	0.366	0.454	0.149	0.312	0.405	0.550	0.474	0.410	0.443	0.374	0.390	0.400	0.424
	O	0.671	0.591	0.926	0.776	0.782	0.791	0.774	0.789	0.155	0.446	0.795	0.782	0.791	0.784	0.787	0.791
	ln(N)	0.449	0.469	0.456	0.494	0.459	0.457	0.463	0.456	0.455	0.464	0.457	0.452	0.457	0.455	0.457	0.448
	U	0.245	0.228	0.235	0.243	0.296	0.531	0.263	0.251	0.083	0.223	0.254	0.263	0.270	0.252	0.259	0.254
	M	-0.581	-0.618	-0.486	-0.104	-0.495	-0.490	-0.514	-0.429	-0.504	-0.470	-0.506	-0.532	-0.399	-0.325	-0.456	-0.502
	F	0.659	0.738	0.711	0.740	0.421	0.696	0.345	0.765	0.694	0.674	0.702	0.338	0.706	0.744	0.701	0.702
	V	-1.625	-1.346	-1.431	-1.523	-2.074	-1.407	-0.537	-1.491	-1.462	-1.666	-1.436	-1.005	-1.436	-1.459	-1.438	-1.486
	L	0.207	0.298	0.302	0.313	0.291	0.302	0.417	0.303	0.300	0.292	0.300	0.262	0.302	0.306	0.296	0.296
	Y ₀₉	–	-0.820	-0.796	-0.816	-0.817	-0.811	-0.833	-0.815	-0.815	-0.799	-0.811	-0.815	-0.810	-0.811	-0.811	-0.813
	Y ₁₀	–	-0.758	-0.743	-0.747	-0.723	-0.750	-0.752	-0.756	-0.749	-0.740	-0.752	-0.740	-0.751	-0.759	-0.752	-0.753
	Y ₁₁	–	-0.455	-0.414	-0.431	-0.404	-0.418	-0.414	-0.423	-0.358	-0.389	-0.418	-0.417	-0.416	-0.420	-0.420	-0.419
	Y ₁₂	–	-0.689	-0.672	-0.669	-0.667	-0.675	-0.698	-0.682	-0.605	-0.657	-0.676	-0.692	-0.675	-0.678	-0.675	-0.676
	Y ₁₃	–	-0.706	-0.690	-0.691	-0.693	-0.694	-0.699	-0.699	-0.640	-0.683	-0.694	-0.689	-0.693	-0.696	-0.691	-0.694
	Y ₁₄	–	-0.181	-0.156	-0.146	-0.168	-0.160	-0.178	-0.162	-0.132	-0.151	-0.161	-0.169	-0.159	-0.160	-0.135	-0.160
	Y ₁₅	–	-0.503	-0.479	-0.475	-0.463	-0.486	-0.519	-0.493	-0.446	-0.486	-0.486	-0.503	-0.485	-0.492	-0.461	-0.486

^A. The 16 models are ranked in order of increasing model support from left to right. Note that *greater* support for the model lacking a given variable corresponds to *less* support for including that variable (reflected in a lower evidence ratio (bottom row). Models include the global model (containing all main effects and interactions) and 12 models each lacking one interaction term, indicated with a minus (-), one model lacking year effects (seven parameters: Y₀₈-Y₁₅), and one model evaluating effect of replacing M*V (removed from global model, -) with M*F (added to global model, +). Coefficients not included in each model are indicated with a dash (–) and have values of 0.0 for that model.

^B. Parameter name explanations are shown in Table 1.

^C. “Common” parameters apply to all observations, including both front and rear seat observer sighting probabilities.

^D. Evidence ratios compare AIC_c model weights for models without the parameter indicated in each column relative to model weight of the global model containing all parameters. Higher evidence ratios indicate stronger support for the parameter indicated in that column. Evidence ratio for the model that substituted M*V for M*F is the ratio of support for including M*F to that for M*V.

Table 6 (continued). Coefficient estimates and model support statistics for each of 16 contributing MDSH models used in model averaging. Alternative models are titled with the single term that was removed (-) from the global model and the term substituted (+) for the one removed.

Type of Parameter	Parameter ^B	Model ^A															
		-Y ₀₈ -Y ₁₅	-M*O	-P*O	-ln(N)*M	-F*V	-U*R	-V*L	-M*F +M*V	-U*O	-V*O	Global	-F*L	-M*R	-M*F	-M*O*Y ₁₄ -Y ₁₅	-ln(N)*V
Common ^C Interaction Parameter Estimates	U*O	-0.477	-0.515	-0.628	-0.646	-0.674	-0.657	-0.623	-0.647	–	-0.498	-0.656	-0.642	-0.650	-0.648	-0.643	-0.649
	M*O	-1.019	–	-1.009	-0.815	-1.105	-1.009	-1.051	-1.052	-0.911	-1.106	-1.016	-1.026	-1.008	-1.055	-1.011	-1.019
	V*O	-0.619	-1.029	-0.799	-0.734	-0.586	-0.794	-0.806	-0.776	-0.538	–	-0.796	-0.784	-0.790	-0.750	-0.797	-0.805
	ln(N)*M	0.305	0.231	0.291	–	0.289	0.301	0.300	0.305	0.298	0.290	0.297	0.309	0.299	0.315	0.290	0.295
	ln(N)*V	-0.073	-0.064	-0.023	0.008	-0.014	-0.036	-0.068	-0.026	-0.009	-0.060	-0.032	-0.038	-0.035	-0.023	-0.027	–
	M*F	0.402	0.435	0.364	0.421	0.311	0.365	0.388	–	0.358	0.342	0.369	0.393	0.368	–	0.373	0.365
	M*V	–	–	–	–	–	–	–	0.328	–	–	–	–	–	–	–	–
	F*V	-0.909	-1.167	-1.026	-0.987	–	-1.023	-1.058	-1.028	-1.044	-0.870	-1.019	-1.029	-1.016	-0.958	-1.027	-1.018
	F*L	-0.438	-0.474	-0.456	-0.499	-0.473	-0.445	-0.001	-0.475	-0.440	-0.446	-0.453	–	-0.458	-0.472	-0.449	-0.453
	V*L	1.234	1.133	1.025	1.023	1.121	1.014	–	1.065	0.990	1.058	1.039	0.524	1.038	1.049	1.041	1.052
	M*O*Y ₁₄₋₁₅	0.429	0.195	0.204	0.125	0.227	0.209	0.204	0.224	0.181	0.209	0.208	0.201	0.203	0.225	–	0.209
Front Seat Effects	P	-0.942	-0.971	-0.878	-0.970	-0.972	-0.985	-0.974	-0.973	-0.973	-0.976	-0.974	-0.976	-0.969	-0.972	-0.974	-0.974
	P*O	0.520	0.541	–	0.536	0.549	0.566	0.544	0.548	0.537	0.545	0.547	0.548	0.533	0.545	0.546	0.546
Rear Seat Effects	R	-0.836	-0.809	-0.847	-0.825	-0.820	-0.295	-0.811	-0.817	-0.817	-0.818	-0.820	-0.817	-0.744	-0.820	-0.820	-0.820
	U*R	0.584	0.548	0.588	0.563	0.559	–	0.547	0.555	0.554	0.555	0.557	0.553	0.515	0.558	0.557	0.558

^A. The 16 models are ranked in order of increasing model support from left to right. Note that *greater* support for the model lacking a given variable corresponds to *less* support for including that variable (reflected in a lower evidence ratio (bottom row). Models include the global model (containing all main effects and interactions) and 12 models each lacking one interaction term, indicated with a minus (-), one model lacking year effects (seven parameters: Y₀₈-Y₁₅), and one model evaluating effect of replacing M*V (removed from global model, -) with M*F (added to global model, +). Coefficients not included in each model are indicated with a dash (–) and have values of 0.0 for that model.

^B. Parameter name explanations are shown in Table 1.

^C. “Common” parameters apply to all observations, including both front and rear seat observer sighting probabilities.

^D. Evidence ratios compare AIC_c model weights for models without the parameter indicated in each column relative to model weight of the global model containing all parameters. Higher evidence ratios indicate stronger support for the parameter indicated in that column. Evidence ratio for the model that substituted M*V for M*F is the ratio of support for including M*F to that for M*V.

Table 6 (continued). Coefficient estimates and model support statistics for each of 16 contributing MDSH models used in model averaging. Alternative models are titled with the single term that was removed (-) from the global model and the term substituted (+) for the one removed.

Type of Parameter	Parameter ^B	Model ^A															
		-Y ₀₈ -Y ₁₅	-M*O	-P*O	-ln(N)*M	-F*V	-U*R	-V*L	-M*F +M*V	-U*O	-V*O	Global	-F*L	-M*R	-M*F	-M*O*Y ₁₄ -Y ₁₅	-ln(N)*V
Rear Seat Effects (continued)	M*R	0.245	0.232	0.220	0.243	0.240	0.195	0.243	0.241	0.237	0.239	0.241	0.244	–	0.244	0.239	0.241
Model Fit and Support Statistics	Dev=-2ln(L)	3515.6	3490.9	3490.1	3489.5	3488.1	3488.0	3487.2	3485.0	3487.0	3486.1	3483.9	3485.9	3485.5	3485.4	3484.2	3483.9
	n	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0	1759.0
	K	24	30	30	30	30	30	30	31	30	30	31	30	30	30	30	30
	AIC _c	3564.3	3552.0	3551.2	3550.5	3549.2	3549.1	3548.2	3548.1	3548.0	3547.2	3547.0	3547.0	3546.6	3546.5	3545.3	3545.0
	ΔAIC _c	19.27	7.00	6.21	5.53	4.20	4.05	3.22	3.13	3.02	2.20	2.02	1.96	1.58	1.49	0.28	0.00
	AIC _c Model relative Rel-Weight ($\hat{w}_k$, %)	0.0%	0.6%	0.9%	1.3%	2.5%	2.7%	4.1%	4.3%	4.5%	6.8%	7.4%	7.7%	9.3%	9.7%	17.8%	20.4%
	Evidence Ratio ^D	5572	12.1	8.11	5.78	2.98	2.76	1.82	1.74	1.65	1.10	1.00	0.97	0.80	0.77	0.42	0.36

^A. The 16 models are ranked in order of increasing model support from left to right. Note that *greater* support for the model lacking a given variable corresponds to *less* support for including that variable (reflected in a lower evidence ratio (bottom row). Models include the global model (containing all main effects and interactions) and 12 models each lacking one interaction term, indicated with a minus (-), one model lacking year effects (seven parameters: Y₀₈-Y₁₅), and one model evaluating effect of replacing M*V (removed from global model, -) with M*F (added to global model, +). Coefficients not included in each model are indicated with a dash (–) and have values of 0.0 for that model.

^B. Parameter name explanations are shown in Table 1.

^C. “Common” parameters apply to all observations, including both front and rear seat observer sighting probabilities.

^D. Evidence ratios compare AIC_c model weights for models without the parameter indicated in each column relative to model weight of the global model containing all parameters. Higher evidence ratios indicate stronger support for the parameter indicated in that column. Evidence ratio for the model that substituted M*V for M*F is the ratio of support for including M*F to that for M*V.

The direction of most model effects matched *a priori* expectations. The heterogeneity effect, U , was positive, indicating that groups detected by helicopter observers were more easily detected than groups detected via radio telemetry. The heterogeneity effect was somewhat reduced in OLYM compared to MORA ($U*O$). The heterogeneity effect was stronger for back-seat observers ($U*R$) than for front-seat observers. Sighting probability was greater in OLYM than MORA (O), for larger elk groups than smaller groups ($\ln[N]$), and under flat lighting conditions compared to bright lighting (L). Elk sightability was reduced when elk were in greater vegetation cover (V) and was less for back-seat observers (R) compared to front-seat observers, and for front-seat observers when groups were on the pilot's side (P), although this latter effect was not as great in OLYM as in MORA ($P*O$). The negative effect of vegetation was substantially less negative when lighting was flat ($V*L$) than under bright lighting. The positive effect of group size was more positive when elk were moving ($\ln[N]*M$) than when they were stationary. For some larger groups, this positive effect outweighed the baseline negative effects of motion, making large moving groups easier to detect than similarly sized stationary groups. The effect of vegetation was not as negative in OLYM as it was in MORA ($V*O$). Sighting probability was highest in the first survey year (intercept, 2008), lowest in the next one (Y_{09} , 2009), and intermediate in other years.

The effect of forest cover on elk detectability was complex. The intercept for forest cover was positive, suggesting higher sighting probability in forest vegetation than other vegetation types. However, when combined with percent vegetation cover (V) and the interaction between these ($V*F$), which were both negative, net effect of moderate to heavy forest cover on elk detectability was negative. Sighting probability was even more negative when high-contrast lighting was combined with forest cover ($F*L$). On the other hand, motion in forest cover resulted in a somewhat less negative effect overall ($M*F$); in other words, movement in forest cover aided detection.

The effects of elk motion were unexpected and appeared to reflect a complex interaction of motion with park, seat location, and group size. The main effect of motion (M) was to make moving groups less likely to be seen, perhaps indicating that evasive movements prior to detection may have reduced aerial sighting probabilities. The negative effect of motion on aerial detection probability was several times greater in OLYM than in MORA ($M*O$). We speculated that more recent and frequent helicopter capture operations conducted in OLYM than in MORA may have caused elk to move more evasively in response to helicopters in OLYM than MORA. We tested this hypothesis by including the $M*O*Y_{14-Y_{15}}$ 3-way interaction. The positive estimated value of this parameter indicates that there has been some reversal of greater negative effect of motion on detection probability in OLYM relative to that seen in MORA. The effect of movement was not as strongly negative for rear-seat observers as for front-seat observers ($M*R$).

Elk Population Trends in Trend Count Areas of Mount Rainier National Park

We estimated elk abundance and population composition using M_{DSH} models presented above. Because model parameters have been updated from the previous summary report (Jenkins et al. 2015) to reflect annual variations in sightability and a larger sample of DO and DO-S trials, there are minor variations in numbers of elk and composition of elk groups reported here from those reported in the previous summary (Jenkins et al. 2015).

Abundance

Survey crews counted a mean of 301 elk per survey (range: 106-468) in North Rainier TCA, and 389 elk per survey (range: 190-706) in South Rainier TCA (Table 7). After imputing values for non-surveyed units and applying the M_{DSH} models to account for detection biases, we estimated a mean of 359 elk present in North Rainier TCA and 477 elk in South Rainier TCA during surveys conducted from 2008-2017 (Table 7). These means equate to 3.5 elk/km² present in North Rainier TCA (103.1 km²) and 5.3 elk/km² in South Rainier TCA (89.3 km²) during surveys. On average, survey crews detected approximately 81-83% of elk estimated present in North and South Rainier TCAs.

Table 7. Raw counts and estimated abundance ($\hat{N}_{a,t}^*$) of elk in surveyed units in MORA, 2008-2011, including directly estimated abundance ($\hat{N}_{a,t}$) and associated standard error (SE), and imputed abundance ($\hat{N}_{a,t}'$) and associated SE for surveys with >1 non-surveyed units in North Rainier TCA and South Rainier TCA. Percent seen was estimated as raw count divided by $\hat{N}_{a,t}^*$. Bootstrapped estimates of SE and CV were not computed in 2017.

