STAFF SUMMARY FOR JUNE 24-25, 2020

2. GENERAL PUBLIC COMMENT (DAY 1)

Today's Item **Information** ☒ **Action** ☐

Receive public comments, petitions for regulation change, and requests for non-regulatory actions for items not on the agenda.

Summary of Previous/Future Actions

- **Today receive requests and comments** **Jun 24-25, 2020; Webinar/teleconference**
- Consider granting, denying or referring Aug 19-20, 2020; Fortuna

Background

This agenda item is to provide the public an opportunity to address FGC on topics not on the agenda. Staff may include written materials and comments received prior to the meeting as exhibits in the meeting binder (if received by written comment deadline), or as supplemental comments at the meeting (if received by the supplemental comment deadline).

Public comments are generally categorized into three types under general public comment: (1) petitions for regulation change; (2) requests for non-regulatory action; and (3) informational-only comments. Under the Bagley-Keene Open Meeting Act, FGC cannot discuss or take action on any matter not included on the agenda, other than to schedule issues raised by the public for consideration at future meetings. Thus, petitions for regulation change and non-regulatory requests generally follow a two-meeting cycle (receipt and direction); FGC will determine the outcome of the petitions for regulation change and non-regulatory requests received at today's meeting at the next regular FGC meeting, following staff evaluation (currently Aug 19-20, 2020).

As required by the Administrative Procedure Act, petitions for regulation change will be either denied or granted and notice made of that determination. Action on petitions received at previous meetings is scheduled under a separate agenda item titled "Petitions for regulation change." Action on non-regulatory requests received at previous meetings is scheduled under a separate agenda item titled "Non-regulatory requests."

Significant Public Comments

1. The new petition for regulation change is summarized in Exhibit 1, and the original petition is provided as Exhibit 2.
2. Informational comments are provided as exhibits 3-5.

Recommendation

FGC staff: Consider whether any future agenda items are needed to address issues that are raised during public comment.

Exhibits

1. Summary of new petition for regulation change received by June 11, 2020 at 5:00 p.m.

2. Petition #2020-008: Elk hunting closure, received Jun 10, 2020
3. Email from Action for Animals, regarding China and wildlife trade, received Apr 19, 2020
4. Letter from Kathy Lynch, regarding state Senate hearings on wildlife trade, received May 26, 2020
5. Letter from Peter Flournoy, regarding restoration of a fishing license for Adam Aliotti, received Jun 9, 2020

Motion/Direction (N/A)

CALIFORNIA FISH AND GAME COMMISSION
RECEIPT LIST FOR PETITIONS FOR REGULATION CHANGE: RECEIVED BY 5:00 PM ON JUNE 17, 2020
Revised 6/15/2020

Tracking No.	Date Received	Name of Petitioner	Subject of Request	Short Description	FGC Receipt Scheduled	FGC Action Scheduled
2020-008	6/10/2020	Thomas Wheeler	Elk hunting suspension	Suspend indefinitely all elk hunting (excluding by DFW depredation permit) in the Northwestern Elk Hunt Area or reduce tags issued under 14 Cal. Code Regs §§ 364, 364.1 to zero.	6/25/20	

Tracking Number: (_2020-008_)

To request a change to regulations under the authority of the California Fish and Game Commission (Commission), you are required to submit this completed form to: California Fish and Game Commission, (physical address) 1416 Ninth Street, Suite 1320, Sacramento, CA 95814, (mailing address) P.O. Box 944209, Sacramento, CA 94244-2090 or via email to FGC@fgc.ca.gov. Note: This form is not intended for listing petitions for threatened or endangered species (see Section 670.1 of Title 14).

Incomplete forms will not be accepted. A petition is incomplete if it is not submitted on this form or fails to contain necessary information in each of the required categories listed on this form (Section I). A petition will be rejected if it does not pertain to issues under the Commission's authority. A petition may be denied if any petition requesting a functionally equivalent regulation change was considered within the previous 12 months and no information or data is being submitted beyond what was previously submitted. If you need help with this form, please contact Commission staff at (916) 653-4899 or FGC@fgc.ca.gov.

SECTION I: Required Information.

Please be succinct. Responses for Section I should not exceed five pages

1. **Person or organization requesting the change (Required)**
   Name of primary contact person: Thomas Wheeler
   Address: 145 G St., Ste. A, Arcata, CA 95521
   Telephone number: (707) 822-7711
   Email address: tom@wildcalifornia.org

2. **Rulemaking Authority (Required) -** Reference to the statutory or constitutional authority of the Commission to take the action requested: Government Code § 11342.545; Fish and Game Code §§ 200, 332, 339

3. **Overview (Required) -** Summarize the proposed changes to regulations:

   14 Cal. Code Regs. § 364.2

   All elk hunting, excluding hunting conducted pursuant to a depredation permit issued by the California Department of Fish and Wildlife, in the Northwestern Elk Hunt Area is indefinitely suspended.

   Alternatively, the same effect of the proposed regulation could be achieved by reducing the tags issued under 14 Cal. Code Regs §§ 364, 364.1 to zero.

4. **Rationale (Required) -** Describe the problem and the reason for the proposed change:

In early April 2020, the California Department of Fish and Wildlife discovered the presence of a novel disease, treponema-associated hoof disease, affecting the hooves of Roosevelt elk in Del Norte County. Shortly thereafter, on April 16, 2020, the California Fish and Game Commission approved new hunting regulations providing for tag numbers for elk in California. Unfortunately, the discovery of the disease was not disclosed to the Commission. Until the Department and Commission have the opportunity to consider the ramifications of the disease (including the cumulative effects of the disease together with approved hunting), ways to minimize the spread of the disease and measures to mitigate the harm to infected individuals and herds, it is necessary to rein back elk hunting in the Northwest Elk Hunt Area. The proposed rule would institute a temporary moratorium on hunting elk within the infected area thereby providing time for the Department to issue a containment and management strategy. The proposed rule, as written, would continue to allow hunting pursued under a depredation permit issued by the Department.

As explained below, the disease may cause population declines in affected herds and the effects of the disease were never studied by the Commission before making its decision, in the mandated Elk Management Plan, or in the environmental impact documents prepared for the Commission.

TAHD May Affect Elk Populations

Research concerning the effects of the disease on local herd populations is scant. Existing information does raise a logical conclusion that the disease may affect herd populations by reducing the fitness of elk.

In an infected herd near Mount St. Helens, populations have declined by approximately 30-35% over a four-year period (2009-2013). (McCorquodale et al. 2014.) It is unclear what role the disease may have played in this decline because this period coincided with an effort to reduce the population of elk through increased hunting and severe weather in winter 2012. While researchers were unable to untangle the role of the disease in the population decline, the authors did note that the "seemingly logical assumption that some additional mortality risk is likely associated with advanced disease." (McCorquodale et al. 2014.)

Additional research from Washington State is ongoing and a final reported is anticipated in 2020. A preliminary report on findings, Hoenes et al. (2018), expresses why TAHD has the potential to inflict population-level impacts:

> It is reasonable to assume that elk with advanced stages of TAHD have a decreased probability of survival because their infirmities may predispose them to predation, harvest, severe weather events, or other types of disease (Bender et al. 2008). For example, mule deer with chronic wasting disease (CWD), prior to developing obvious clinical signs, have been shown to be more vulnerable to predation (Miller et al. 2008, Krumm et al. 2009), vehicle collisions (Krumm et al. 2005), and possibly harvest (Conner et al. 2000). This is an important consideration because the growth rate of large ungulate populations, such as elk, is highly sensitive to changes in adult female survival (Nelson and Peek 1982, Eberhardt 2002) and strongly correlated with the production and survival of juveniles (Gaillard et al. 2000; see also Smith and Anderson 1998, Raithel et al. 2007). When adult female and juvenile survival are concurrently reduced, populations would be expected to decline (Gaillard et al. 2000; see also Bender et al. 2007, McCorquodale et al. 2014). Consequently, if TAHD reduces the survival of adult females and calves, it has the potential to have a negative effect on the population dynamics of impacted elk herds.

Preliminary results also raise concerns, although the author notes it is too soon to make any definitive statement about the effect of the disease. Among the preliminary conclusions:

> Elk affected by TAHD have had lower levels of condition in December, lower pregnancy rates, lower lactation rates, and lower annual survival rates. Our estimates of IFBF in December indicate elk in the Mount St. Helens elk herd area continue to experience strong nutritional limitations during late-summer and autumn, regardless of disease status. Irrespective of proximate cause, 0.88 of the mortalities we have documented for elk affected by TAHD, have

included animals that had bone marrow content levels indicative of a severe negative energy balance. (Hoenes et al., 2018.)

The Commission was Unable to Consider the TAHD During its April Deliberations

Although the disease was discovered in early April 2020, the Commission was seemingly not informed about its discovery before the April 16, 2020 meeting where the Department approved new elk tag quotas for the coming year. EPIC has an outstanding Public Records Act request with the Department to ascertain what was known and by whom by the date of this meeting.

Environmental advocates raised their alarm at the May 14, 2020 teleconference and the May 14, 2020 Wildlife Resources meeting. At these meetings, the Department expressed that the disease was a concern and that they were in talks with sister agencies in Oregon and Washington about the disease. Furthermore, at the meeting, the Department promised to produce a specific plan to address TAHD. This plan has not yet been issued.

The Statewide Elk Management Plan Does Not Consider TAHD

As directed by the California legislature, elk within the state are to be managed by a "statewide elk management plan." Fish and Game Code § 3952. This plan is directed to consider, inter alia, "[m]ajor factors affecting elk within the state," including disease. The current elk management plan, published by the Department in 2018, does not consider TAHD.

Environmental Impact Analysis Did Not Consider TAHD

Because the issue of TAHD was unknown to the Commission at the time, the environmental documents necessary for compliance with the California Environmental Quality Act failed to consider the direct and cumulative impacts of TAHD on the species. Without study, it is unknown what the impacts of the disease, together with other stressors, such as hunting, will be on the species.

Northcoast Elk are Irreplaceable

Northcoast Roosevelt elk are irreplaceable between these elk have not undergone hybridization with other elk subspecies. Although Roosevelt elk exist across four U.S. states (Alaska, California, Oregon, and Washington), the Northcoast population is perhaps the only that has not experienced recent hybridization with other sympatric elk species. (Meredith et al., 2007.) In other words, the Northcoast Roosevelt elk possess unique genetics and represent a "pure" Roosevelt elk without the effects of crossbreeding. For this reason, Meredith et al. (2007) has proposed that these elk constitute an "evolutionarily significant unit." Population declines in herds of this region are therefore significant in a manner that similar declines in other areas would not be.

SECTION II: Optional Information

5. **Date of Petition:** June 10, 2020

6. **Category of Proposed Change**
   ☐ Sport Fishing
   ☐ Commercial Fishing
   X Hunting
   ☐ Other, please specify: Click here to enter text.

7. **The proposal is to:** (*To determine section number(s), see current year regulation booklet or https://govt.westlaw.com/calregs*)
☐ Amend Title 14 Section(s):Click here to enter text.
X Add New Title 14 Section(s): 364.2
☐ Repeal Title 14 Section(s): Click here to enter text.

8. **If the proposal is related to a previously submitted petition that was rejected, specify the tracking number of the previously submitted petition** Click here to enter text.
Or ☐ Not applicable.

9. **Effective date**: If applicable, identify the desired effective date of the regulation.
If the proposed change requires immediate implementation, explain the nature of the emergency: This petition is in response to a novel threat to Roosevelt elk in the Northwest Elk Management Area. Accordingly, we file this petition as an emergency petition and ask for the rule to come into effect immediately.

10. **Supporting documentation:** Identify and attach to the petition any information supporting the proposal including data, reports and other documents:

Attached to this petition are the following publications concerning TAHD in Roosevelt elk:

Hoenes, B., George, B., Holman, E. and Stephens, N. 2018. Assessing the potential effects of treponeme associated hoof disease (TAHD) on elk population dynamics in Southwest Washington. Washington Department of Fish and Wildlife, Olympia, Washington USA.

McCorquodale, S. M., P. J. Miller, S. M. Bergh and E. W. Holman. 2014. Mount St. Helens elk population assessment: 2009-2013. Washington Department of Fish and Wildlife, Olympia, Washington, USA.

Meredith, E., Rodzen, J., Banks, J., Schaefer, R., Ernest, H., Famula, T., May, B. 2007. Microsatellite Analysis of Three Subspecies of Elk (*Cervus elaphus*) in California, *Journal of Mammalogy*, Volume 88, Issue 3, Pages 801–808, https://doi.org/10.1644/06-MAMM-A-014R.1

11. **Economic or Fiscal Impacts:** Identify any known impacts of the proposed regulation change on revenues to the California Department of Fish and Wildlife, individuals, businesses, jobs, other state agencies, local agencies, schools, or housing:

Fiscal impacts of the proposed regulation are unknown.

12. **Forms:** If applicable, list any forms to be created, amended or repealed:

Click here to enter text.

SECTION 3: FGC Staff Only

Date received: Click here to enter text.

FGC staff action:

☐ Accept - complete
☐ Reject - incomplete
☐ Reject - outside scope of FGC authority

Tracking Number

Date petitioner was notified of receipt of petition and pending action: _______________

Meeting date for FGC consideration: ___________________________

FGC action:

☐ Denied by FGC
☐ Denied - same as petition _____________________
Tracking Number

☐ Granted for consideration of regulation change

Journal of Mammalogy, 88(3):801–808, 2007

MICROSATELLITE ANALYSIS OF THREE SUBSPECIES OF ELK (*CERVUS ELAPHUS*) IN CALIFORNIA

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A total of 676 elk (*Cervus elaphus*) were genotyped at 16 tetranucleotide microsatellite loci to evaluate genetic differences among 3 subspecies of elk in California: tule (*C. e. nannodes*), Roosevelt (*C. e. roosevelti*), and Rocky Mountain (*C. e. nelsoni*) elk. Of the 13 populations analyzed, 5 represented tule elk herds, 3 were Roosevelt elk, 2 were Rocky Mountain elk, and 3 were of uncertain taxonomic status. Overall, populations averaged between 7 and 8 alleles per locus, with observed heterozygosity values ranging from 0.33 to 0.58 per population. Tule elk, which experienced a severe bottleneck in the 1870s, had consistently less genetic diversity than the other subspecies. All 3 subspecies were significantly differentiated, with the greatest genetic distance seen between the tule and Roosevelt subspecies. Assignment of individuals to subspecies using microsatellite data was nearly 100% accurate. Despite the past population bottleneck, significant differences were found among the tule elk herds. Assignment testing of elk from Modoc, Siskiyou, and Shasta counties to determine subspecific status of individuals suggested that these populations contained both Roosevelt and Rocky Mountain elk and their hybrids, indicating that these elk subspecies interbreed where subspecies coexist.