TCA	Year	Repli- cate	Raw count	$\hat{N}_{a,t}$	SE	CV	$\hat{N}_{a,t}^*$	SE	CV	Percent Seen
North	2008	1	216	228	12.0	0.05	290	16.1	0.06	94.6%
North	2008	2	246	272	23.6	0.09	290	23.8	0.08	90.3%
North	2009	1	365	449	29.5	0.07	449	29.5	0.07	81.2%
North	2010	1	290	315	12.1	0.04	315	12.1	0.04	92.1%
North	2010	2	375	431	29.5	0.07	431	29.5	0.07	87.0%
North	2011	1	373	418	54.9	0.13	426	55.0	0.13	89.3%
North	2011	2	267	302	29.5	0.10	316	30.4	0.10	88.4%
North	2012	1	229	287	30.8	0.11	296	30.9	0.10	79.8%
North	2013	1	247	333	52.2	0.16	333	52.2	0.16	74.1%
North	2013	2	106	193	34.4	0.18	193	34.4	0.18	54.9%
North	2014	1	468	561	60.0	0.11	565	60.0	0.11	83.4%
North	2015	1	297	349	41.5	0.12	349	41.5	0.12	85.0%
North	2017	1	431	533	–	–	533	–	–	–
Means	–	–	301	359	34.2	0.10	368	34.6	0.10	83.3%
South	2008	1	337	385	29.7	0.08	385	29.7	0.08	87.5%
South	2008	2	279	319	28.6	0.09	320	28.6	0.09	87.3%
South	2009	1	393	511	64.2	0.13	556	65.1	0.12	77.0%
South	2009	2	225	300	33.8	0.11	300	33.8	0.11	75.0%
South	2010	1	602	718	46.5	0.06	718	46.5	0.06	83.8%
South	2010	2	327	410	33.3	0.08	410	33.3	0.08	79.7%
South	2011	1	529	642	72.2	0.11	688	73.0	0.11	82.4%

Table 7 (continued). Raw counts and estimated abundance ($\hat{N}_{a,t}^*$) of elk in surveyed units in MORA, 2008-2011, including directly estimated abundance ($\hat{N}_{a,t}$) and associated standard error (SE), and imputed abundance ($\hat{N}_{a,t}'$) and associated SE for surveys with >1 non-surveyed units in North Rainier TCA and South Rainier TCA. Percent seen was estimated as raw count divided by $\hat{N}_{a,t}^*$. Bootstrapped estimates of SE and CV were not computed in 2017.

TCA	Year	Repli- cate	Raw count	$\hat{N}_{a,t}$	SE	CV	$\hat{N}_{a,t}^*$	SE	CV	Percent Seen
South	2012	1	706	866	106.4	0.12	866	106.4	0.12	81.6%
South	2012	2	494	631	63.5	0.10	631	63.5	0.10	78.3%
South	2013	1	501	625	77.3	0.12	625	77.3	0.12	80.1%
South	2014	1	339	419	41.4	0.10	419	41.4	0.10	80.9%
South	2014	2	388	455	42.4	0.09	455	42.4	0.09	85.4%
South	2015	1	280	333	33.5	0.10	345	33.7	0.10	84.1%
South	2015	2	190	250	27.5	0.11	250	27.5	0.11	76.1%
South	2017	1	246	285	—	—	302	—	—	—
Means	—	—	389	477	50.0	0.10	485	50.2	0.10	81.4%

Weak evidence suggests estimated numbers of elk in North Rainier TCA may have increased from 2008-2017 (Table 8, Figure 5). Model selection and multi-model inferences, however, indicated that the null model (the model of no change in elk estimates) garnered the greatest percentage of model weight ($\hat{w}_k = 25.7\%$, Table 8). The most strongly supported model containing a weather or seasonal effect (i.e., any effect other than time) was the model containing a positive association of MaxT with abundance, which had nearly the same model weight as the null model. The coefficient for the linear model of $\ln(N)$ versus time, which corresponds with observed exponential rate of increase (r_o), averaged 0.039 (95% CI=-0.02, 0.10; Table 8), indicating abundance estimates increased by about 4% annually from 2008-17, although with considerable statistical uncertainty. In fact, linear time effect alone garnered approximately $\hat{w}_k=12\%$. The evidence ratio against a linear time effect alone was ER=2.1 compared to the null model. However, after accounting for MaxT effect, the ratio of evidence against an additional time effect was much stronger (ER=5.1). The model-weighted estimate of a linear time effect after controlling for other covariates was 0.9% annual increase (slope of exponential model represented by the black dashed line in Figure 5). Hence, there was moderate evidence for weather effects and weaker evidence for a linear time effect after controlling for weather-related changes.

Table 8. Model selection results for covariates that potentially affect elk abundance estimates in North and South Rainier TCAs during aerial surveys in MORA, 2008-2017. The number of model parameters (k), Akaike's Information Criterion (AIC_c), change in AIC_c relative to the top model (ΔAIC_c), model weights ($\hat{w}_k$), and evidence ratios (ER) are presented as defined in Burnham and Anderson (1998).

TCA	Model	k	AIC_c	ΔAIC_c	$(\hat{w}_k)$	ER ^B	Estimated Model Coefficients ^A							
							Intercept	Time	Time ²	Julian	MaxT	SHI	SMD	LI
North Rainier	Null	2	-29.07	0.00	0.26	1.00	5.91	–	–	–	–	–	–	–
	MaxT	3	-28.67	0.41	0.21	0.82	5.54	–	–	–	0.020	–	–	–
	Time	3	-27.62	1.46	0.12	0.48	5.78	0.039	–	–	–	–	–	–
	Julian	3	-27.58	1.49	0.12	0.47	8.82	–	–	-0.012	–	–	–	–
	SHI	3	-26.28	2.80	0.06	0.25	5.95	–	–	–	–	0.000	–	–
	LI	3	-25.75	3.33	0.05	0.19	5.86	–	–	–	–	–	–	0.001
	SMD	3	-25.67	3.40	0.05	0.18	5.90	–	–	–	–	–	0.000	–
	Time+MaxT	4	-25.40	3.68	0.04	0.16	5.52	0.027	–	–	0.016	–	–	–
	Time+Julian	4	-24.06	5.02	0.02	0.08	7.78	0.026	–	-0.008	–	–	–	–
	Time+Time ²	4	-23.50	5.57	0.02	0.06	5.72	0.076	-0.004	–	–	–	–	–
	Time+LI	4	-23.41	5.66	0.02	0.06	5.74	0.038	–	–	–	–	–	0.001
	Time+SMD	4	-23.38	5.69	0.01	0.06	5.77	0.039	–	–	–	–	0.000	–
	Time+SHI	4	-23.28	5.79	0.01	0.06	5.78	0.039	–	–	–	0.000	–	–
	Time+Time ² +MaxT	5	-20.21	8.87	0.00	0.01	5.53	-0.038	0.006	–	0.021	–	–	–
	Time+Time ² +Julian	5	-18.60	10.47	0.00	0.01	7.61	0.054	-0.003	-0.008	–	–	–	–
	Time+Time ² +SMD	5	-17.96	11.12	0.00	0.00	5.72	0.072	-0.003	–	–	–	0.000	–
	Time+Time ² +LI	5	-17.94	11.13	0.00	0.00	5.71	0.070	-0.003	–	–	–	–	0.000
	Time+Time ² +SHI	5	-17.93	11.15	0.00	0.00	5.72	0.076	-0.004	–	–	0.000	–	–

^A. Julian = Julian date of survey; MaxT = maximum temperature on survey day(s). For surveys spanning multiple days, daily maxima were averaged; SHI = summer heat index on first survey day; SMD = soil moisture deficit on first survey day; LI = lunar illumination averaged among survey days.

^B. ER = evidence ratio of AIC_c weight for each alternative model to AIC_c weight for the null model ($\hat{w}_k / \hat{w}_{Null}$). Ratios >1 indicate support for an alternative model and effects contained in it, compared to no effects (constant), whereas ER<1 indicate greater support for no effect.

Table 8 (continued). Model selection results for covariates that potentially affect elk abundance estimates in North and South Rainier TCAs during aerial surveys in MORA, 2008-2017. The number of model parameters (k), Akaike's Information Criterion (AIC_c), change in AIC_c relative to the top model (ΔAIC_c), model weights ($\hat{w}_k$), and evidence ratios (ER) are presented as defined in Burnham and Anderson (1998).

TCA	Model	k	AIC_c	ΔAIC_c	$(\hat{w}_k)$	ER ^B	Estimated Model Coefficients ^A							
							Intercept	Time	Time ²	Julian	MaxT	SHI	SMD	LI
South Rainier	Time+Time ² +SHI	5	-38.61	0.00	0.24	9.69	5.29	0.360	-0.030	–	–	-0.002	–	–
	Time+Time ² +MT	5	-38.08	0.53	0.18	7.44	5.00	0.317	-0.036	–	0.036	–	–	–
	Time+Time ² +SMD	5	-36.65	1.96	0.09	3.64	5.68	0.246	-0.026	–	–	–	-0.002	–
	Julian	3	-36.53	2.08	0.08	3.42	10.90	–	–	-0.020	–	–	–	–
	Time+Time ²	4	-35.82	2.80	0.06	2.40	5.61	0.297	-0.032	–	–	–	–	–
	Time+Time ² +Julian	5	-34.34	4.27	0.03	1.15	9.04	0.204	-0.023	-0.014	–	–	–	–
	Time+Julian	4	-34.33	4.28	0.03	1.14	11.33	-0.030	–	-0.022	–	–	–	–
	Time+SMD	4	-34.22	4.39	0.03	1.08	6.07	-0.003	–	–	–	–	-0.002	–
	SHI	3	-34.13	4.48	0.03	1.03	6.02	–	–	–	–	-0.001	–	–
	Null	2	-34.07	4.54	0.02	1.00	6.02	–	–	–	–	–	–	–
	Time+SHI	4	-32.42	6.19	0.01	0.44	5.73	0.067	–	–	–	-0.002	–	–
	MaxT	3	-31.85	6.76	0.01	0.33	5.70	–	–	–	0.018	–	–	–
	Time	3	-31.44	7.17	0.01	0.27	6.11	-0.021	–	–	–	–	–	–
	Time+Time ² +LI	5	-31.23	7.38	0.01	0.24	5.53	0.317	-0.034	–	–	–	–	0.001
	LI	3	-31.22	7.39	0.01	0.24	6.10	–	–	–	–	–	–	-0.002
	Time+MaxT	4	-29.51	9.10	0.00	0.10	5.71	-0.036	–	–	0.026	–	–	–
	Time+LI	4	-28.86	9.75	0.00	0.07	6.35	-0.038	–	–	–	–	–	-0.003

^A. Julian = Julian date of survey; MaxT = maximum temperature on survey day(s). For surveys spanning multiple days, daily maxima were averaged; SHI = summer heat index on first survey day; SMD = soil moisture deficit on first survey day; LI = lunar illumination averaged among survey days.

^B. ER = evidence ratio of AIC_c weight for each alternative model to AIC_c weight for the null model ($\hat{w}_k / \hat{w}_{Null}$). Ratios >1 indicate support for an alternative model and effects contained in it, compared to no effects (constant), whereas ER<1 indicate greater support for no effect.

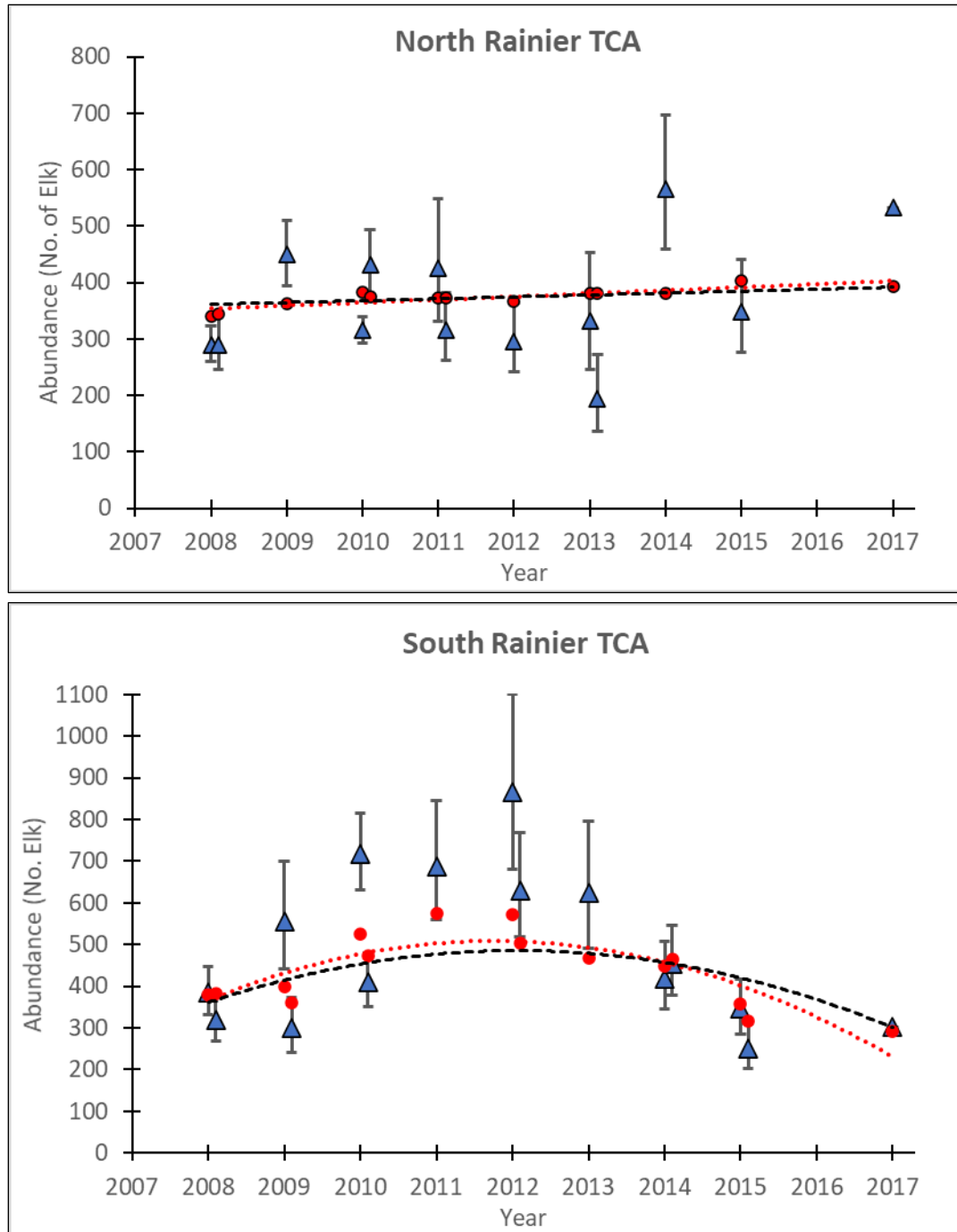


Figure 5. Trends in estimated elk abundance in North and South Rainier TCAs, 2008-2017. Blue triangles and error bars represent estimated elk abundances $\pm 95\%$ log-normal confidence intervals ($\hat{N}_{a,t}^*$). Red dots represent model-weighted predicted abundances including effects of season and weather variables. The dashed red line represents a quadratic model fitted to predicted abundances for North Rainier TCA and a quadratic fit for South Rainier TCA. The black dashed line represents predicted effect of time with all season and weather variables held constant.

Estimated numbers of elk in South Rainier TCA increased and subsequently decreased from 2008-2017 (Figure 5). Elk abundance in South TCA decreased at a per-capita exponential rate (r_o) of -0.02 (95% CI=-0.05, 0.01), as derived from the linear model of $\ln(N)$ versus time; however, this model received minimal support ($\hat{w}_k = <1\%$, Table 8). The most highly supported model of trend in elk numbers estimated within South Rainier TCA included both linear and quadratic effects and a negative effect of SHI on abundance. The second- and fourth-best models also included both linear and quadratic time effects and a weather covariate, either MaxT (ER=1.3) or SMD (ER=2.7). Evidence for including SHI was 4.0 times higher than excluding it. After controlling for SHI, support for the two terms for time effects was 9.4 times higher than excluding them. Evidence for quadratic time effect was 22.1 times greater than evidence for excluding it. In summary, variation in elk abundance due to both weather and time was strongly supported, but there was no detectable net decline over the study period.

Distribution

There was considerable variation in estimated densities of elk among survey units in both North and South Rainier TCAs (Figures 6, 7). Densities of elk within individual survey units ranged from <1 to nearly 20 elk/km² in North Rainier TCA, with highest densities recorded in parts of Units 11, 12, and 17 (Table 9). Similarly, densities of elk in South Rainier TCA ranged from <1 to approximately 10 elk/km², with lowest densities in the southeastern 1/3 of the TCA and greatest densities in units 11 and 20 (Table 9).

The distribution of elk within each TCA remained relatively constant through the survey period. Trends in relative elk density among count units, which would indicate changes in elk distribution and use over the 10-yr period, were significant ($P<0.10$) in only a few survey units within each TCA. Most count units in which relative densities increased throughout the period were units of low elk abundance (Table 9) where changes in just a few elk among count units were significant while having a small impact on overall distribution elk throughout TCAs.