Key words: California, *Cervus elaphus*, elk, genetics, hybrid, microsatellite, population

Elk (*Cervus elaphus*) herds that roamed a large portion of North America have been reduced in both area and number due to hunting pressure and loss of habitat. Although management strategies have aimed to reintroduce elk to some of their original range, these programs are not without potential genetic consequence. Genetic bottlenecks and founder effects are of great concern, and exacerbated by harem mating structure and high variability in male reproductive success (Clutton-Brock 1989).

California contains 3 of the described subspecies of free-ranging elk: tule elk (*C. e. nannodes*; historic resident of oak woodlands and grasslands), Roosevelt elk (*C. e. roosevelti*; northwestern coastal area), and Rocky Mountain (*C. e. nelsoni*; occupying the extreme northeastern corner of California, including Modoc County) elk. The remaining extant subspecies, Manitoban elk (*C. e. manitobensis*), occurs east of the Rocky Mountains in the northern plains states and into central Canada but does not inhabit California. Although each subspecies naturally occurs in different locations within California, there are potential geographic regions of overlap between Roosevelt and Rocky Mountain elk, allowing for the possibility of hybrid zones.

Tule elk residing in the Central Valley and oak woodlands of the foothills of California were almost eliminated after the gold rush of 1849 (McCullough et al. 1996). Historically estimated at more than 500,000 animals, tule elk were compromised by extreme hunting pressure and conversion of grass and woodland habitat into farming and agricultural operations. In 1873, when tule elk were thought to be extinct, protection was granted by the state of California (McCullough 1969; McCullough et al. 1996). Although exact numbers vary, it is believed that at least a single breeding pair of tule elk was found and protected in the southern San Joaquin Valley in Kern County, California, in 1874. Those remaining elk are believed to be the ancestors of extant tule elk populations in California (McCullough 1969; McCullough et al. 1996).

Roosevelt elk inhabit their historical range in the northwestern coastal mountain ranges of California (O'Gara 2002), mainly Humboldt and Del Norte counties. Only elk inhabiting these 2 counties are categorized as Roosevelt elk by the Boone

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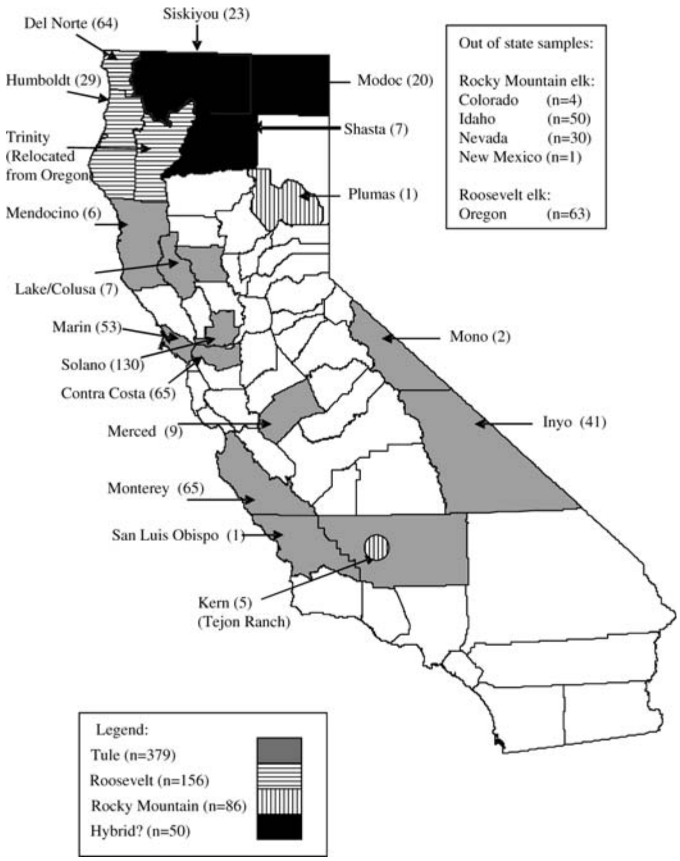

Fig. 1.—Map depicting number of individuals sampled at each herd location given by county name. Gray shaded areas represent counties that contain herds of tule elk, horizontal lines indicate counties with herds of Roosevelt elk, vertical lines indicate counties with herds of supposed Rocky Mountain elk, and diagonal lines indicate potential hybrid zones of Roosevelt and Rocky Mountain elk.

and Crockett Club (Missoula, Montana) for trophy-hunting purposes (Reneau and Reneau 1993). Discrimination of distinct herds of Roosevelt elk is difficult because of the dense forest habitat. Examination of satellite tracking data indicates restricted movement of animals and the possibility of distinct herds (R. Schaefer, in litt.).

Examination of satellite data (R. Schaefer, in litt.) provides evidence that Rocky Mountain Elk of northeastern California may migrate between Modoc County and Oregon, Idaho, and Nevada. Circa 1913, approximately 50 Rocky Mountain elk from Montana were introduced into Shasta County, California (R. Schaefer, in litt.).

Shasta, Siskiyou, and Modoc counties in northern California are considered to be potential hybrid zones for Roosevelt and Rocky Mountain elk by California Department of Fish and Game wildlife managers. For the purpose of our study, the term ''hybrid'' refers to an intraspecific cross. Interstate 5, a major north–south highway in Washington, Oregon, and California, has been used as an arbitrary management boundary for subspecies delineation: elk occurring west of Interstate 5 have been designated Roosevelt and those to the east of Interstate 5 as Rocky Mountain elk. Lone elk are known to wander and travel great distances (>150 miles—R. Schaefer, in litt.), and crossing the unfenced Interstate 5 is likely, as inferred by presence of road-killed elk (R. Schaefer, in litt.). Because Roosevelt and Rocky Mountain trophy elk are recorded separately by hunting organizations, determination of the genetic lineage of animals in these areas will benefit trophy hunters and wildlife managers.

Subspecific status of North American elk has been hotly debated (see O'Gara [2002] for discussion of the taxonomy of North American elk). Overlap of morphological differences among tule, Roosevelt, and Rocky Mountain subspecies demands that other discriminating criteria, such as molecular genetic analyses, are used to address taxonomic status. Tule elk are considered the smallest subspecies of North American elk (Merriam 1905) and are typified by having lower body masses, lighter pelage, and the longest toothrows of any North American subspecies. Roosevelt elk reportedly have the largest body mass and display different antler and jaw morphologies from the others (McCullough 1969; O'Gara 2002). Of the 3 subspecies, Rocky Mountain elk typically have the largest antlers (Reneau and Reneau 1993).

Evidence derived from mitochondrial DNA indicates that tule elk are more closely related to Rocky Mountain than Roosevelt elk, and supports the subspecific status of these 3 categories of elk (Polziehn et al. 1998, 2000; Polziehn and Strobeck 1998, 2002). Using microsatellite data, Williams et al. (2004) showed that tule elk display reduced genetic variation relative to Rocky Mountain and Manitoban elk; however, small sample size prevented robust tests of genetic differentiation among populations of tule elk.

The primary goal of our study was to measure the degree of nuclear genetic differentiation between tule, Roosevelt, and Rocky Mountain elk and evaluate whether the populations of elk in California warrant status as evolutionarily significant units. Given that Roosevelt and Rocky Mountain elk are sympatric in California, yet recorded separately for trophy records, wildlife managers will benefit from genetic information that identifies subspecies composition, particularly in potential hybrid zones. Genetic discriminators will allow identification of subspecies in trophy animals, hair samples from field sampling efforts, and forensic samples. Toward these objectives, we used 2 population assignment programs, WHICHRUN (Banks and Eichert 2000) and STRUCTURE 2.1 (Pritchard et al. 2000), to test the accuracy of assignment to subspecies from multilocus genotype data. Lastly, we assessed the risks and degree of inbreeding faced by herds of tule elk and make recommendations for monitoring and managing these herds.

Materials and Methods

Sample collection and DNA isolation.—A total of 676 elk were analyzed in this study (Fig. 1). The majority of the samples were from a large tissue archive maintained by the California Department of Fish and Game's Wildlife Forensic Laboratory (Rancho Cordova, California). Tissue and blood samples were collected from road-killed animals or animals legally taken at scheduled hunts and elk relocations throughout

California from 1997 through 2003. Samples were shipped frozen on ice to the Wildlife Forensic Laboratory and maintained at −20°C until DNA extraction.

Tule elk from 8 herds were sampled, including 2 of the original 3 surviving herds established in the 1930s: the Owens Valley herd (Inyo County) and the Cache Creek herd (Colusa and Lake counties). The remaining 6 herds of tule elk sampled were created by later translocations; however, all herds of tule elk are descendants from 1 original remnant population.

Samples of Rocky Mountain elk collected from Nevada and Idaho served as reference samples for comparison to Rocky Mountain elk in California. Five Rocky Mountain elk originally translocated from Wyoming to Tejon Ranch in Kern County, California, were sampled. Roosevelt elk from Jewell, Oregon, and translocated to Trinity County, California, between 1988 and 1995 were examined. The Nevada Department of Wildlife supplied muscle tissue samples of 30 Rocky Mountain elk, and the Idaho Department of Fish and Game provided 49 diluted DNA extracts (10 ng/μl) and 1 muscle tissue sample.

The DNA was isolated from all tissue and blood samples using Qiagen QIAmp tissue isolation kits and procedures (Qiagen, Chatsworth, California). After extraction, DNA was quantified using a Molecular Dynamics model 595 Fluorimager (Molecular Dynamics, Sunnyvale, California) using human DNA reference standards of known concentration. DNA from extracted tissue samples was diluted to a concentration of 10 ng/μl; blood extracts were not diluted.

Microsatellite analysis.—Multiplex polymerase chain reaction was used to amplify 16 tetranucleotide microsatellite markers developed specifically for elk or mule deer (*Odocoileus hemionus*; see Table 1 for references). All loci used were developed from enriched libraries by GIS Inc. (Chatsworth, California). These primers were selected based upon their highly repeatable polymerase chain reaction products and variability within and among the 3 subspecies of elk described herein.

Forward primers were fluorescently labeled with 6FAM, VIC, or NED (Applied Biosystems, Foster City, California) and the reverse primer had a 5′-GTTTCTT-3′ extension added to the 5′ end to reduce split peaks and drive the reaction to the ''plus A'' band (Brownstein et al. 1996). Polymerase chain reaction fragments were detected using a BaseStation DNA Fragment Analyser (MJ Research, Inc., Waltham, Massachusetts).

Each amplification cocktail included up to 20 ng of template DNA, 1X PCR buffer (Applied Biosystems), 2.4 μl of multiplex specific primer concentrations (see below), 0.2 mM of each deoxynucleoside triphosphate, 2 mM $MgCl_2$, and 0.2 U (Multiplex D, A, and E) or 0.25 U (Multiplex N) Amplitaq (Applied Biosystems) and double-distilled H_2O to total 20 μl per reaction. Polymerase chain reaction primer concentrations are indicated in Table 1. Reactions containing at least 5 ng/μl DNA were run on a PTC-100 thermalcycler (MJ Research, Inc.) with the following amplification parameters: 94°C for 3 min, followed by 26 cycles of 94°C for 30 s, 58°C for 30 s, 72°C for 40 s, a final extension at 72°C for 20 min, and a final hold at 10°C. All blood samples and tissue samples containing less than 5 ng/μl DNA were amplified for 30 cycles. One microliter of polymerase chain reaction product was then added to 4 μl of loading buffer (double-distilled H_2O, formamide, blue dextran, Genescan 400HD ROX [Applied Biosystems], and Genescan 500 ROX [Applied Biosystems] mixed in a ratio of 220 μl : 155.2 μl : 51.7 μl : 12 μl : 12 μl). Polymerase chain reaction products were separated using a denaturing 5.5% acrylamide gel (Long Ranger Gel Solution, Cambrex Bio Science Rockland Inc., Rockland, Maine). Gel data analysis and allele sizing were performed using Cartographer (MJ Research, Inc.).

TABLE 1.—Summary of loci examined in this study. This table shows in which multiplex each locus was amplified, polymerase chain reaction (PCR) primer concentration (each primer), 5′ fluorescent dye label used, number of alleles, heterozygosity values observed (H_O), and the reference in which the original primer sequences can be found. Note that all the reverse primers were modified with a 5′-GTTTCTT sequence to reduce split peaks and encourage the formation of ''+A'' bands during polymerase chain reaction. References: 1 = Jones et al. (2002); 2 = Meredith et al. (2005); 3 = Jones et al. (2000).

Locus	Multiplex	PCR concentration (μM)	5′ dye label	No. alleles	Size range (base pairs)	H_O	Reference
T108	D	0.100	6Fam	8	136–181	0.540	1
T26	D	0.483	6Fam	12	328–398	0.565	1
T172	D	0.017	Vic	7	174–198	0.450	1
T501	D	0.600	Ned	9	252–290	0.576	1
T268	N	0.092	6Fam	6	228–256	0.437	1
T156	N	0.062	Vic	15	143–249	0.545	1
T507	N	0.062	Ned	11	148–202	0.390	1
C273	N	0.985	6Fam	8	132–166	0.553	2 and 3
T193	A	0.706	6Fam	10	184–220	0.599	1
C217	A	0.212	Vic	2	185–193	0.415	1
T123	A	0.282	Ned	4	155–186	0.399	1
C180	E	0.048	6Fam	4	156–168	0.507	2
T107	E	0.144	Vic	4	242–265	0.326	2
C229	E	0.144	6Fam	5	299–319	0.363	2
C143	E	0.240	Ned	4	166–178	0.492	2
C01	E	0.624	Ned	5	342–358	0.433	2

Statistical methods.—Genotypic data were collected on all 676 samples. However, only those counties or states (Idaho, Nevada, and Oregon) with at least 20 animals ($n = 632$) were used in frequency-based analyses, specifically the calculation of F-statistics and log-likelihood statistics of population differentiation. Because the alleles were not sequenced to determine the actual number of tetranucleotide repeat units, statistical models conforming to the infinite alleles model were used.

Allele frequencies, unique alleles, and observed and expected heterozygosities within counties or states (''populations'') with a minimum of 20 individuals and within each of the 3 subspecies were calculated using GENEPOP on the Web (http://www.biomed.curtin.edu.au/genepop—Raymond and Rousset 1995). For frequency-based analyses, the populations of Roosevelt elk used were from Humboldt and Del Norte counties (California) and Jewell, Oregon; the populations of Rocky Mountain elk used were from Nevada and Idaho. Deviations from linkage equilibrium between all pairs of loci across all populations and conformation to Hardy–Weinberg equilibrium on a locus-by-locus basis within populations also were tested using GENEPOP. The *P*-value for a significant deviation from Hardy–Weinberg equilibrium using the exact test (Guo and Thompson 1992) was adjusted from 0.05 to 0.00027 using a Bonferroni adjustment for 186 tests of the same hypothesis (16 loci by 12 populations with 6 loci being monomorphic in a population). A Bonferroni-adjusted *P*-value of 0.0014 was used to assess significance for multiple tests of deviation from Hardy–Weinberg equilibrium at the subspecies level (3 subspecies and 16 loci).