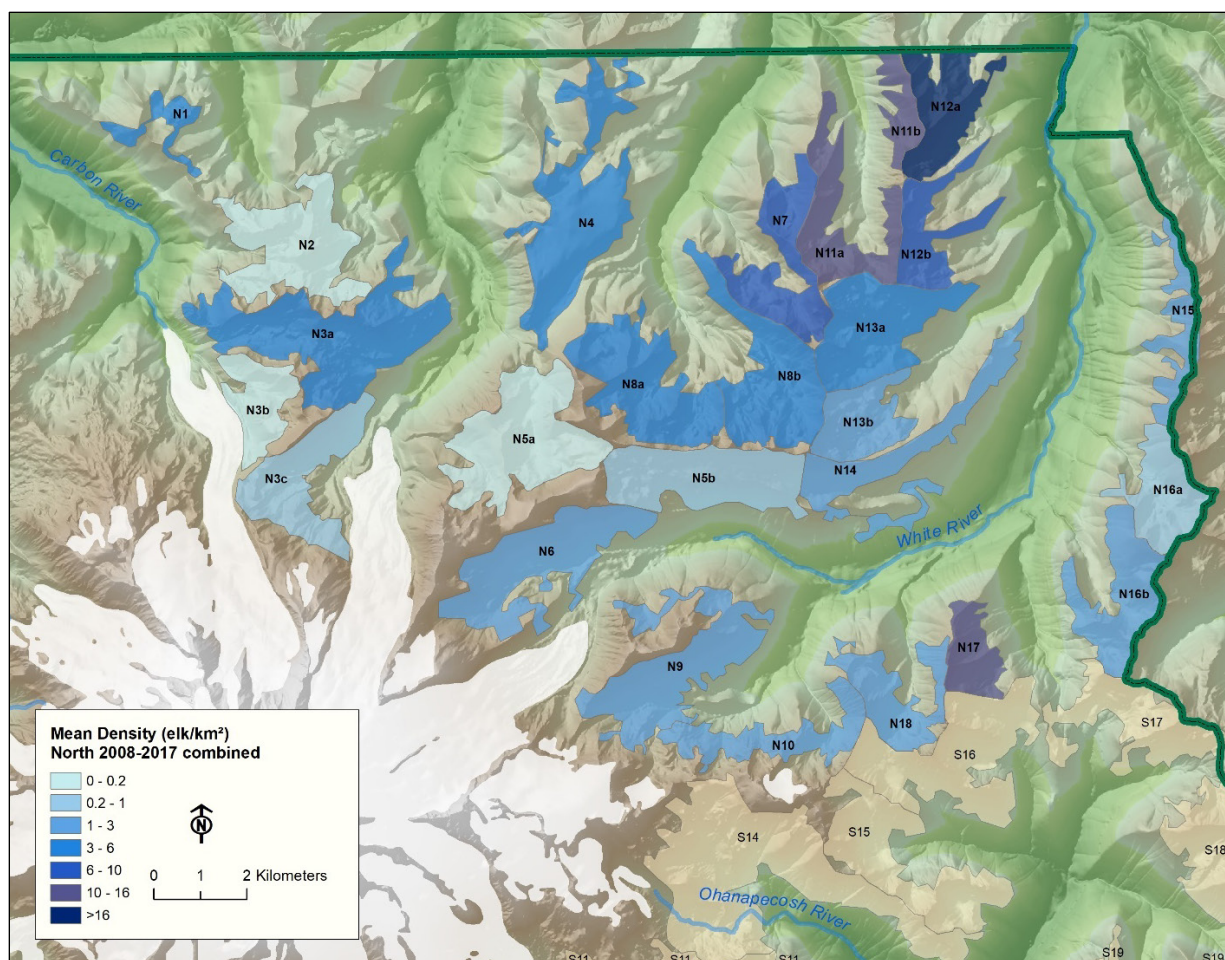


Figure 6. Mean estimated elk density (elk/km²) in survey units of North Rainier TCA, 2008-2017. Survey units of South Rainier TCA are coded in tan color; local variations in elk densities among survey units of South TCA are presented in Figure 7.

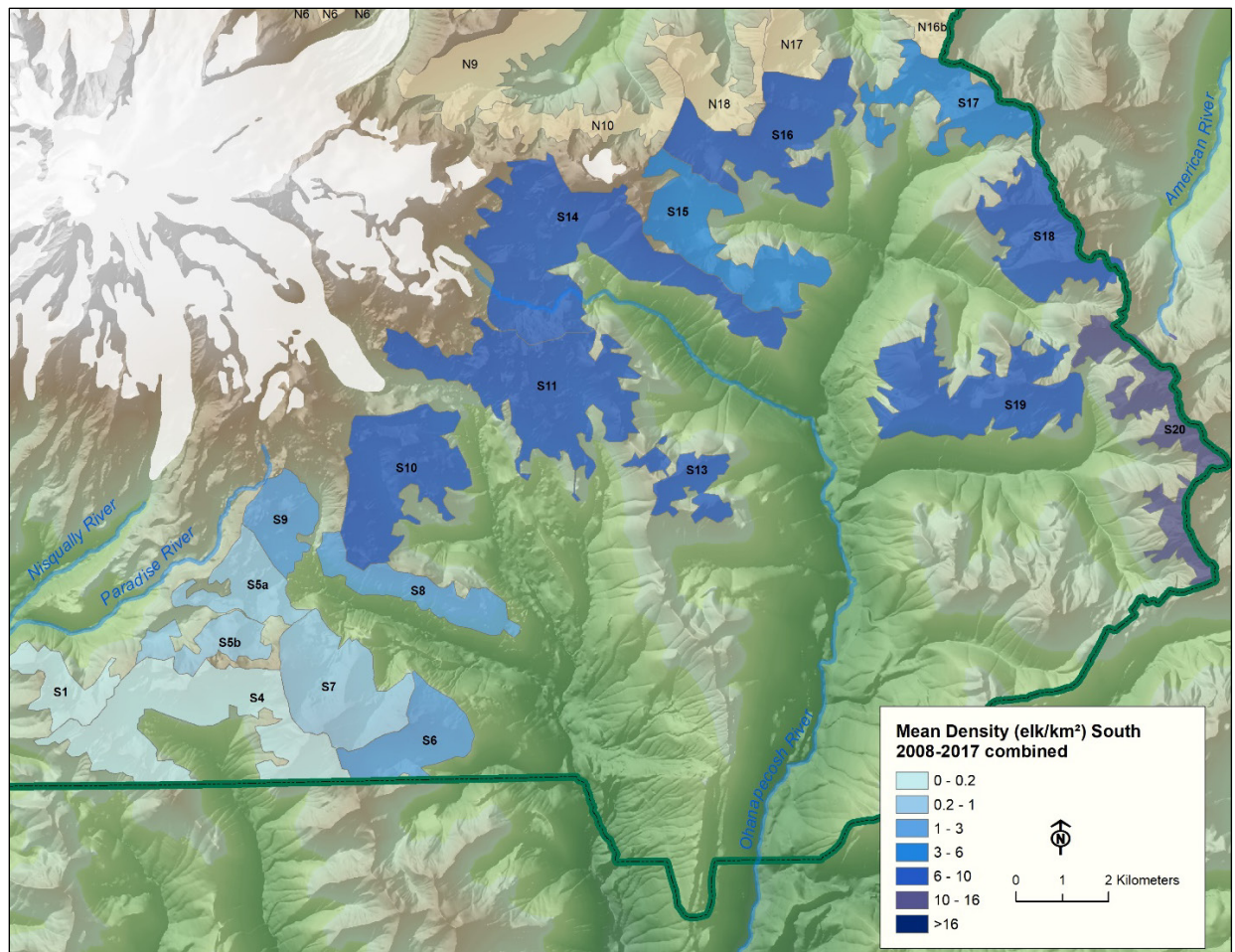


Figure 7. Mean estimated elk density (elk/km²) in survey units of South Rainier TCA, 2008-2017. Survey units of North Rainier TCA are coded in tan color; local variations in elk densities among survey units of North TCA are presented in Figure 6.

Table 9. Mean abundance, relative density, and trends in relative density of elk in survey units of North and South Rainer TCAs, 2008-2017. Units with relative density <1 have less than mean density of elk and units with relative density >1 have greater than mean density. The slope in relative density (and SE) describes the linear relationship between relative densities over time (2008-17).

TCA	Survey Unit	Area (km ²)	No. Surveys	Mean abundance ($\bar{N}$)	$\widehat{\text{Var}}(\hat{N}_{a,t})$	Mean Density (elk/km ²)	Mean Relative Density ^A	Slope, Relative Density	SE (Slope)	P (Slope)
North	N1	1.04	12	4.29	5.17	4.12	1.20	0.19	0.23	0.43
North	N2	5.08	13	0.18	0.03	0.04	0.01	0.00	0.00	0.39
North	N3a	7.83	13	30.79	67.22	3.93	1.11	-0.05	0.11	0.67
North	N3b	2.30	12	0.35	0.12	0.15	0.05	0.01	0.02	0.69
North	N3c	4.02	13	1.51	0.29	0.38	0.11	0.01	0.02	0.50
North	N4	6.68	13	23.97	82.53	3.59	0.89	0.11	0.11	0.34
North	N5a	6.21	12	0.78	0.18	0.12	0.03	0.00	0.01	0.97
North	N5b	5.10	12	1.41	0.65	0.28	0.10	0.03	0.03	0.40
North	N6	5.67	12	6.12	2.28	1.08	0.27	0.04	0.02	0.10^B
North	N7	3.95	13	30.44	42.36	7.71	2.15	0.01	0.19	0.97
North	N8a	5.44	13	16.46	24.70	3.03	0.77	0.03	0.09	0.72
North	N8b	5.11	13	29.82	106.36	5.84	1.70	-0.16	0.24	0.52
North	N9	5.71	11	8.89	5.25	1.56	0.40	-0.02	0.04	0.70
North	N10	2.90	12	5.79	3.60	2.00	0.55	-0.12	0.07	0.14
North	N11a	3.60	13	33.73	108.13	10.97	2.82	0.36	0.40	0.39
North	N11b	1.34	12	14.35	55.74	10.71	3.43	0.11	0.71	0.88
North	N12a	3.30	13	65.22	192.32	19.76	5.33	-0.49	0.39	0.23
North	N12b	2.54	13	19.19	77.76	9.58	2.25	0.61	0.38	0.14
North	N13a	4.90	13	21.90	21.08	4.98	1.45	-0.18	0.12	0.17
North	N13b	2.68	13	5.55	3.31	2.62	0.76	-0.05	0.13	0.71

^A. Mean relative density was computed as elk density in the survey unit divided by mean elk density in the TCA.

^B. Signifies trends were significant ($P \leq 0.10$) (also bolded).

Table 9 (continued). Mean abundance, relative density, and trends in relative density of elk in survey units of North and South Rainer TCAs, 2008-2017. Units with relative density <1 have less than mean density of elk and units with relative density >1 have greater than mean density. The slope in relative density (and SE) describes the linear relationship between relative densities over time (2008-17).

TCA	Survey Unit	Area (km ²)	No. Surveys	Mean abundance ($\bar{N}$)	$\widehat{\text{Var}}(\hat{N}_{a,t})$	Mean Density (elk/km ²)	Mean Relative Density ^A	Slope, Relative Density	SE (Slope)	P (Slope)
North	N14	3.84	12	9.06	7.25	2.36	0.66	-0.13	0.06	0.07^B
North	N15	2.19	12	2.60	2.19	1.19	0.27	0.13	0.04	0.01^B
North	N16a	3.12	12	1.34	1.14	0.43	0.21	0.04	0.07	0.56
North	N16b	3.89	11	8.12	8.65	2.09	0.66	0.11	0.11	0.34
North	N17	1.86	12	21.73	19.16	11.68	3.08	0.00	0.24	0.99
North	N18	2.83	12	4.07	1.19	1.44	0.42	0.08	0.04	0.09^B
South	S1	2.10	14	0.22	0.05	0.11	0.02	0.01	0.01	0.43
South	S4	8.50	15	1.89	0.58	0.22	0.05	0.02	0.01	0.03^B
South	S5a	2.60	15	0.74	0.26	0.28	0.05	-0.01	0.01	0.32
South	S5b	2.02	13	0.62	0.17	0.30	0.06	-0.01	0.01	0.48
South	S6	3.35	15	5.66	2.36	1.69	0.33	-0.05	0.04	0.24
South	S7	5.36	15	2.16	0.46	0.40	0.10	0.00	0.01	0.95
South	S8	3.00	15	5.70	2.80	1.90	0.41	-0.06	0.04	0.15
South	S9	2.29	15	3.03	1.49	1.32	0.31	0.13	0.04	0.01^B
South	S10	6.11	15	60.73	37.00	9.94	1.92	0.02	0.08	0.84
South	S11	8.65	15	86.49	90.97	10.00	1.88	-0.05	0.05	0.34
South	S13	1.87	14	12.44	16.41	6.65	1.16	-0.11	0.12	0.39
South	S14	11.33	15	87.45	130.74	7.72	1.42	-0.06	0.05	0.19
South	S15	5.29	15	21.25	18.86	4.02	0.75	0.10	0.05	0.05^B
South	S16	6.36	15	51.53	119.73	8.10	1.46	0.10	0.07	0.14

^A. Mean relative density was computed as elk density in the survey unit divided by mean elk density in the TCA.

^B. Signifies trends were significant ($P \leq 0.10$) (also bolded).

Table 9 (continued). Mean abundance, relative density, and trends in relative density of elk in survey units of North and South Rainer TCAs, 2008-2017. Units with relative density <1 have less than mean density of elk and units with relative density >1 have greater than mean density. The slope in relative density (and SE) describes the linear relationship between relative densities over time (2008-17).

TCA	Survey Unit	Area (km ²)	No. Surveys	Mean abundance ($\bar{N}$)	$\widehat{\text{Var}}(\hat{N}_{a,t})$	Mean Density (elk/km ²)	Mean Relative Density ^A	Slope, Relative Density	SE (Slope)	P (Slope)
South	S17	4.08	14	16.93	17.20	4.15	0.73	0.13	0.06	0.05^B
South	S18	4.76	15	30.79	50.65	6.47	1.08	0.00	0.07	0.97
South	S19	6.98	15	49.77	53.00	7.13	1.34	-0.03	0.07	0.67
South	S20	4.70	13	45.29	120.47	10.53	1.86	-0.04	0.11	0.73

^A. Mean relative density was computed as elk density in the survey unit divided by mean elk density in the TCA.

^B. Signifies trends were significant ($P \leq 0.10$) (also bolded).

Population Composition

Survey crews classified 3,785 and 5,744 elk on North and South Rainier TCAs, respectively, from 2008 to 2017 (Table 10). The weighted mean ratio of calves:100 AF was 42:100 (SE=2.3) in North TCA and 36:100 (SE=2.0) in South TCA over the study period. The weighted mean ratio of males:100 AF was 41:100 in both North and South TCAs. Additional details on ratios of specific age-classes of males are provided in Table 10.

There was variable support for models relating time, Julian date, and weather variables with population composition measured in both North and South Rainier TCAs (Table 11). In North TCA, there was low to moderate support for any time effects on estimated composition ratios, with greatest support for the temporal model seen in ratios of subadult males:100 AF. However, the linear time trend model received only 77% as much support as the null (constant) model ($ER = \hat{w}_{Time} / \hat{w}_{Null} = 0.77$; Table 11, Figure 8). There was strong support for an effect of MaxT on the ratio of calves:100 AF (ER=5.5) and of Julian date on the ratio of mature males:100 AF; Table 11).

In South Rainier TCA, there was strong support for linear temporal trends in ratio of mature males:100 AF (ER=65.0) and weak support for all male age-classes combined:100 AF (ER=1.02). There was also strong evidence for a quadratic effect on all males:100 AF (ER=5.3). The ratio of mature males and of all male age classes combined increased during the time series, although ratios of all males combined leveled off by 2017 (Figure 9). As in North TCA, there was moderate support (ER 1.7) for an effect of MaxT on the ratio of calves:100 AF. Because calves and adult females are closely associated throughout late-summer survey season, however, there is no compelling explanation for this apparent relationship between calf ratios and ambient temperature.