Quantitative measures of population differentiation (F_{ST}) and inbreeding (F_{IS}) were made among subspecies and among populations within subspecies using the software package FSTAT (FSTAT, a program to estimate and test gene diversities and fixation indices, version 2.9.3, J. Goudet, 2001; http://www.unil.ch/izea/softwares/fstat.html) as described in Weir and Cockerham (1984) after Bonferroni-adjusted pairwise significance levels. Samples from Modoc, Shasta, and Siskiyou counties were not used in the comparisons of subspecies populations because the taxonomy of elk from these 3 counties was uncertain.

Analysis of molecular variance (AMOVA; ARLEQUIN—Schneider et al. 2000) was used to evaluate the degree of population differentiation based on the relative number of repeats. Genotypic data were analyzed using subspecies, populations within subspecies, and individuals within populations as sources of variation.

The measure of genetic distance among 12 of the county or state sampling groups was Nei's standard distance (Ds—Nei 1972), calculated in PHYLIP, version 3.5c (Felsenstein 1993) using GENDIST. The neighbor-joining method was used in NEIGHBOR (PHYLIP, version 3.5c—Felsenstein 1993).

Animals were assigned to subspecies using genotypic data and 2 population assignment software packages, WHICHRUN (Banks and Eichert 2000) and STRUCTURE 2.1 (Pritchard et al. 2000), to test accuracy of assigning to presumptive subspecies. Elk from the hybrid zones were excluded because of the confounding effects of uncertain lineage. A baseline genotype data file was constructed using known reference animals, including 367 tule elk, 156 Roosevelt elk, and 80 Rocky Mountain elk. The tule elk baseline reference samples consisted of animals from Contra Costa County ($n = 65$), Inyo County ($n = 41$), Lake County ($n = 5$), Marin County ($n = 53$), Monterey County ($n = 65$), and Solano County ($n = 130$). Roosevelt elk baseline samples included Del Norte County ($n = 64$), Humboldt County ($n = 29$), and Oregon ($n = 63$). Rocky Mountain elk baseline samples included elk from the states of Idaho ($n = 50$) and Nevada ($n = 30$).

In WHICHRUN, the probability of a given sample belonging to a "critical population" was generated by a likelihood ratio log of odds score of the probabilities of the 1st and 2nd most probable population assignment given that sample's genotype. The baseline data file of the 603 samples was jackknifed, a log of odds score was generated for the most probable population assignment, and each sample was assigned to that subspecies with log of odds score of $\geq$1.0.

WHICHRUN was then used to assign individual elk from Modoc, Siskiyou, and Shasta counties to Rocky Mountain or Roosevelt subspecies with log of odds score of $\geq$1.0. Five elk from the Tejon Ranch (Kern County) and 6 elk from Mendocino County also were analyzed for subspecies verification. The 6 elk from Mendocino County were collected in 2 different locations. An individual was assumed to be a possible hybrid if the log of odds score for both Roosevelt and Rocky Mountain was $\leq$1.0. The same analysis parameters were used for assignment testing of baseline data and for animals of unknown ancestry.

The baseline genetic data also were tested for assignment accuracy using the program STRUCTURE using 100,000 rounds of iteration after a 10,000-round burn-in. The STRUCTURE genetic analysis program also was used to test assignment of reference elk and samples from Modoc, Siskiyou, and Shasta counties. STRUCTURE was used to estimate the number of lineages that comprise the counties or states without using a priori population information. The number of populations (K) was evaluated for 1–20 populations. Most likely number of populations was determined by $\Delta(K)$ as described in Evanno et al. (2005).

Elk were classified as potential hybrids if the most probable subspecies was <10 times more likely than the 2nd most probable subspecies, indicative of past introgression. This is mathematically equivalent to the log of odds score threshold of 1.0 used in WHICHRUN for subspecies assignment.

Results

Measures of genetic diversity.—Within the 676 samples, loci possessed from 2 alleles (locus C217) to 15 (locus T156; average = 7.3) with observed heterozygosity values ranging from 0.33 (locus T107) to 0.60 (locus T193). F_{IS} estimated for the 5 herds of tule elk analyzed ranged from −0.038 (Contra Costa County) to 0.079 (Inyo County). Tule elk displayed the lowest allelic diversity and showed no more than 5 alleles at each locus (average number of alleles = 3.2), with several loci being monomorphic in some of the tule elk herds. Rocky Mountain elk averaged 6.8 alleles per locus and Roosevelt elk were intermediate with an average of 5.2.

The 16 loci did not show departures from Hardy–Weinberg equilibrium within analyzed counties or states after a Bonferroni correction. However, when data were pooled by subspecies, several loci departed from Hardy–Weinberg equilibrium. No loci deviated significantly from Hardy–Weinberg equilibrium in the 80 samples of Rocky Mountain elk, 6 loci deviated from Hardy–Weinberg equilibrium within the samples of tule elk, and 1 locus deviated significantly from Hardy–Weinberg equilibrium within the samples of Roosevelt elk.

Relationships among subspecies and populations (Table 2).—There were significant differences in allele frequencies among populations of tule elk. Exact tests of population differentiation yielded a *P*-value of <0.0002 and significance at all pairwise comparisons of the tule elk herds (1% level after Bonferroni corrections). The overall value of F_{ST} for the 5 populations of tule elk was 0.11.

Table 2.—Genetic distances among the 3 subspecies of elk (*Cervus elaphus*) in California and their populations. Data are presented for both the population and subspecific levels of comparison. Nei's standard genetic distance values are above the diagonal and F_{ST} values are below. Significance levels for pairwise tests are: *** $P = 0.001$, ** $P = 0.01$, and * $P = 0.05$ after a Bonferroni correction. The Oregon samples were collected from animals released into California from Oregon. Sample sizes for each population or herd are given in Fig. 1.

	Tule elk herds					Roosevelt elk populations			Rocky Mountain elk populations		Subspecies		
	Contra Costa	Inyo	Marin	Monterey	Solano	Del Norte	Humboldt	Oregon	Idaho	Nevada	Tule	Roosevelt	Rocky Mountain
Tule													
Contra Costa	—	0.03	0.12	0.03	0.07	0.49	0.64	0.42	0.46	0.62			
Inyo	0.06**	—	0.11	0.02	0.08	0.54	0.74	0.50	0.47	0.63			
Marin	0.19**	0.14**	—	0.10	0.08	0.42	0.61	0.34	0.37	0.45			
Monterey	0.07**	0.03**	0.13**	—	0.06	0.55	0.71	0.45	0.45	0.56			
Solano	0.12**	0.12**	0.10**	0.10**	—	0.41	0.59	0.39	0.39	0.53			
Roosevelt													
Del Norte	0.37**	0.33**	0.25**	0.34**	0.29**	—	0.18	0.09	0.31	0.53			
Humboldt	0.47**	0.42**	0.34**	0.42**	0.37**	0.12*	—	0.25	0.47	0.61			
Oregon	0.40**	0.37**	0.27**	0.37**	0.31**	0.06*	0.16*	—	0.17	0.31			
Rocky Mountain													
Idaho	0.33**	0.28**	0.21**	0.28**	0.27**	0.14**	0.19**	0.13**	—	0.09			
Nevada	0.38**	0.33**	0.25**	0.33**	0.31**	0.20**	0.24**	0.18**	0.03*	—			
Subspecies													
Tule											—	0.55	0.48
Roosevelt											0.30*	—	0.31
Rocky Mountain											0.28*	0.14*	—

Exact tests of population differentiation, as measured by allele frequencies, were highly significant ($P < 0.0002$) among populations of Roosevelt elk (Oregon and Humboldt and Del Norte counties) and among populations of Rocky Mountain elk (Nevada and Idaho). F_{ST} values among populations of Roosevelt elk ($F_{ST} = 0.096$) and between populations of Rocky Mountain elk ($F_{ST} = 0.03$) were less than those observed among herds of tule elk. Individual populations of Roosevelt and Rocky Mountain elk showed significant differentiation at the 5% nominal level after Bonferroni corrections.