Table 10. Ratios of sex and age classes of elk (n :100 Adult Females [AF]) in Trend Count Areas (TCAs) in MORA, 2008–17. Weighted means ($\bar{x}_w$) and weighted standard errors using sample size as weights are presented for each TCA. Bootstrapped estimates of SE and CV were not computed in 2017.

TCA	Year	Replicate	N Elk Classified	Calves: 100 AF		Males: 100 AF		Yearling males: 100 AF		Subadult males: 100 AF		Mature males: 100 AF	
				Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
North	2008	1	199	48	1.7	34	3.6	12	1.1	6	1.3	16	2.8
North	2008	2	249	44	2.2	40	2.6	18	1.4	7	0.7	14	1.7
North	2009	1	363	37	1.5	31	4.6	1	0.2	9	1.7	21	3.6
North	2010	1	267	33	0.8	50	5.4	4	0.6	8	1.6	38	4.5
North	2010	2	312	49	2.1	47	4.2	9	0.8	10	2.4	28	3.6
North	2011	1	328	36	1.4	55	5.2	12	2.2	20	2.8	23	3.6
North	2011	2	261	25	1.6	25	4.5	6	1.4	6	1.7	13	3.1
North	2012	1	256	50	3.2	49	7.0	12	1.2	16	3.5	21	4.0
North	2013	1	190	47	4.6	43	8.8	6	1.9	5	1.6	31	7.4
North	2013	2	101	33	5.4	39	8.1	0	0.0	21	6.1	18	3.8
North	2014	1	503	50	1.8	36	5.0	7	0.9	10	2.0	20	3.2
North	2015	1	237	44	2.0	41	4.2	14	1.8	9	1.9	18	3.2
North	2017	1	430	42	–	33	–	3	–	13	–	17	–
North	($\bar{x}_w$)	–	–	42	2.3	41	5.3	8	1.3	10	2.3	22	3.8
South	2008	1	312	37	1.5	31	2.6	10	1.3	9	1.4	12	1.3
South	2008	2	264	31	1.9	35	4.1	6	0.9	12	2.2	18	2.4
South	2009	1	419	35	1.9	34	6.9	5	0.6	11	3.0	19	4.3
South	2009	2	243	35	3.6	32	5.7	1	0.1	5	1.9	27	5.3
South	2010	1	541	32	1.6	33	3.0	4	0.4	10	1.1	18	2.7
South	2010	2	356	39	2.4	53	7.0	1	0.3	8	1.5	44	6.3
South	2011	1	549	35	1.7	50	3.7	7	0.7	25	2.3	18	2.2
South	2012	1	649	36	1.5	43	5.1	5	0.8	11	1.5	27	3.9
South	2012	2	434	40	2.9	49	4.4	11	1.4	21	2.4	17	2.6

Table 10 (continued). Ratios of sex and age classes of elk (n :100 Adult Females [AF]) in Trend Count Areas (TCAs) in MORA, 2008–17. Weighted means ($\bar{x}_w$) and weighted standard errors using sample size as weights are presented for each TCA. Bootstrapped estimates of SE and CV were not computed in 2017.

TCA	Year	Replicate	N Elk Classified	Calves: 100 AF		Males: 100 AF		Yearling males: 100 AF		Subadult males: 100 AF		Mature males: 100 AF	
				Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
South	2013	1	495	30	1.6	38	5.2	3	0.5	4	1.0	31	4.9
South	2014	1	388	38	2.1	48	4.5	9	1.2	9	1.5	30	3.4
South	2014	2	395	33	1.5	41	3.9	9	1.0	11	1.6	21	2.3
South	2015	1	236	38	1.6	35	5.1	3	0.7	5	1.4	27	4.1
South	2015	2	207	45	3.0	46	6.3	3	1.3	18	3.7	25	4.1
South	2017	1	256	29	–	36	–	3	–	1	–	32	–
South	($\bar{x}_w$)	–	–	36	2.0	41	4.9	6	0.9	12	2.0	24	3.7

Table 11. Candidate linear regression models of factors affecting composition ratios of elk in North Rainier TCA and South Rainier TCA, based on all available estimates from 2008-2017, and associated ΔAIC_c values, model weights ($\hat{w}_k$), and evidence ratios (ER).

TCA	Model ^A	Calves:100 AF			All males:100 AF			Yearling males:100 AF			Subadult males:100 AF			Mature males:100 AF		
		ΔAIC_c	$\hat{w}_k$	ER ^B	ΔAIC_c	$\hat{w}_k$	ER ^B	ΔAIC_c	$\hat{w}_k$	ER ^B	ΔAIC_c	$\hat{w}_k$	ER ^B	ΔAIC_c	$\hat{w}_k$	ER ^B
North	Null	3.32	0.10	1.00	0.00^C	0.48^C	1.00^C	0.00^C	0.44^C	1.00^C	0.00^C	0.31^C	1.00^C	1.58^C	0.21^C	1.00^C
	Time	6.19	0.02	0.24	3.46	0.08	0.18	2.37	0.13	0.31	0.53	0.24	0.77	4.46	0.05	0.24
	Time+Time ²	8.04	0.01	0.09	6.66	0.02	0.04	6.34	0.02	0.04	4.86	0.03	0.09	5.95	0.02	0.11
	Julian	6.58	0.02	0.20	1.82	0.19	0.40	2.36	0.14	0.31	1.26	0.17	0.53	0.00	0.47	2.20
	Julian +Time	10.40	0.00	0.03	5.70	0.03	0.06	6.17	0.02	0.05	4.37	0.04	0.11	4.18	0.06	0.27
	MaxT	0.00^C	0.55^C	5.25^C	3.20	0.10	0.20	2.50	0.13	0.29	3.00	0.07	0.22	2.84	0.11	0.53
	MaxT+Time	1.83	0.22	2.10	7.46	0.01	0.02	6.15	0.02	0.05	4.83	0.03	0.09	7.17	0.01	0.06
	SHI	4.49	0.06	0.56	3.42	0.09	0.18	3.12	0.09	0.21	3.08	0.07	0.21	4.67	0.05	0.21
	SHI+Time	8.82	0.01	0.06	7.67	0.01	0.02	6.69	0.02	0.04	3.68	0.05	0.16	8.78	0.01	0.03
South	Null	1.02	0.25	1.00	3.33	0.08	1.00	0.00^C	0.39^C	1.00^C	0.67	0.25	1.00	8.35	0.01	1.00
	Time	4.20	0.05	0.20	3.29	0.08	1.02	3.07	0.08	0.22	2.29	0.11	0.44	0.00^C	0.54^C	65.0^C
	Time+Time ²	7.66	0.01	0.04	0.00^C	0.43^C	5.29^C	6.53	0.01	0.04	4.59	0.04	0.14	3.80	0.08	9.73
	Julian	3.65	0.07	0.27	6.29	0.02	0.23	3.18	0.08	0.20	3.23	0.07	0.28	11.36	0.00	0.22
	Julian +Time	7.44	0.01	0.04	6.57	0.02	0.20	6.89	0.01	0.03	5.77	0.02	0.08	3.80	0.08	9.75
	MaxT	0.00^C	0.42^C	1.67^C	5.51	0.03	0.34	1.67	0.17	0.43	3.00	0.08	0.31	6.93	0.02	2.03
	MaxT+Time	2.93	0.10	0.38	2.17	0.15	1.78	5.48	0.03	0.06	5.77	0.02	0.08	3.13	0.11	13.6
	SHI	3.72	0.07	0.26	6.48	0.02	0.21	1.53	0.18	0.46	0.00^C	0.35^C	1.40^C	3.84	0.08	9.54
	SHI+Time	6.53	0.02	0.06	1.82	0.17	2.13	4.36	0.04	0.11	3.59	0.06	0.23	3.63	0.09	10.6

^A. Julian = Julian date of the survey; MaxT = maximum temperature on survey day(s). For surveys spanning multiple days, daily maxima were averaged; SHI = summer heat index on first survey day.

^B. ER = evidence ratio of AIC_c weight for each alternative model to AIC_c weight for the null model ($\hat{w}_k / \hat{w}_{Null}$). ER >1 indicates support for an alternative model and effects contained in it, compared to no effects (constant), whereas ER<1 indicates greater support for no effect.

^C. Top-ranked model in each group (also shown in bold font).

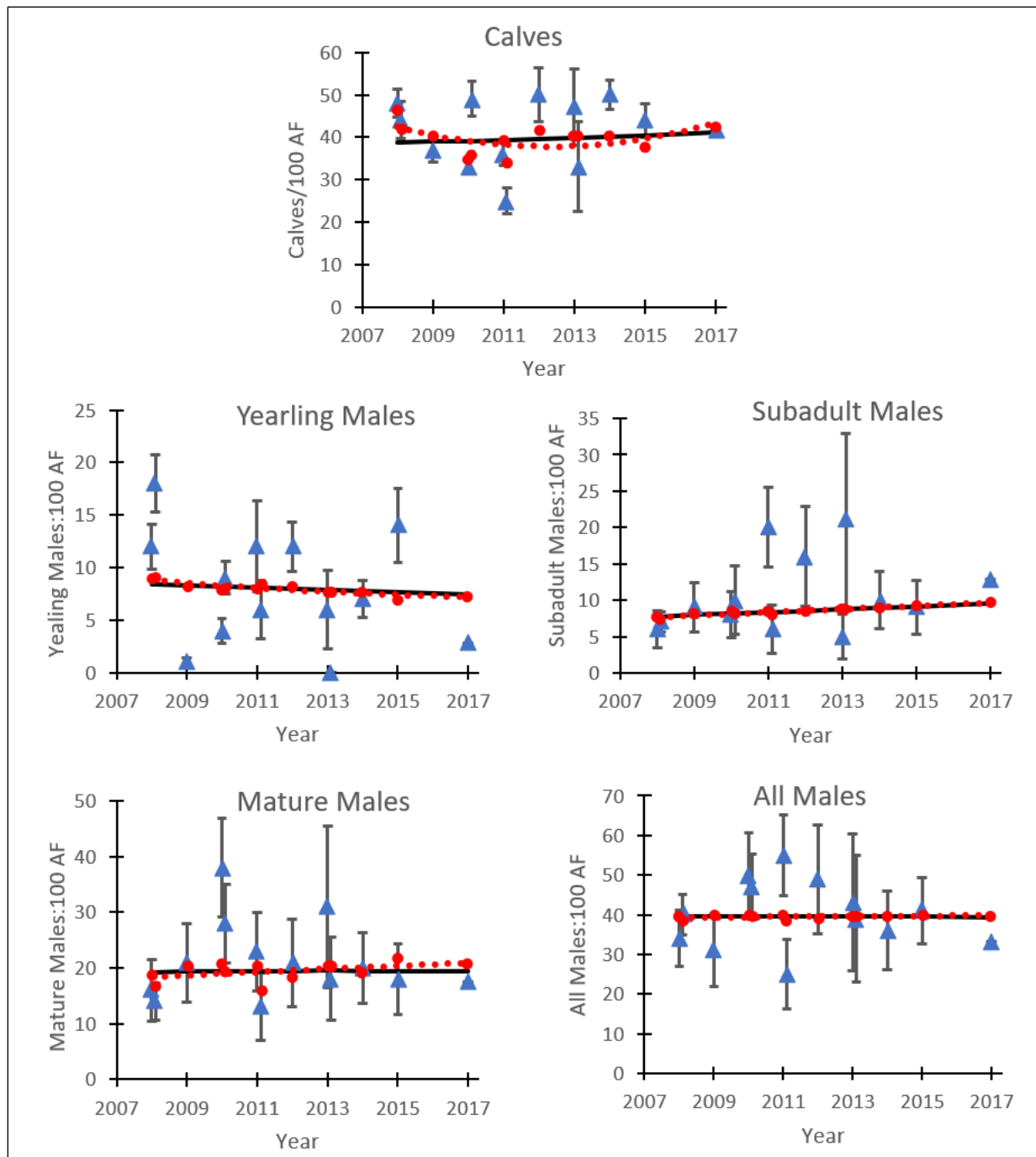


Figure 8. Trends in sex and age ratios of elk in the North Rainier TCA, 2008-2017. Blue triangles and error bars represent ratio estimates $\pm 95\%$ confidence intervals. Red dots represent the model-weighted predicted ratios. The dashed red line is the linear or quadratic model fit to the predicted ratios, whereas the solid black line represents the predicted effect of time with all seasonal and weather variables held constant.

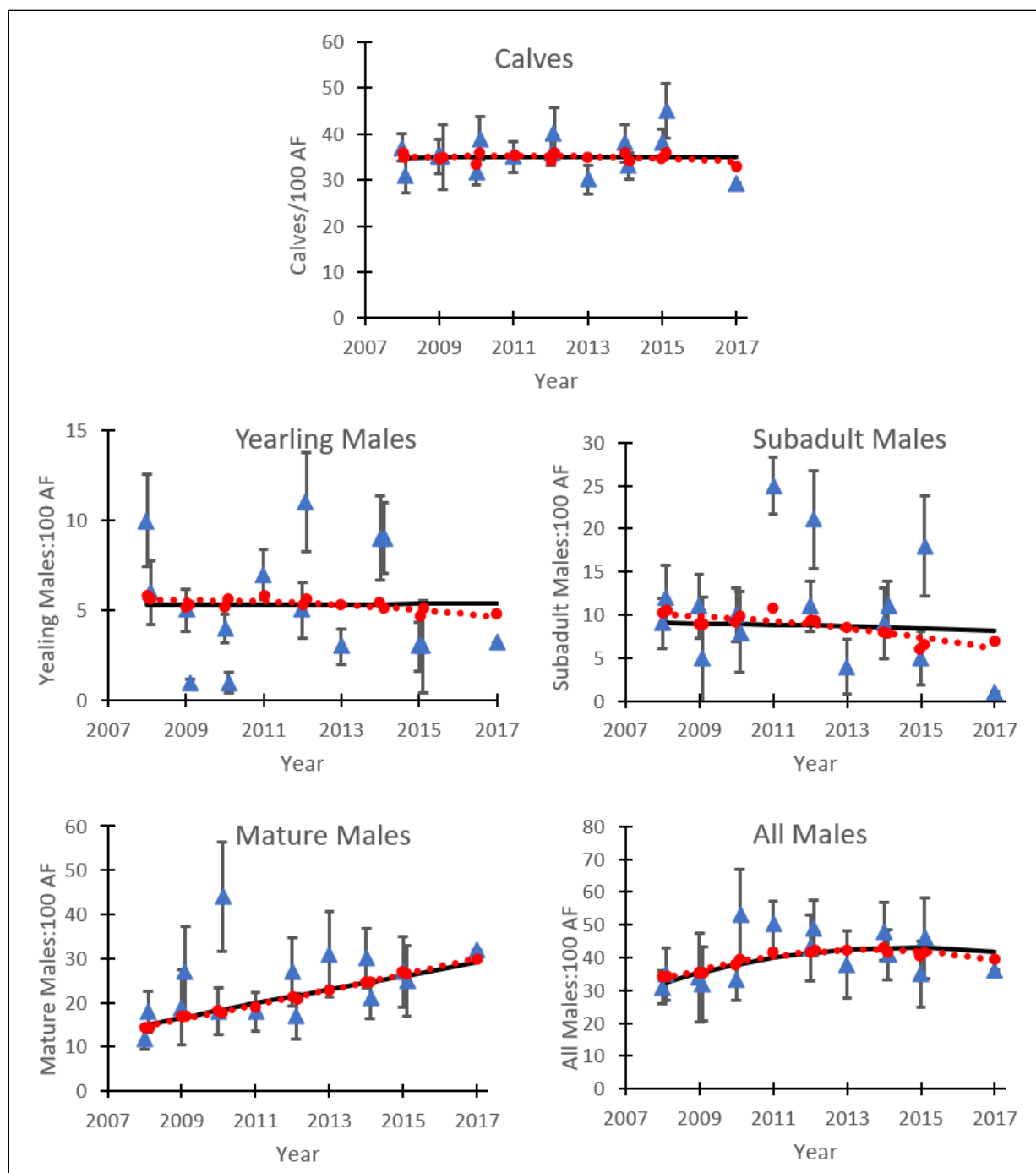


Figure 9. Trends in sex and age ratios of elk in the South Rainier TCA, 2008-2017. Blue triangles and error bars represent ratio estimates $\pm 95\%$ confidence intervals. Red dots represent the model-weighted predicted ratios. The dashed red line is the linear or quadratic model fit to the predicted ratios, whereas the solid black line represents the predicted effect of time with all seasonal and weather variables held constant.

Elk Population Trends in Trend Count Areas of Olympic National Park

Abundance

We estimated a mean of 236 elk present during six surveys completed in OLYM's Core TCA or 2.3 elk/km² (Table 12). In two surveys of Elwha TCA, a mean of 81 elk was present or approximately 1 elk/km². In single surveys of Northwest, Quinault, and Southeast TCAs, we estimated 15, 213, and 100 elk present during surveys, respectively, corresponding to about 0.2, 2.9, and 1.2 elk/km², respectively. In OLYM, survey crews generally detected about 91% of elk estimated to be present in Core TCA, and 63-97% of elk present during surveys of other Olympic TCAs.

Table 12. Raw counts and total estimated abundance of elk ($\hat{N}_{a,t}$) and associated standard error in surveyed units in OLYM TCAs, 2008-2015. Percent seen was estimated as the raw count divided by $\hat{N}_{a,t}$.

TCA	Year	Replicate	Raw count	$\hat{N}_{a,t}$	SE	CV	Percent Seen
Core	2008	1	285	297	18.9	0.06	95.9%
Core	2011	1	237	250	20.5	0.08	94.9%
Core	2012	1	351	378	21.0	0.06	92.8%
Core	2013	1	241	280	21.7	0.08	86.0%
Core	2014	1	116	132	13.8	0.10	88.1%
Core	2015	1	72	80	11.0	0.14	89.7%
Means	–	–	217	236	17.8	0.09	91.2%
Elwha	2012	1	76	94	21.1	0.22	81.0%
Elwha	2014	1	43	68	22.5	0.33	63.4%
Means	–	–	60	81	21.8	0.28	72.2%
Northwest	2011	1	13	15	4.1	0.27	85.7%
Quinault	2014	1	207	213	19.7	0.09	97.2%
Southeast	2013	1	90	100	13.4	0.13	90.3%

Estimated elk abundance appeared to decrease in the Core TCA of OLYM from 2008-2015 (Figure 10). The coefficient for the linear time model, corresponding with observed exponential rate of increase (r_o), was -0.157 ± 0.084 SE (95% CI = $-0.32, -0.03$; Table 13), indicating abundance estimates decreased by about 16% annually from 2008-15, but with low confidence due to substantial year-to-year variation in estimates and limited sample size (6 surveys). Model selection and multi-model inferences, however, indicated that the null model (the model of no change in elk estimates) garnered by far the greatest model support, with $\hat{w}_k = 61\%$. A model reflecting a negative association between elk abundance and SHI ranked second with ER = 0.23 (only 23% as much support as the null model). Other seasonal and weather covariates (e.g., Julian, SMD, MaxT, and LI) had decreasing levels of support. The linear time effect was not supported (ER = 0.04). The model-weighted estimate of a linear time effect after controlling for other covariates was -0.004 (-0.4% /year, exponential slope of black dashed line in Figure 10), demonstrating there was minimal effect of time on estimated abundance after controlling for seasonal and weather variations (Figure 10).

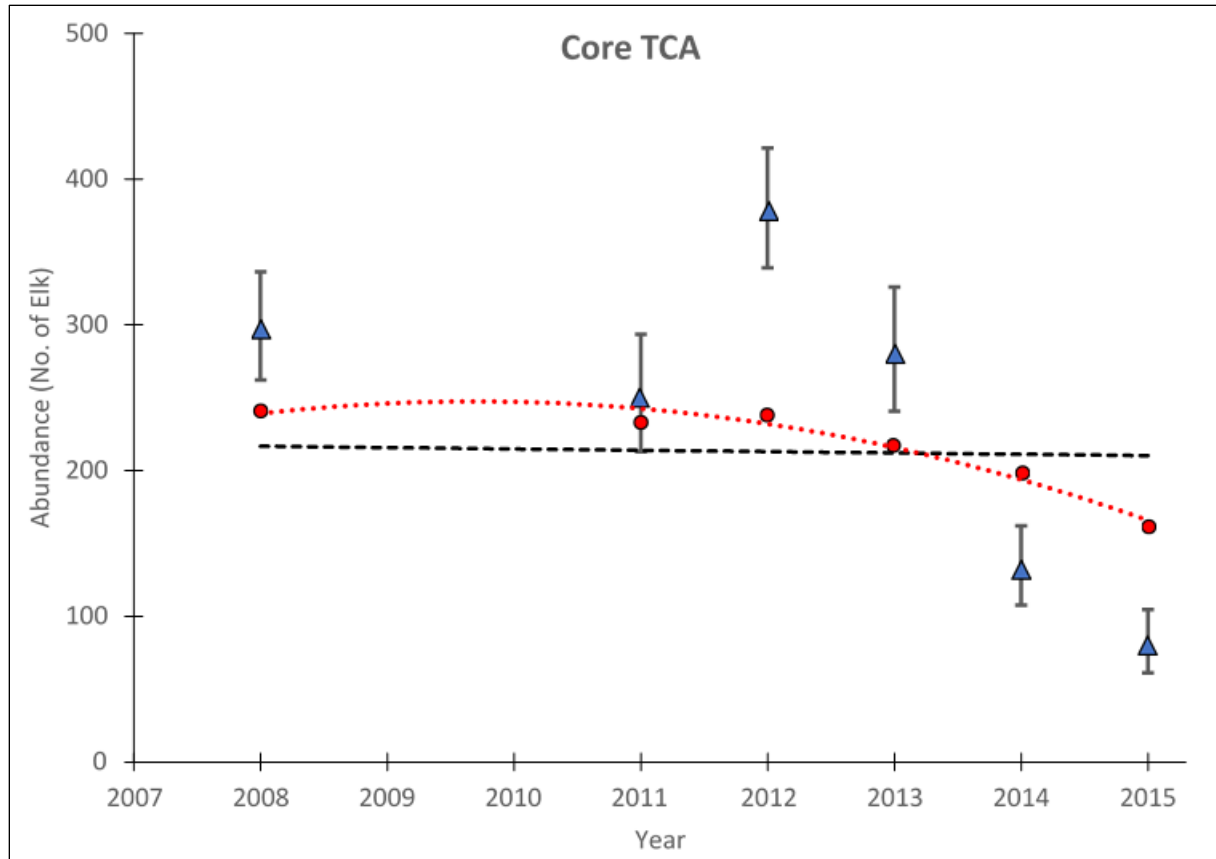


Figure 10. Trends in estimated elk abundance in Core TCA, OLYM, 2008-2015. Blue triangles and error bars represent estimated abundances $\pm 95\%$ log-normal confidence intervals ($\hat{N}_{a,t}$). Red dots represent the model-weighted predicted abundances including effects of season and weather variables. The dashed red line is a quadratic model fitted to the predicted abundance, whereas the black dashed line represents the predicted effect of time with all seasonal and weather variables held constant.

Table 13. Model selection results for covariates that potentially affect elk abundance estimates in Core TCA during aerial surveys in OLYM, 2008-2015. The numbers of estimated parameters in each model (k), Akaike's Information Criterion (AIC_c), changes in AIC_c relative to the top model (ΔAIC_c), model weights ($\hat{w}_k$), and evidence ratios (ER) are presented as defined in Burnham and Anderson (1998).

Model	k	AIC_c	ΔAIC_c	$\hat{w}_k$	ER ^B	Estimated Model Coefficients ^A							
						Intercept	Time	Time ²	Julian	MaxT	SHI	SMD	LI
Null	2	4.46	0.00	0.61	1.00	5.37	–	–	–	–	–	–	–
SHI	3	7.36	2.90	0.14	0.23	5.35	–	–	–	–	-0.003	–	–
MaxT	3	7.92	3.47	0.11	0.18	7.08	–	–	–	-0.106	–	–	–
SMD	3	8.26	3.80	0.09	0.15	5.35	–	–	–	–	–	-0.001	–
Time	3	10.67	6.21	0.03	0.04	6.15	-0.157	–	–	–	–	–	–
Julian	3	12.06	7.60	0.01	0.02	-4.16	–	–	0.040	–	–	–	–
LI	3	14.06	9.61	0.01	0.01	5.16	–	–	–	–	–	–	0.006
Time+Time ²	4	32.19	27.73	0.00	0.00	5.29	0.419	-0.066	–	–	–	–	–
Time+SMD	4	35.73	31.27	0.00	0.00	5.81	-0.091	–	–	–	–	-0.001	–
Time+MaxT	4	36.55	32.09	0.00	0.00	7.06	-0.074	–	–	-0.082	–	–	–
Time+SHI	4	37.35	32.89	0.00	0.00	5.38	-0.008	–	–	–	-0.003	–	–
Time+LI	4	39.51	35.06	0.00	0.00	5.92	-0.162	–	–	–	–	–	0.008
Time+Julian	4	40.66	36.20	0.00	0.00	5.24	-0.147	–	0.004	–	–	–	–

^A. Julian = Julian date of the survey; MaxT = maximum temperature on survey day(s). For surveys spanning multiple days, daily maxima were averaged; SHI = summer heat index on first survey day; SMD = soil moisture deficit on first survey day; LI = lunar illumination averaged among survey days

^B. ER = evidence ratio of AIC_c weight for each alternative model to AIC_c weight for the null model ($\hat{w}_k / \hat{w}_{Null}$). ER > 1 indicates support for an alternative model and effects contained in it, compared to no effects (constant), whereas ER < 1 indicates greater support for no effect.

Distribution

Mean estimated elk abundance ranged from 0.28-4.6 elk/km² among count units in OLYM's Core TCA (Figure 11, Table 14). Trends in relative elk density among count units, which would indicate changes in elk distribution and use over the 8-yr period, were only significant ($P < 0.10$) in one count unit (Unit 6b, Table 14). As was also the case in MORA, only units of low elk density tended to change, thus having a minimal effect on distribution throughout the TCA.

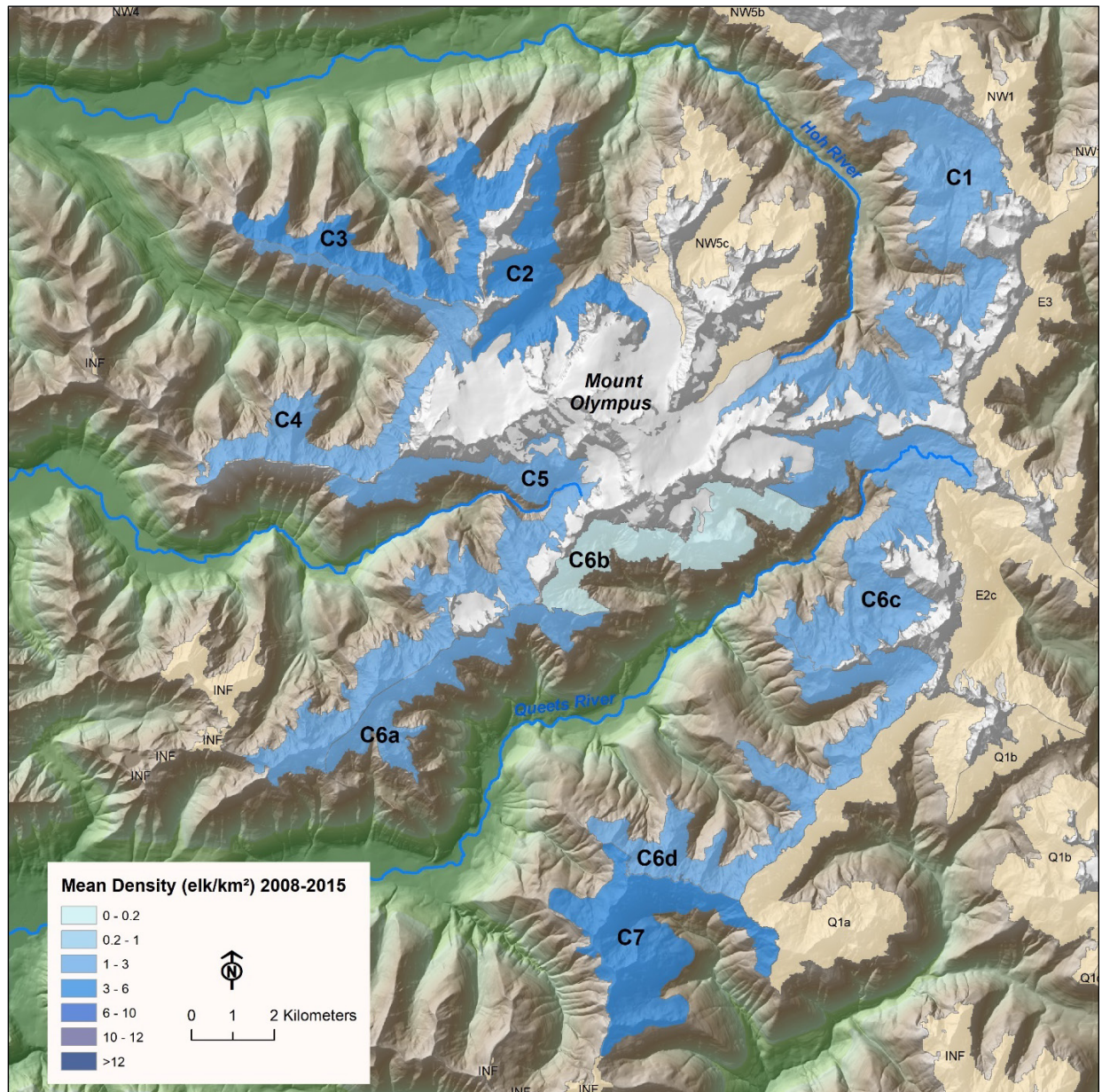


Figure 11. Mean estimated elk density (elk/km²) in survey units of Core TCA in OLYM, 2008-2015. Survey units outside Core TCA are coded in tan color.

Table 14. Mean abundance, relative density, and trends in relative density of elk in survey units of North and South Rainer TCAs, 2008-2017. Units with relative density <1 have less than mean density of elk and units with relative density >1 have greater than mean density. The slope in relative density (and SE) describes the linear relationship between relative densities over time (2008-17).

Survey unit	Area (km ²)	No. surveys	Mean abundance ($\hat{N}_{a,t}$)	$\widehat{\text{Var}}(\hat{N}_{a,t})$	Mean density (elk/km ²)	Mean relative density ^A	Slope, relative density	SE (Slope)	p (Slope)
C1	17.52	6	43.59	177.92	2.49	1.37	0.24	0.27	0.42
C2	7.06	6	20.53	22.16	3.56	1.37	-0.20	0.15	0.24
C3	7.76	6	27.39	169.30	3.53	1.15	-0.19	0.20	0.39
C4	7.66	6	22.14	110.84	2.89	0.99	-0.16	0.20	0.49
C5	14.03	8	17.93	54.46	1.62	0.59	-0.11	0.09	0.24
C6a	5.51	6	12.89	48.74	2.34	0.85	0.03	0.19	0.89
C6b	7.17	6	2.02	0.46	0.28	0.18	0.07	0.02	0.02^B
C6c	13.16	6	25.01	92.13	1.90	0.95	0.14	0.27	0.63
C6d	10.68	8	8.50	9.65	1.01	0.70	0.18	0.17	0.34
C7	10.12	6	46.58	169.06	4.60	1.68	-0.25	0.15	0.16

^A. Mean relative density was computed as elk density in the survey unit divided by mean elk density in the TCA.

^B. Signifies trends were significant ($p \leq 0.10$) (also bolded).

In addition to Core TCA, abundance was estimated in four other elk range areas of OLYM (Figures 12-15). These surveys, which were conducted on a rotating basis, were not conducted with enough frequency to evaluate temporal changes in relative density and distribution. Of the remaining summer range areas counted, estimated densities of summering elk ranged from 0-15.6 elk/km², reaching greatest densities in upper Quinault and Hoh Valleys (Quinault and Northwest TCAs; Figures 12, 13).