Data from the 3 subspecies were analyzed as a whole and tested for population differentiation using subspecies as the source of variation (Table 2). A highly significant Exact test ($P < 0.0002$) suggested that there were greater differences in allele frequencies among the 3 subspecies than among populations or herds within any of the 3 subspecies. Pairwise tests of differentiation between the 3 subspecies were all significant at the 5% nominal level of significance after a Bonferroni correction. The AMOVA results (Table 3) indicated that the subspecies are well differentiated.

STRUCTURE yielded results, both in terms of K populations and $\Delta(K)$, that suggested the sampled elk are from 2 "populations": tule and Roosevelt–Rocky Mountain elk lineages. Although the likelihood values for $K = 1$–20 populations approached a maximum at $K = 3$ populations, the $\Delta(K)$ values spiked at $K = 2$ populations.

Subspecies clustered distinctly, with 100% bootstrap support between tule elk and the other 2 subspecies (Fig. 2). The node separating the 2 Rocky Mountain elk populations (Idaho and Nevada) from the other subspecies populations had a 94% level of bootstrap support.

Assignment testing.—All of the 367 samples presumptively categorized by wildlife managers as tule elk assigned correctly using both WHICHRUN and STRUCTURE (Table 4). STRUCTURE was slightly more accurate in assigning reference elk to their presumptive subspecies, although both programs yielded a very high success rate of correct assignment. Population assignment of Roosevelt and Rocky Mountain elk had a small error rate (<5%), which varied by analysis program. One presumptive Roosevelt elk collected from eastern Oregon (Bend, Oregon) was assigned to the Rocky Mountain subspecies with >3.0 log of odds score.

Assignment testing of individual elk using both STRUCTRE and WHICHRUN (Table 5) revealed that Modoc, Shasta, and Siskiyou counties were inhabited by Rocky Mountain, Roosevelt, and hybrid elk. The same individuals were identified as hybrids by both programs. The 5 individuals from the Tejon Ranch in Kern County were correctly assigned as Rocky Mountain elk. The 6 elk from Mendocino County consisted of 2 Roosevelt elk and 4 tule elk.

Table 3.—Analysis of molecular variance of 3 subspecies of elk (*Cervus elaphus*) in California using subspecies, populations within subspecies, and individuals as sources of variation. Samples were collected from 1997 through 2003.

Source of variation	*d.f.*	Sum of squares	Variance components	Percentage of variation (%)
Among subspecies	2	905.12	1.253 Va	24.18
Among populations within subspecies	7	319.94	0.3631 Vb	7.00
Within populations	1,170	4,174.93	3.568 Vc	68.81
Total	1,179	5,399.99	5.185	

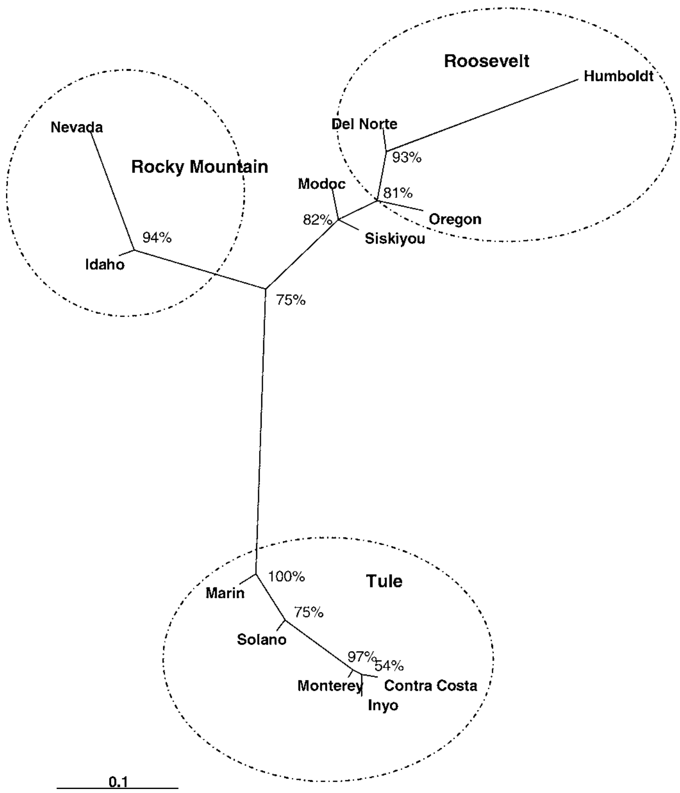

Fig. 2.—Unrooted tree of Nei's standard genetic distance after bootstrapping the data 1,000 times. The bootstrap level of support (out of 1,000) is indicated at each node. Included are all populations of elk with at least 20 samples.

Discussion

Tule elk have much reduced microsatellite variation compared to the Roosevelt and Rocky Mountain elk subspecies, as expected given the severe population bottleneck in the late 1800s. The low level of genetic variability in the tule elk was likely due to the low numbers of founders rather than insufficient sampling, because sampling collections were well distributed among herds. Thus, the molecular genetic uniqueness of the tule elk resulted from lack of genetic variation, not from novel genetic variability.

Tule elk may have been reduced to 1 breeding pair in 1874 (McCullough et al. 1996). Barring a mutation event or experimental error, the presence of 5 alleles at 1 locus requires that the tule elk subspecies was reduced to no fewer than 1 female and 2 males, or vice versa. Allele frequencies varied significantly among the herds of tule elk. The results also suggest that the herds in Contra Costa, Inyo, and Monterey counties were more closely related than the other 2 herds of tule elk; the Marin herd was the most distantly related. This also was reflected in the phylogenetic results (Fig. 2) and follows logically from historical information on relocations (McCullough et al. 1996). Because all tule elk originated from the same herd, founder effects and genetic drift likely caused the herds to diverge genetically in spite of relocation efforts.

Table 4.—Assignment test results for 3 subspecies of elk (*Cervus elaphus*) in California using programs WHICHRUN and STRUCTURE 2.1. The numbers of correct assignments are on the diagonal and incorrect assignment counts are off the diagonal for each program.

Software	Subspecies	*n*	Tule	Roosevelt	Rocky Mtn.
WHICHRUN	Tule	367	367	—	—
	Roosevelt	156	—	151	5
	Rocky Mountain	80	—	1	79
STRUCTURE 2.1	Tule	367	367	—	—
	Roosevelt	156	—	154	1
	Rocky Mountain	80	—	—	80

Table 5.—Assignment tests of elk from Modoc, Siskiyou, Shasta, and Kern counties, California, using programs WHICHRUN and STRUCTURE. Animals are noted as potential hybrids using WHICHRUN when the log of odds score of assignment was less than 1.0, and when the probability of assignment was less than 10 times the 2nd most probable subspecies using STRUCTURE.