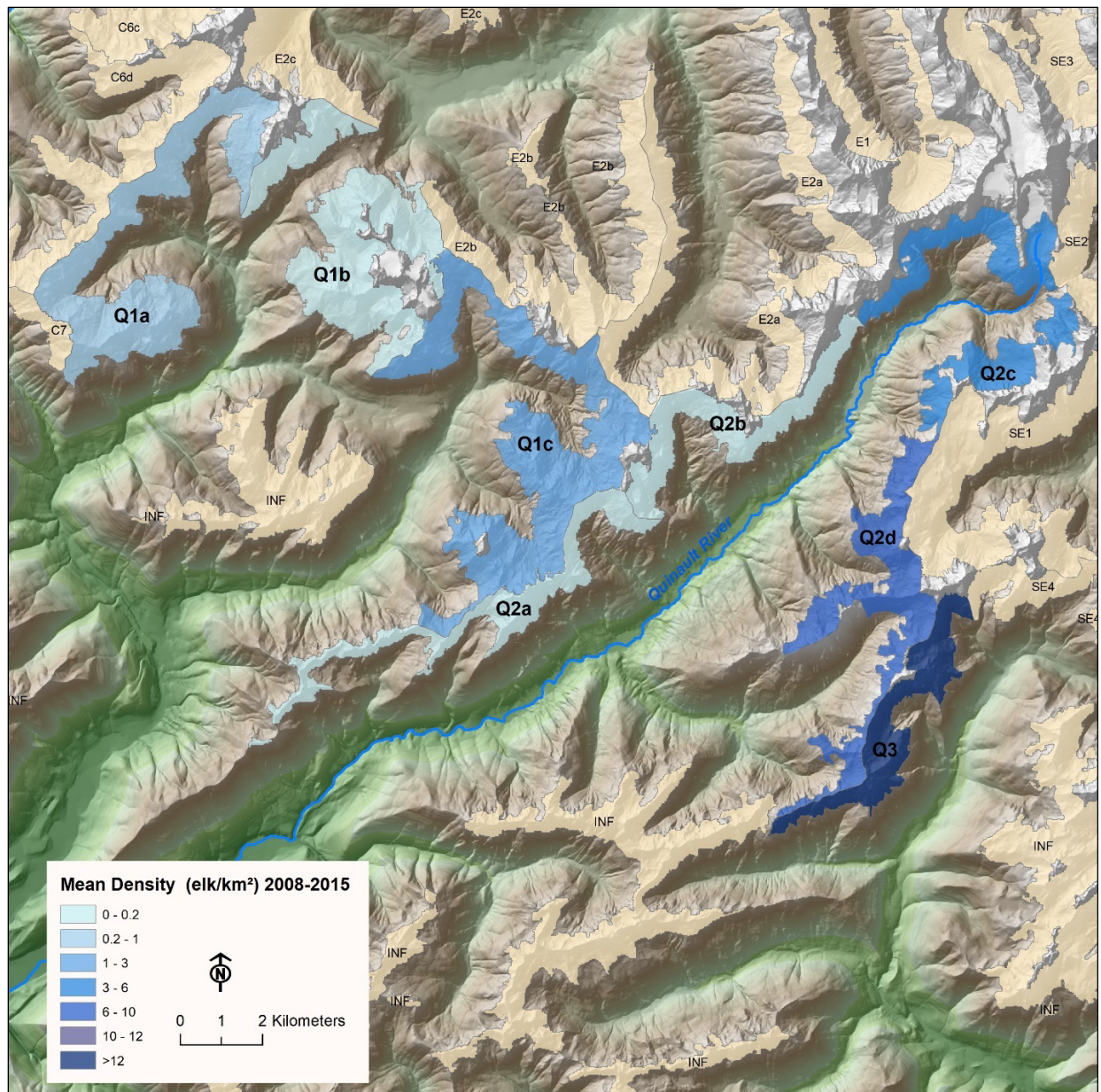


Figure 12. Mean estimated elk density (elk/km²) in survey units of Quinault TCA in OLYM, 2008-2015. Survey units outside Quinault TCA are coded in tan color.

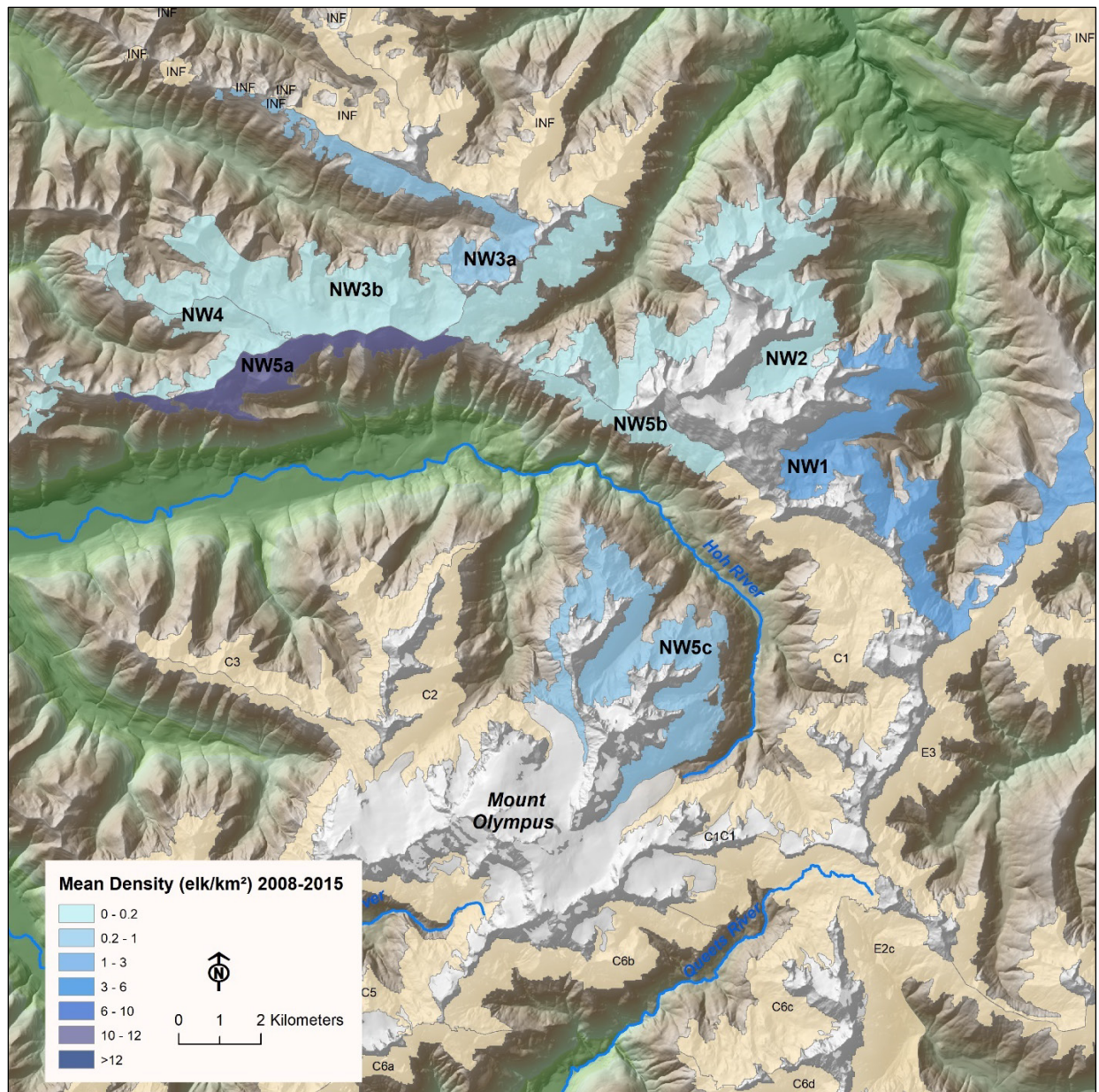


Figure 13. Mean estimated elk density (elk/km²) in survey units of Northwest TCA in OLYM, 2008-2015. Survey units outside Northwest TCA are coded in tan color.

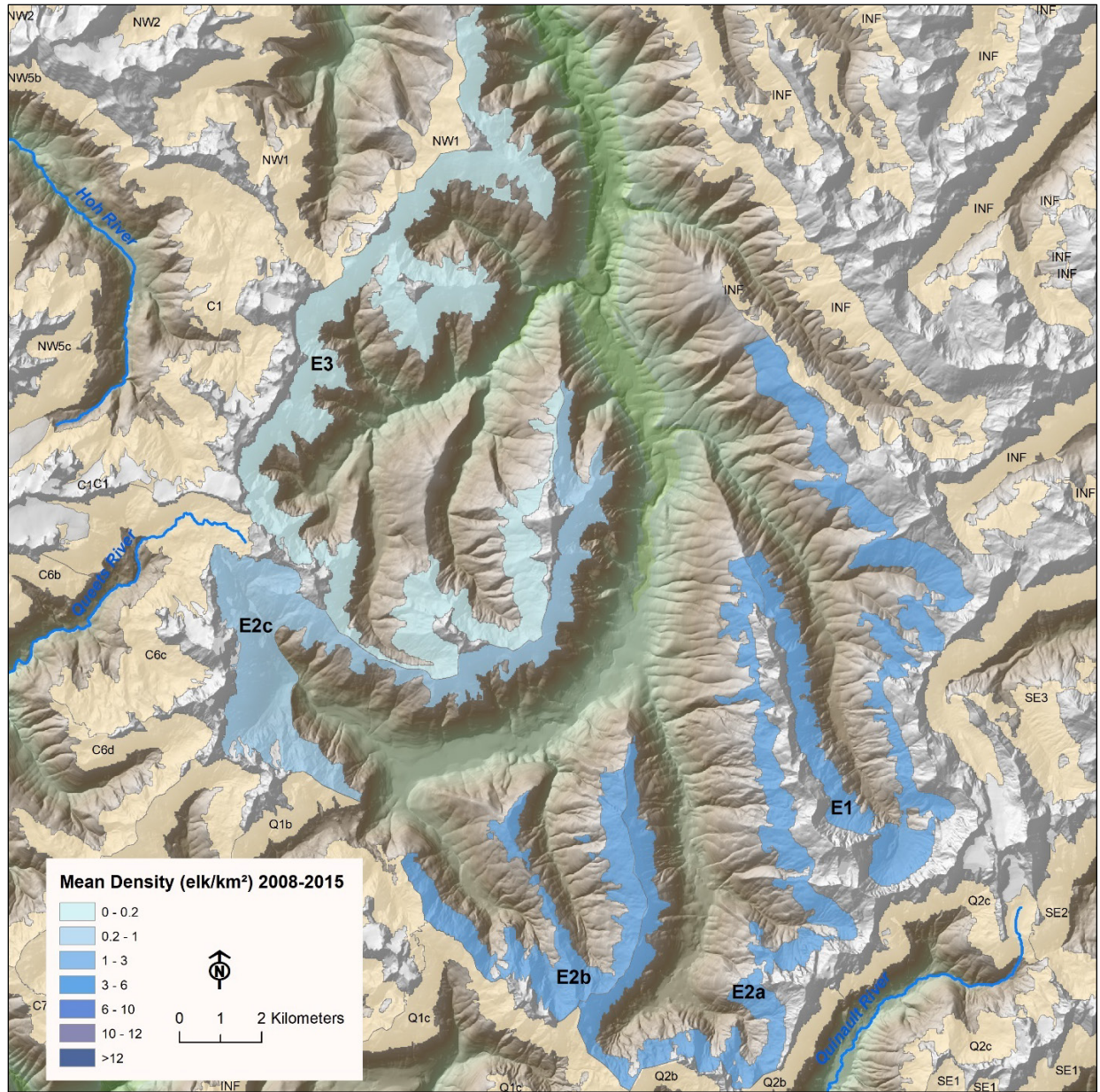


Figure 14. Mean estimated elk density (elk/km²) in survey units of Elwha TCA in OLYM, 2008-2015. Survey units outside Elwha TCA are coded in tan color.

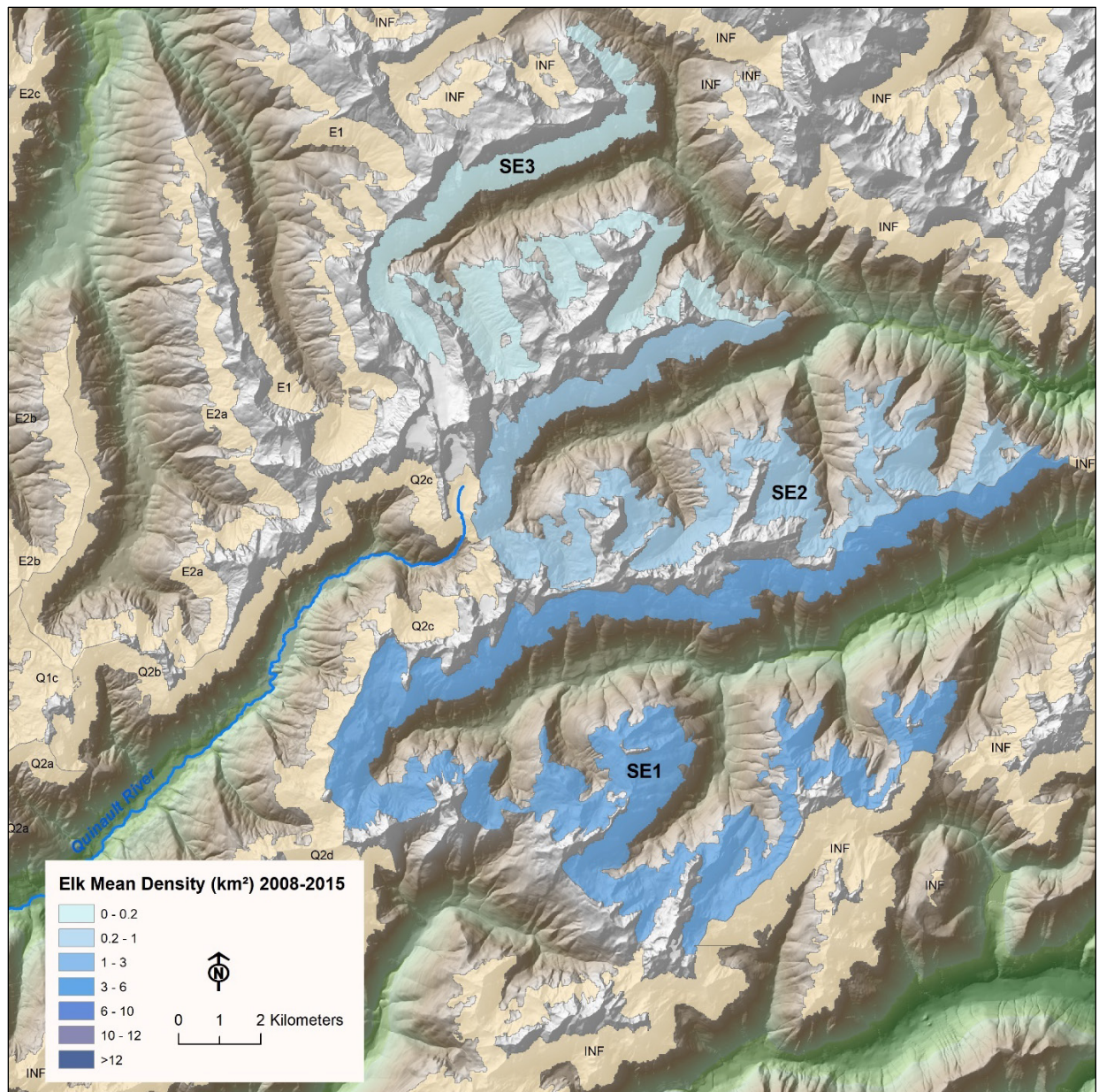


Figure 15. Mean estimated elk density (elk/km²) in survey units of Southeast TCA in OLYM, 2008-2015. Survey units outside Southeast TCA are coded in tan color.

Population Composition

Survey crews classified 1,964 elk according to sex and age categories in OLYM from 2008-2015, including 1,235 elk in Core TCA and 729 elk among the remaining Olympic TCAs (Table 15). The weighted mean estimated ratio of calves was 36:100 AF (SE=1.6) in Core TCA and 37:100 AF (SE=2.7) in the other Olympic TCAs. The weighted mean ratio of all male classes combined was 60:100 AF (SE=7.5) in Core TCA and 48:100 AF (SE=28.9) in the other Olympic TCAs. The weighted mean ratio of mature males was 48:100 AF in Core TCA and 34:100 AF (SE=27.3) in all other TCAs combined. Individual TCA composition ratios are provided in Table 15.

The null model was the most highly ranked and strongly supported model of population composition change in the Core and all other Olympic TCAs, indicating there was minimal influence of temporal trend, Julian date, or weather variables on composition estimates (Table 16, Figure 16). There was negligible evidence of temporal trend in composition ratios among elk observed ($ER \leq 0.03$). Nor was there appreciable evidence for Julian date ($ER \leq 0.02$) or weather variables ($ER \leq 0.03$) affecting observed sex and age ratios of males. There was moderate evidence for a positive association between calf ratio and SHI ($ER = 0.94$).

Table 15. Estimated relative abundance of sex and age classes of elk (n:100 Adult Females [AF]) in Trend Count Areas (TCAs) of OLYM, 2008–17. Note that relative abundance estimates are provided for all TCAs including for years when incomplete survey coverage did not permit estimation of abundance (*). Weighted means ($\bar{x}_w$) and weighted standard errors (SE) using sample size as weights are presented for each TCA.

TCA	Year	Replicate	N Elk Classified	Calves: 100 AF		All males: 100 AF		Yearling males: 100 AF		Subadult males: 100 AF		Mature males: 100 AF	
				Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
Core	2008	1	282	40	0.9	54	3.5	5	0.4	4	0.4	45	3.4
	2011	1	229	30	1.9	57	6.8	6	0.8	9	1.4	41	6.0
	2012	1	347	33	0.8	59	5.0	6	0.3	5	0.8	48	4.9
	2013	1	194	34	1.9	68	11.1	3	0.6	9	1.7	57	10.8
	2014	1	114	34	3.2	80	12.7	5	0.8	3	0.6	72	12.3
	2015	1	69	54	0.7	45	7.5	11	0.8	3	0.3	32	7.6
	$\bar{x}_w$	–	–	36	1.6	60	7.5	5	0.6	6	1.0	49	7.2
Elwha	2012	1	82	24	2.9	122	22.4	14	1.9	18	5.9	91	19.9
	2014	1	22	5	22.7	104	330.5	11	5.4	13	22.1	81	312.4
	$\bar{x}_w$	–	–	20	10.7	119	153.3	13	3.0	17	11.4	89	144.8
Northwest	2008*	1	88	34	3.7	23	7.0	6	0.6	2	0.2	16	7.6
	2011	1	13	20	0.0	169	51.4	20	0.0	0	0.0	149	51.4
	2012*	1	139	52	0.0	15	1.9	1	0.0	1	0.0	12	1.9
	$\bar{x}_w$	–	–	43	2.2	26	12.8	4	0.4	1	0.1	21	12.9
Quinault	2008*	1	3	100	0.0	100	0.0	0	0.0	0	0.0	100	0.0
	2011	1	139	29	0.6	47	5.1	0	0.0	12	1.8	35	4.3
	2014	1	154	48	0.5	28	2.3	10	0.6	8	1.1	10	1.0
	$\bar{x}_w$	–	–	39	0.6	38	3.9	5	0.4	10	1.5	23	3.0
Southeast	2013	1	89	32	1.8	61	10.4	14	1.1	7	1.8	41	9.9

Table 16. Candidate linear regression models of factors potentially affecting composition ratios of elk in TCAs of OLYM, based on all available estimates from 2008-2017, and associated ΔAIC_c values, model weights ($\hat{w}_k$), and evidence ratios (ER).

Model ^A	Calves:100 AF			All males:100 AF			Yearling males:100 AF			Subadult males:100 AF			Mature males:100 AF		
	ΔAIC_c	$\hat{w}_k$	ER ^B	ΔAIC_c	$\hat{w}_k$	ER	ΔAIC_c	$\hat{w}_k$	ER	ΔAIC_c	$\hat{w}_k$	ER	ΔAIC_c	$\hat{w}_k$	ER
Null ^C	0.00	0.47	1.00	0.00	0.97	1.00	0.00	0.94	1.00	0.00	0.93	1.00	0.00	0.97	1.00
Time	7.33	0.01	0.03	9.83	0.01	0.01	8.83	0.01	0.01	8.84	0.01	0.01	9.99	0.01	0.01
Time+Time ²	18.20	0.00	0.00	38.02	0.00	0.00	36.67	0.00	0.00	35.13	0.00	0.00	39.49	0.00	0.00
Julian	7.60	0.01	0.02	9.92	0.01	0.01	8.86	0.01	0.01	7.61	0.02	0.02	9.88	0.01	0.01
Julian +Time	37.28	0.00	0.00	39.82	0.00	0.00	38.71	0.00	0.00	34.30	0.00	0.00	39.68	0.00	0.00
MaxT	4.07	0.06	0.13	9.93	0.01	0.01	8.09	0.02	0.02	8.71	0.01	0.01	9.30	0.01	0.01
MaxT+Time	34.06	0.00	0.00	39.43	0.00	0.00	37.88	0.00	0.00	38.69	0.00	0.00	38.97	0.00	0.00
SHI	0.12	0.44	0.94	9.76	0.01	0.01	7.31	0.02	0.03	7.27	0.02	0.03	9.86	0.01	0.01
SHI+Time	19.87	0.00	0.00	38.08	0.00	0.00	37.18	0.00	0.00	35.75	0.00	0.00	39.70	0.00	0.00

^A. Julian = Julian date of the survey; MaxT = maximum temperature on survey day(s). For surveys spanning multiple days, daily maxima were averaged; SHI = summer heat index on first survey day.

^B. ER = evidence ratio of AICc weight for each alternative model to AICc weight for the null model ($\hat{w}_k / \hat{w}_{Null}$). ER >1 indicates support for an alternative model and effects contained in it, compared to no effects (constant), whereas ER<1 indicates greater support for no effect.

^C. Top-ranked model (also shown in bold font).

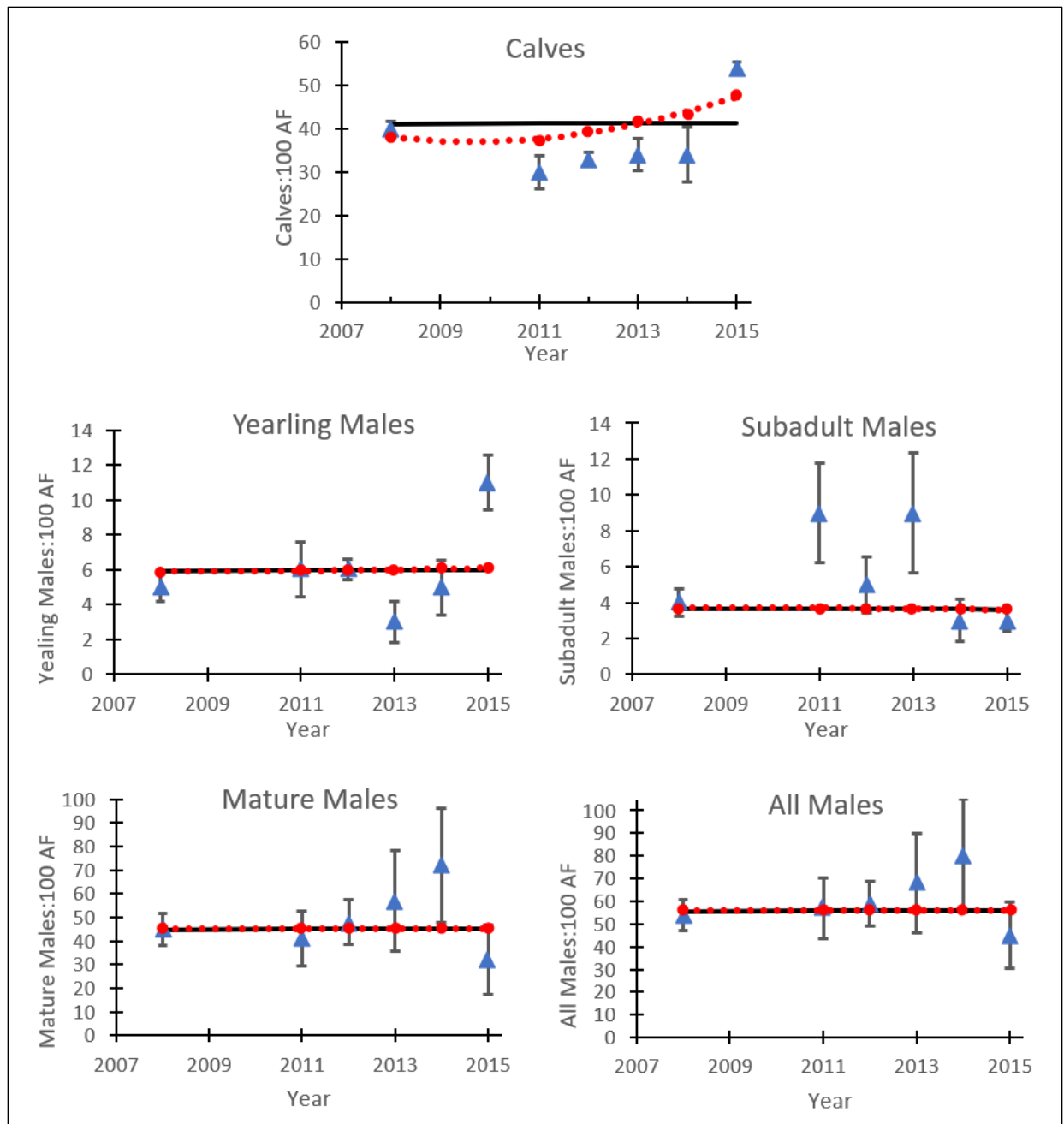


Figure 16. Trends in sex and age ratios of elk in Core TCA in OLYM, 2008-2015. Blue triangles and error bars represent ratio estimates $\pm 95\%$ confidence intervals. Red dots represent model-weighted predicted ratios. The dashed red line is the linear or quadratic model fit to predicted ratios, whereas the black dashed line represents predicted effect of time with all seasonal and weather variables held constant.

Discussion

Elk Population Trends in MORA and OLYM Trend Count Areas

Relatively small sample sizes (number of surveys) and substantial variability among survey occasions made detecting trends difficult. In fact, no time trend was the most strongly supported conclusion in several cases. Nevertheless, monitoring revealed some less conclusive support for trends in numbers of elk using key summer ranges within MORA and OLYM during 2008-2017. There was weak evidence of increasing elk abundance in North Rainier TCA, whereas there was weak evidence for a decrease in elk abundance in Core TCA of OLYM. There was strong evidence for a quadratic trend for elk using South Rainier TCA. Abundance increased initially during 2008-2011, substantiating trends reported previously (Jenkins et al. 2015), but then declined resulting in a minor and weakly supported net linear decline over the 10-year survey period.

Variation in weather, either during surveys (MaxT) or cumulatively during summer leading up to the surveys (SHI and SMD), confounded interpretation of abundance trends within the TCAs. MaxT, SHI, and SMD were all positively correlated with time, increasing from 2008-2017 (Figure 17). SMD was highly and positively correlated with SHI ($r > 0.68$ and $P < 0.02$ in both parks) and is not shown in the figure. The last four years of surveys were warmer and drier than average, whereas the first four years were cooler and moister than average (Figure 17). Consequently, it is difficult to discern whether changes in abundance reflected actual changes in elk populations over time or, instead, changes in elk distribution either due to or independent of changing weather patterns.

To the extent that trends were distinguishable from random variation, estimates of elk abundance appeared to increase from 2008-2017 in North Rainier TCA ($r_o = 0.039$; 95% CI = -0.02, 0.09), but the weight of model evidence supported the interpretation that the increase was most closely associated with a trend in increasing summer temperatures during the surveys (MaxT). We cannot explain the positive association of elk abundance with ambient temperatures during surveys because counts are generally depressed during hot weather (D. Vales, MIT, personal communication). Estimates of elk population abundance on neighboring winter range, based on mark-resight surveys of a population containing radio-marked elk, increased at a mean instantaneous rate of $r_o = 0.06$ (95% CI = 0.04, 0.08) during the same years as our summer range estimates (MIT data published in WDFW 2020). Consequently, we speculate that hot and dry conditions on the summer range may have obscured a corresponding population increase on the summer range.

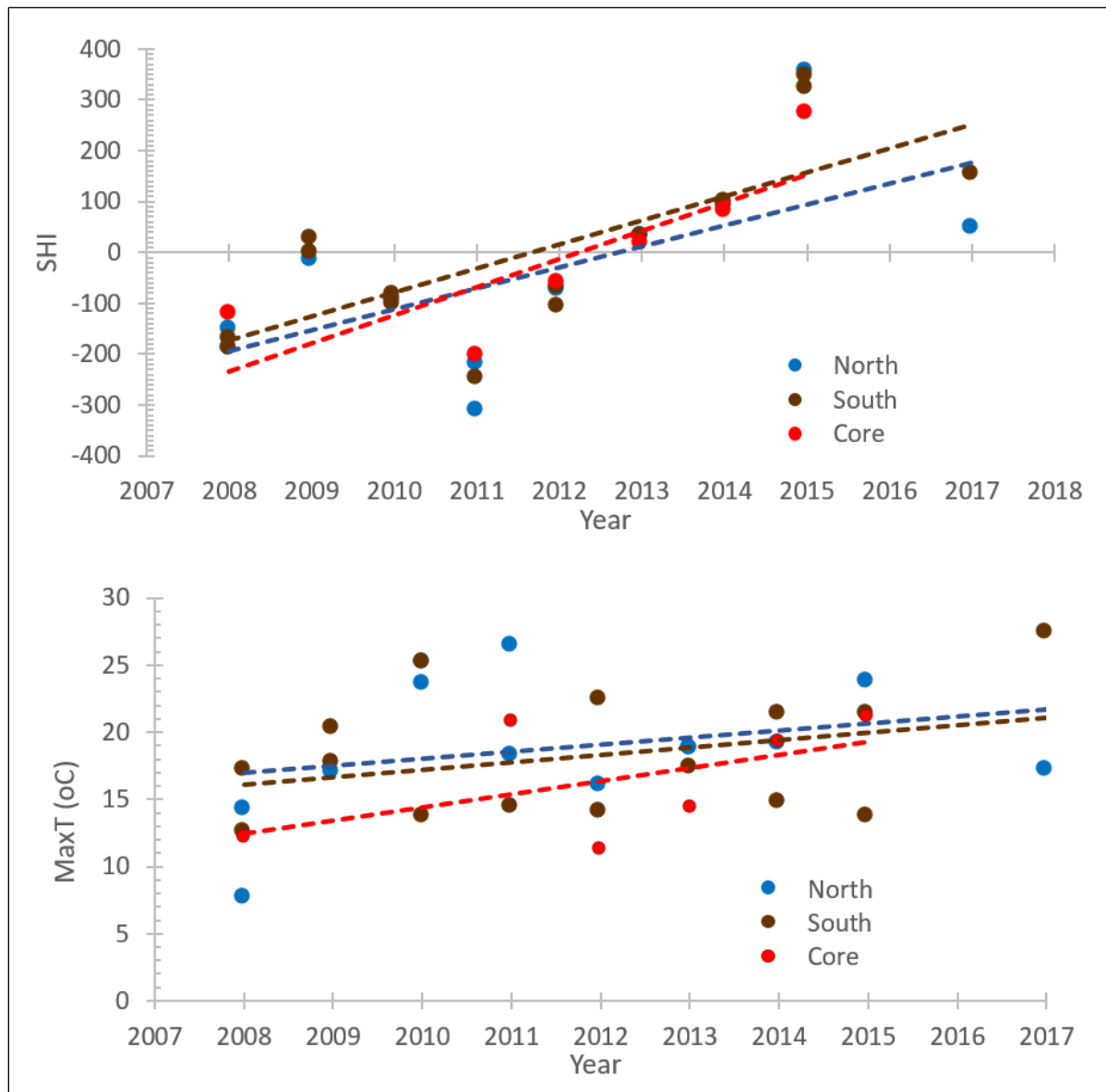


Figure 17. Correlations of Summer Heat Index (SHI) and Maximum Temperature (MaxT) with time during years of study from 2008-2017 in the North and South Rainier TCAs in MORA and 2008-2015 in the Core TCA in OLYM.