	County			
Program	Modoc ($n = 20$)	Siskiyou ($n = 23$)	Shasta ($n = 7$)	Kern ($n = 5$)
WHICHRUN				
Roosevelt	9	15	1	0
Rocky Mountain	10	2	5	5
Hybrid	1	5	1	0
STRUCTURE 2.1				
Roosevelt	9	15	1	0
Rocky Mountain	10	2	5	5
Hybrid	1	5	1	0

Although tule elk do not currently display the effects of reduced fitness, such as low reproductive output and morphological deformities, the individual herds are definitely at risk if they remain genetically isolated. However, reduced genetic variation at neutral loci does not necessarily indicate a lack of adaptability (Hedrick 1999, 2001) and would not warrant intentional crossbreeding with Roosevelt or Rocky Mountain elk.

We propose the following management recommendations for tule elk given the genetic data and their life-history characteristics. Management of tule herds should continue to involve the movement of animals, preferably mature females, between the tule herds. Adult female elk would be much more likely to contribute genetically because of the harem mating structure, because an introduced male elk would likely have to establish dominance before breeding. Translocating elk among Inyo, Contra Costa, and Monterey counties should not negatively impact genetic diversity of these 3 herds, because they are closely related.

Periodic monitoring of the physical health and genetics of the tule herds is required in order to detect a rise in frequency of deleterious inherited phenotypes, reduced fitness, and other effects of inbreeding. Although the 6 elk samples from Mendocino County were either pure tule or pure Roosevelt and did not indicate crossbreeding, the elk in the Mendocino and Lake county areas should be monitored for hybridization. The tule and Roosevelt elk sampled were from 2 different locations and did not occur sympatrically. Tule elk in Mendocino County have recently been detected in close proximity to Roosevelt elk (R. Schaefer, in litt.). Introgression of Roosevelt elk into these tule herds should prohibit their use for future transplants.

The reproductive strategy of elk makes this species vulnerable to the loss of genetic diversity. Williams et al. (2002, 2004) applied theory and computer simulation to conclude that elk in small isolated herds tend to lose genetic variation and heterozygosity. The effect of small population size is magnified by the highly polygynous nature of elk, and even brief bottlenecks can have a large effect on the number of alleles and heterozygosity of species with this mating system.

The effects of a small population size on a mammal are well illustrated by research on Florida panthers (*Puma concolor coryi*). Hedrick (2001) suggested that populations that remain small over a long time period would incur a large genetic load from fixation of many deleterious alleles of small effect, as seen in the Florida panther. Even with an effective population size of 30–50, this subspecies of panther so rapidly accumulated deleterious alleles through drift and inbreeding that it was in serious danger of extinction (Hedrick 1995).

Population assignment for individual reference elk with known source populations using multilocus genotype data was concordant with source population records because of highly significant differences in allele frequencies observed between the subspecies. Two population assignment software programs, WHICHRUN and STRUCTURE, yielded nearly identical assignment accuracies. This high degree of accuracy is important from a forensic standpoint because tule elk are a heavily managed subspecies within California; recaptured escapees from game refuges and evidence from suspected cases of tule elk poaching now can be reliably identified to subspecies.

Elk present in the northern California counties of Modoc, Siskiyou, and Shasta are genetically Roosevelt elk, Rocky Mountain elk, or hybrids of these 2 subspecies. Thus, trophy elk taken by sportsmen from these counties cannot be reliably assigned to subspecies in the absence of molecular genetic information. The unique genetic character of Roosevelt elk from California merits careful monitoring of translocations of elk if new animals are moved into the existing herds in Humboldt and Del Norte counties from areas containing elk of mixed ancestry.

Our analyses lend strong support to previously published work suggesting that tule, Roosevelt, and Rocky Mountain elk should be designated as discrete subspecies (Polziehn et al. 1998, 2000; Polziehn and Strobeck 1998, 2002) and as evolutionarily significant units. Values of F_{ST} and log-likelihood values for tests of population differentiation were highly significant. AMOVA results indicated that the subspecies are well differentiated and gene flow has likely occurred among populations within the subspecies.

The criteria used for determining which populations comprise an evolutionarily significant unit have been the topic of considerable debate (i.e., Crandall et al. 2000; Fraser and Bernatchez 2001; Moritz 1994, 2002). We incorporated criteria from these studies and propose evolutionarily significant units for elk in California. Tule elk displayed highly significant differences in nuclear allele frequencies relative to other elk populations, consistent with the criteria of Waples (1991) and Moritz (1994, 2002). Given its unique ecological niche, evolutionarily significant unit status is warranted under the ''ecological exchangeability'' concept of Crandall et al. (2000).

We propose evolutionarily significant unit status for Roosevelt elk of the north coast of California (Humboldt and Del Norte counties). Again, significant genetic divergence was observed between this group and the other sampled populations. Because Roosevelt elk from the Olympic Peninsula in Washington State may have some Rocky Mountain introgression (Polziehn and Strobeck 2002), care (and perhaps genetic testing) is essential before translocating elk from the Olympic Peninsular to augment Roosevelt elk in other regions, including California.

Rocky Mountain elk are the least populous elk in California, although they exist in great numbers in the mountains of the western United States. They are genetically distinct from both the Roosevelt and tule elk and inhabit environments where the tule elk are absent. The only pure population of Rocky Mountain elk within California identified from this study occurs at Tejon Ranch (Kern County). These animals originally were imported from Yellowstone National Park, Wyoming. California Department of Fish and Game managers had expressed concern that these animals had bred with tule elk at 1 point in time; this concern appears unfounded. Rocky Mountain elk and tule elk are held at 2 physically separated ranches in Kern County. Although Rocky Mountain elk are sympatric with Roosevelt elk in northern California, their range extends beyond that of Roosevelt elk east into the Rocky Mountains. Elk taken from the counties containing hybrids should be genetically tested on an individual basis to determine the subspecies of their source. Polziehn et al. (2000) documented that population subdivision and restricted gene flow occurs in herds of Rocky Mountain elk, many of which were relocated or reintroduced. Considering that this subspecies covers a large geographic area, future studies covering larger geographic areas are likely to identify additional Rocky Mountain elk evolutionarily significant units.

To date, our study is the most comprehensive population genetic analysis of the 3 subspecies of elk inhabiting California and should provide valuable information for elk managers and wildlife law enforcement. Future conservation efforts should focus on ensuring connectivity between herds or populations within each evolutionarily significant unit to ensure that adaptive genetic variation is maintained in a large population and not removed by genetic drift or fixed by inbreeding in small isolated populations. Current population management efforts focus primarily on the protected tule elk, maintained as several distinct, isolated herds across the state. We recommend the continued translocation of tule elk between the herds in order to maintain the genetic diversity of the tule subspecies and avoid the potential inbreeding that can occur in small polygynous herds.

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Mount St. Helens Elk Population Assessment: 2009-2013

March 2014

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Mount St. Helens Elk Population Assessment:

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EXECUTIVE SUMMARY

In 2009, we initiated a study of the Mount St. Helens elk population to better quantify elk abundance, develop a practical and defensible population monitoring approach, and document recent trends in elk condition, productivity, and survival. During 2009-2012, we captured and radiomarked 150 unique elk aged ≥ 1-yr-old (110 F: 40 M) by helicopter darting in a 5-Game Management Unit (GMU) study area (GMUs 520, 522, 524, 550, and 556) in the core of the Mount St. Helens elk herd area. Among the issues motivating our work were episodic high overwinter elk mortality, recent evidence of sub-par condition among elk translocated to the North Cascades in 2003 and 2005, and apparent elk herbivory impacts on plant communities in the vicinity of Mount St. Helens. In response to these issues and concurrent with the initiation of our work, antlerless elk harvesting was liberalized across several GMUs to reduce local elk densities.