Estimated elk abundance in South TCA increased during relatively cool summers from 2008-2011 and declined with warming summers during 2012-2017. Estimates of population trend of South Rainier Herd on its winter range based on previously developed models of detection biases (Gilbert and Moeller 2008) substantiated the downward trend in numbers of elk estimated on South Rainier TCA from 2011-2017 (PTOI, unpublished data). Elk abundance estimated on Cowlitz winter range decreased at a per-capita exponential rate (r_0) of -0.035 (95% CI=-0.024, 0.045) from approximately 1,616 elk in 2011 to 1,272 elk in 2017. Elk abundance declined during the same time at an even greater rate on South Rainier TCA, but this result may be overly influenced by a low abundance estimate obtained during the hot dry summer of 2015.

Elk abundance appeared to decline steeply in Core TCA over the 8-years sampled in OLYM ($r_o = -0.157$; 95% CI = -0.32, -0.03); however, statistical support for this trend was weak due to the small number of estimates and considerable unexplained year-to-year variability. To the extent there was support for declining abundance, it was most closely associated (negatively) with annual variation in SHI. The decline in estimated numbers was influenced by one particularly low count of elk obtained during summer 2015, following one of the lowest snowpacks on record, early disappearance of snow, and hot dry conditions (Marlier et al. 2017). We postulated that observed trends in elk use within the TCA more likely reflected a shift in elk distribution to lower elevations during hot dry summers (hence outside the TCA) than declining abundance, although a combination of factors cannot be ruled out.

Collectively, these findings imply, with various levels of support, that changes in elk abundance in TCAs of both OLYM and MORA are most closely associated with hotter and drier summers observed recently. Studies of movements of radio-collared ungulates in other regions of North America indicate that warming summers may affect forage production and quality with potential adverse effects on elk demography and population trends (Middleton et al. 2013, Mysterud 2013, Aikens et al. 2020). Additional research on climate effects on distribution, nutritional status, and demography of montane elk in NCCN parks would be a fruitful area for future long-term studies.

The confounding of elk population trends with potential changes in distribution hampers interpretation of whether growing elk abundance outside MORA may impact subalpine range conditions within the park—an issue of management concern historically in MORA (Bradley and Driver 1981, Bradley 1982, Ripple et al. 1988). The data suggest most changes in elk abundance on MORA summer ranges is related to weather variation, but surveys outside MORA on the northern winter range suggest the population is growing in response to proactive habitat and population enhancement management practices. These ancillary data point to the importance of data collected by the NPS partners on winter ranges outside MORA for interpreting range trends on summer ranges within the park. Moreover, deficiencies in the interpretation of elk trends on elk summer ranges in OLYM echo the value of developing robust methods of population estimation on corresponding winter ranges to provide a more robust interpretation of parkwide trends. Current numbers of elk using subalpine summer ranges within MORA are less than was commonly estimated during the 1970's period of management concern, however, impacts of elk on subalpine meadows under emerging drier climate regimes also warrants additional scrutiny.

With few exceptions, elaborated below, sex and age composition of elk herds remained stable during surveys. There were no pronounced trends in ratios of calves estimated within summering elk herds in either MORA or OLYM. Calf ratios during late summer appeared slightly higher among North Rainier TCA than in South Rainier and OLYM's Core TCA, potentially reflecting differences in nutritional plane that affect reproduction (Cook et al. 2016), or differences in predator densities that affect survival and recruitment of elk calves (Griffin et al. 2011, Clark et al. 2014). Previous studies of elk body condition and reproduction in the Pacific Northwest revealed that elk in the North Rainier Herd were among the best conditioned elk studied and achieved high pregnancy rates compared to several other elk populations in the region (Cook et al. 2013). Moreover, limited cougar

control efforts exercised in the 2000's may also have contributed to elevated calf ratios in the North Rainier TCA (MIT, unpublished data).

The proportion of males in the population (all age classes considered collectively) also remained constant in North Rainier TCA (MORA) and Core TCA (OLYM), whereas the proportion of mature males increased in South Rainier TCA. The ratios of mature males could be influenced by changing harvest pressures among years, which was not examined here. However, the increasing trend may also reflect the relatively low estimate of mature males:100 AF measured in 2008 and relatively high proportion of mature males estimated in 2017 at the respective ends of the time series.

High ratios of males indicated that healthy numbers of breeding males were found across both parks. The weighted mean ratios of males estimated in MORA (41:100 AF in both North and South Rainier TCAs) were greater than in many other managed herds in Washington (WDFW 2019) and were greater than the State's management guidelines for preseason bull:cow ratios (i.e., 15-35 bulls:100 cows, WDFW 2014). Ratios of males estimated in MORA were also appreciably higher than post-season ratios estimated during spring annually in Game Management Unit (GMU) 653, which encompasses primary wintering area of migratory herds leaving Mount Rainier's Northern TCA during fall (mean=12.2 males:100 AF from 2008-2016; WDFW 2020). The disparity between the pre-season bull:cow ratios estimated in MORA and post-season ratios estimated outside the park would reflect, in part, natural mortality that occurs between the two survey periods. But such a large difference likely also reflects unaccounted differences in male detectability on the two ranges as well as differences in hunting-caused mortality among population segments covered in the two surveys. Higher ratios of males measured in the pre-season MORA surveys may indicate that MORA provides sanctuary from hunting during at least part of hunting seasons or that male elk leaving the park during fall use more remote areas where harvest pressure is lower than on other more accessible ranges. However, the proportions of males in MORA, which were skewed toward the subadult age class compared to the unhunted population in Core TCA of OLYM, suggests that mature males are harvested disproportionately upon leaving the park. That interpretation is consistent with regulations that restrict the allowable harvest by State hunters to males containing 3 points or better (WDFW 2020). Additionally, there are special permit 'any-bull' harvest opportunities outside the park that are skewed toward the higher antler-point classes (K. Garrison, WDFW, personal communication). Regardless, the total number of bulls in MRNP remains high despite the existing harvest levels outside the park.

The weighted mean proportion of males found in Core TCA of OLYM ($60 \pm 7.5[SE]$) was higher than we found reported in other unmanaged elk populations (Flook 1970, Houston 1982, also see review by DeSimone et al. 1993), including Roosevelt elk in OLYM (Smith 1980). Our findings provide a useful baseline for comparison to other managed populations in the region and for long-term assessment of trends in OLYM. Previous studies indicated that bulls captured in the core of the Olympic Mountains rarely move outside park boundaries where they would be susceptible to legal harvest (NPS, unpublished data). Information on bull elk movements and the high ratio of bulls observed in Core TCA suggest that natural sex ratios and mating systems of elk are intact in the park's interior. Additional information and sampling effort would be needed before sample sizes are

sufficient to compare sex ratios among different segments represented in other TCAs sampled on a 4-year rotation in OLYM.

We also found little evidence of changes in spatial distribution use patterns of elk in MORA or OLYM. The only count units with evidence of temporal change in proportional distribution of elk were found in units with low counts where small shifts of elk across unit boundaries would represent appreciable changes in relative numbers of elk over time, while not indicating major changes in spatial distributions overall.

Elk Monitoring Challenges

Apart from ongoing challenges associated with scheduling and contracting multiple aircraft, survey crews encountered few operational difficulties in conducting elk monitoring surveys from 2012-2017. As crews became more familiar with survey logistics, and less time was required to track GPS-collared elk to gather DO-S data for M_{DSH} model development, we had fewer incomplete surveys during 2012-17 compared to the previous reporting interval (Jenkins et al. 2015). Potential errors associated with missing data for individual survey units were minimized by counting a greater proportion of TCAs, omitting low-density units when surveys needed to be curtailed, and by imputing values for missing survey units using a richer data set than was previously available.

Maintaining funding and participation of survey cooperators represents the greatest operational challenge in sustaining current aerial elk monitoring in NCCN parks. Elk monitoring in MORA is the only resource monitoring protocol in NCCN that relies on cooperator support to fund and implement the surveys. Until 2015, surveys were completed by sharing operational control, funding, and survey implementation among NPS-NCCN, WDFW, PTOI, and MIT. Rising costs associated with maintaining NCCN monitoring programs throughout the Network, however, resulted in loss of NCCN funding for elk surveys in 2015. Similarly, funding constraints and changing priorities of WDFW has also resulted in loss of support for these surveys. As the surveys progressed, WDFW recognized that MORA surveys did not adequately describe trends in the greater North and South Rainier Herds at a scale most useful for management. In the future, WDFW will seek collaborations in developing a more pragmatic and comprehensive survey of elk populations at a broader geographic scale. Tribal partners engaged in surveys have also commented that logistical complexity and costs have reduced their interests in conducting DO-S surveys. In recent years, Tribal partners have conducted abbreviated surveys of population composition uncorrected for detection biases and without precision estimates at a fraction of the cost associated with completing a complete DO-S survey of an entire TCA.

In addition to and related to these practical and logistical challenges, the current analyses revealed the fundamental problem that changing weather patterns and annual variations in elk distribution obscured interpretation of population trends. Intensive radio-telemetry studies of North Rainier Herd have indicated that the proportion of radio-collared elk observed within TCAs during surveys has ranged from 16-55% annually with proportions diminishing particularly over recent years (D. Vales, MIT, unpublished data summarized in WDFW 2020). Telemetry studies of GPS-collared elk in OLYM verify that elk use of the subalpine zone is variable (NPS, unpublished data). Despite measurement of weather to statistically account for nuisance variables that influence elk use of

survey areas, there remains considerable unexplained variation in elk population estimates in TCAs of both parks. Research from other regions provides corroborative evidence that changing climate and weather patterns, particularly decreased snowpack and increased summer warming, influence seasonal patterns of forage phenology and elk distribution (Middleton et al. 2013).

We hypothesized *a priori* that weather variables (particularly heat and associated SMD) would influence distribution of elk relative to TCA boundaries. Hence, we measured these covariates to help disentangle effects of weather variation on abundance trends. Specifically, we hypothesized that elk would use forested areas, avalanche chutes, and riparian or wetland areas at lower elevations during hot, dry summers and years of early snowmelt when subalpine vegetation dried out earlier in the season. We did not anticipate the extent to which increased warming would be so closely correlated with the time sequence that it would thoroughly confound interpretation of trends. Further, initially we envisioned conducting two surveys of each TCA each summer to better account for random weather effects and other variations on elk abundance within TCAs. The steady diminution of funding support for this program coupled with logistical complexity of conducting these surveys, has resulted in a steady reduction in the number of annual surveys completed each season, which has exacerbated our inability to reliably detect trends.

As a result of these complications, abundance estimates for TCAs provided here are best considered estimates of use of subalpine and alpine environments of each park at points in time and not indices of population abundance. This important caveat was recognized during program development and was justified from historical concerns that elk use of subalpine meadows may influence the integrity of subalpine meadows. Moreover, information on summer range trends and population composition of this harvested population segment provides potentially useful information for managing harvests of elk outside the park.

Future Needs and Opportunities

A review of existing monitoring protocols considered in the context of park and partner informational needs and monitoring priorities would help to clarify future monitoring directions in NCCN. Such a review would provide an opportunity for interested partnering agencies and Tribes to reaffirm what information obtained from summer surveys is useful for management decision making, whether the current program is meeting those needs, and whether opportunities exist for further collaboration or program modifications.

When the current monitoring program was established, a team of ungulate survey researchers and practitioners met to evaluate potential monitoring approaches and provide recommendations for monitoring elk in NCCN parks. The team examined the merits and limitations of several commonly used methods of estimating ungulate population abundance in mountain ecosystems, including several aerial survey designs and estimation methods (Samuel et al. 1987, Lubow et al. 2002, McCorquodale et al. 2013, Pollack and Kendall 1987), ground-based fecal pellet surveys (Jenkins and Manly 2008), and methods based on fecal genotyping (Brinkman et al. 2011). A review of these methods is beyond the scope of this report, but summaries resulting from previous evaluation are available for future reference if there is an interest to reexamine past rationales (NCCN Elk Monitoring project archives). The decisions made at the time reflected budget limitations that

prevented maintaining a sample of radio-collared elk on the air in perpetuity as would be necessary for more comprehensive accounting for all sources of survey biases or achieving a more comprehensive population estimate. However, the tendency of cooperating tribes in the Mount Rainier ecosystem to maintain a sample of radio-collared elk in the population may provide opportunities to broaden estimation of detection biases to include variations in elk distribution inside and out of surveyed TCAs, or the use of estimation methods based on animal marking.

During recent years there have been several advances in ungulate population survey methodologies that warrant additional evaluation for applicability to NCCN. Aerial line-transect sampling has been used in other mountain ecosystems to lower costs and wilderness impacts associated with more intensive monitoring (Schmidt et al. 2012, 2019). Moreover, there has been a surge of interest recently in using camera surveys to census wildlife using both thermal imaging cameras mounted on aerial platforms and ground-based camera networks. Thermal imaging equipment has become more cost effective and applications will only continue to grow (Havens and Sharp 2016). Ground-based camera networks have been used to estimate abundance of diverse groups of mammals ranging from deer and elk (Moeller et al. 2018), to wolves (G. Roffler, Wildlife Biologist, Alaska Department of Fish and Wildlife, telephone conversation, 11-5-2018), and cougars (Loonam et al. 2021). Although camera surveys have been used over decades to estimate wildlife abundance using standard mark-resight methods or spatially explicit capture-resight models when individual animals can be recognized either by their tags or individual markings (Karanth 1995, Royal and Gardner 2011), recent statistical advances allow estimation without the need for marking animals. Animal density may be derived through analysis of how much area is sampled per ungulate detection on camera (i.e., the collective area sampled by camera fields of view) or by sampling the lengths of time until detections are recorded (Moeller et al. 2018, Loonam et al. 2021). These methods are being field-tested presently for estimating elk abundance and population composition in broad areas of Idaho, as well as by Tribes on a more localized scale on the Olympic Peninsula as a replacement for dangerous and costly aerial surveys. Pilot studies of elk monitoring using cameras are currently in place in both Lewis and Clark National Historical Parks and OLYM. Additionally, camera-based methods could have applications for use with existing aerial monitoring protocol as a potential means of estimating annual variation in percent of relative occurrence of the population within TCA boundaries.

Recent developments using non-invasive sampling methods to estimate population abundance makes this an opportune time to examine their applicability in NCCN not only for ungulate population monitoring, but also potentially for meeting broader monitoring objectives. When priorities were initially established for guiding development of ecological monitoring programs in NCCN parks, one of the highest priorities across multiple parks was to monitor biodiversity of terrestrial biota. At that time, this priority was essentially disregarded due to the lack of feasible, cost effective methods. New methods are currently being developed, however, for monitoring trends in owl population occupancy (with potential for other bird taxa as well) and that of bats using widespread acoustic recording sampling designs. Furthermore, there are a variety of camera networks being deployed throughout Washington State currently in studies of taxa as diverse as lynx, wolverine, fishers, Cascades red fox, and wolves. Collaborative opportunities exist today to develop multi-taxa monitoring systems that

might include specific ungulate monitoring objectives together with broader goals of monitoring biodiversity of other mammalian and avian groups.

Conclusions

The future of elk monitoring is at a crossroads in NCCN parks—decisions are required whether to abandon, reallocate, or retool sampling efforts to meet future needs. Changes in elk abundance within the selected TCAs of MORA and OLYM do not reliably distinguish between changes in population abundance and changes in elk distribution. Yet a look ahead suggests there are new emerging issues likely to affect elk populations of both MORA and OLYM. To the list of historical issues—those having to do primarily with changing land uses and wildlife management practices outside the parks (Houston et al. 1990, Jenkins and Starkey 1996)—effects of changing climate patterns, emerging diseases, and future range expansion of wolves will all likely influence elk population trajectories in one or both parks. Past monitoring efforts provided a baseline of information on relative use of subalpine summer ranges by elk and population composition for future comparisons and a ready protocol for implementation if changing issues, funding, or priorities present themselves. Furthermore, there are promising new methods of wildlife population estimation on the horizon including noninvasive sampling methods that seem particularly well suited for estimating forest wildlife populations in wilderness ecosystems.

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