Using ultrasound examination and body condition scoring we estimated mean ingesta free body fat (IFBF) for elk we live captured in February, 2009-2012, was 5.64% (95% CI = 5.08-6.21) for non-lactaters and 3.26% (95% CI = 2.34-4.18) for lactaters. These levels suggest food limitation. We found that GMU, lactation status, and pregnancy status affected IFBF, but year did not. Overall, 73 of 109 cow elk (67%) we examined for pregnancy via ultrasound were pregnant. Pregnant elk had higher IFBF than did non-pregnant elk. We also used organ samples from 364 hunter-harvested cow elk to estimate fall (Nov) IFBF for elk in the Mount St. Helens herd, 2009-2011. We detected effects of geographic subarea and lactation status on IFBF, but not effects attributable to year or cow age. IFBF was higher for cow elk harvested in GMU 560 and Columbia Gorge GMUs than from the managed forest portion of our 5-GMU study area. We estimated mean IFBF during the fall at 12.51% for non-lactaters and 10.84% for lactaters, controlling for other factors.

We collected data during intensive late winter helicopter surveys (2 complete survey replicates yearly 2009-2012, 1 survey in 2013) over the 5-GMU study area. We used data from Mar-Apr flights, 2006-2007 to fit logistic regression models to predict the sightability of elk groups based on group and environmental covariates. Several covariates influenced sightability in univariate logistic regression models. We then used multi-model inference and an information-theoretic criterion (AIC_c) to compare several alternative multivariate models of varying complexity; our results indicated the best multivariate model predicted sightability of elk groups based on: 1) transformed (log_2) group size, and 2) forest canopy cover (%). Predicted sightability increased with increasing group size and with decreasing cover.

We also used the logit-normal mixed effects (LNME) mark-resight model to generate estimates (2009-2012) of total elk population size and the sizes of the cow and branch-antlered bull subpopulations at a variety of spatial scales. We explored 11 LNME models to estimate total population size, 10 models to estimate total subpopulation sizes for cow elk and branch-antlered bulls, and 15 models to estimate GMU-specific estimates of cow elk abundance. We also used the Lincoln-Petersen model to generate mark-resight estimates for total population size and total cow elk subpopulation size for 2013 using data from the single survey conducted that year. We again used multi-model inference and AIC_c to evaluate the evidence in our data for the various models in our LNME model sets.

Sightability model estimates appeared to underestimate true abundance, relative to LNME estimates. This result is common and relates to how the 2 types of models account for undetected elk. Mark-resight models are virtually always more effective at accounting for such animals. However, trend estimates from the 2 modeling approaches were relatively congruent and time-specific estimates from both approaches were highly correlated, suggesting that sightability model estimates, although biased low, provided a useful and consistent abundance index. The application of a sightability modeling approach is a much more practical strategy, relative to mark-resight, for large-geographic-scale monitoring such as is needed for elk at Mount St. Helens.

Sightability model and LNME mark-resight estimates, 2009-2013, suggested a decline in overall elk abundance and cow elk abundance; bull abundance estimates indicated a relatively stable bull population. We found evidence of strong spatial variation in the decline in overall elk abundance and cow elk abundance. Estimates indicated substantial a reduction in elk abundance in GMUs 520, 524, and 550. We did not detect any decline in GMU 522 elk abundance, nor in GMU 556 abundance; however, estimated elk abundance in GMU 556 during the last survey year that we report on, spring 2013, was the lowest we recorded across the 5 years of data from GMU 556. Across our individual counting units, the units the furthest west showed the most consistent and dramatic declines in raw elk counts; units further east in the same GMUs produced more stable counts.

For virtually every geographic scale of abundance estimates for total elk and total cow elk, the 2013 point estimate was the lowest estimate obtained 2009-2013, except for GMU 522 estimates. For total elk and total cow elk across the 4-GMU landscape (excluding GMU 522), 2013 estimated abundance was on the order of 30-35% lower than the 2009 estimates. GMU-specific sightability model estimates of total elk and total cow elk abundance were on the order of 60-70% lower in 2013 than in 2009 for GMUs 520 and 550, were ~40-60% lower for GMU 524, and were ~20-25% lower for GMU 556.

We also used radiomarked elk to estimate survival rates and explore possible sources of variation in survival. We explored 15 survival models with known-fate modeling using AIC_c and model weights to draw conclusions about Mount St. Helens elk survival during 2009-2013 (4 survival years). The best model had a common cow survival parameter for GMUs 520, 522, 524, and 556 that was constant during 2009-2011, a common cow survival parameter for all GMUs during the last survival year (2012-2013), a unique survival parameter for GMU 550 cows during 2009-2011, and constant bull survival across years. Bull elk survival was estimated to be 0.56 (95% CI = 0.43-0.68). Annual cow survival was estimated to be 0.85 (95% CI = 0.78-0.91) during 2009-2011 in GMUs 520, 522, 524, and 556. During the same years, cow survival was estimated at 0.64 (95% CI = 0.48-0.78) in GMU 550. Cow survival in the final survival year (2012-2013) was estimated to be 0.52 (95% CI = 0.38-0.65) across all 5 GMUs. Low survival of radiomarked elk, 2012-2013, corresponded to a fairly high number of unmarked, winter-killed elk (n= 71) tallied during the annual mortality survey on the mudflow. During the previous 3 years, the annual winter mortality survey yielded tallies ranging 2-46 elk.

Spring calf recruitment varied considerably during 2009-2013. Calf:cow ratios exceeded 35:100 during 2010 and 2011. Calf recruitment was lower in the spring of 2009 and much lower in 2012, 2013. Overall, observed estimates were in the 25-30:100 range for the study area and in the 25-35:100 range for most GMU-specific estimates. After attempting to correct the observed ratios for fall removals of antlerless elk via hunter harvest, calf recruitment was indexed mostly in the high teens to 100 cows range for 2012, 2013 and in the 20-30-ish calves per 100 cows in 2009. Indexed recruitment in spring 2013 was the lowest—compared to other study years—for almost all GMUs. Depressed calf recruitment in the spring of 2013 corresponded to high mortality among radiomarked elk that same year, high observed overwinter mortality of unmarked elk, and elk abundance estimates that were also low.

Spring calf recruitment, 2009-2013, was strongly related to late summer-fall precipitation metrics (r^2 = 0.91-0.96); calf recruitment was higher in years with significant late summer-fall moisture, presumably because of enhanced forage production/quality during the time when calf elk are becoming increasingly dependent on foraging. Overwinter elk mortality, as indexed by the annual mortality survey on the mudflow, was strongly related (r^2 = 0.90) to a metric reflecting daily snowpack during mid-to-late winter; in years with substantial late winter snowpack, overwinter mortality was higher than in years with milder winter conditions.

Collectively, our estimates of elk condition, productivity, and survival indicated fairly strong food limitation in this population that may have been a function of elk density. Attempts to reduce the elk population via liberalized hunter harvest beginning in 2007 were apparently successful, based on our estimates of elk abundance. However, links between weather covariates and recruitment and survival, coupled with a substantive overwinter mortality event, 2012-2013, suggest that reducing the elk density has not eliminated the risks of overwinter mortality, at least in the short-term. It is likely that plant community responses to lower elk herbivory are still evolving and benefits likely will take some time to be fully realized. We discuss the implications of both density-dependent and density-independent influences on elk demography and management in the Mount St. Helens elk herd. Our work did not address issues surrounding elk hoof disease, as these issues were beyond our research scope. The role of hoof disease in elk population processes at Mount St. Helens remains unclear, as does the degree that the condition's presence will complicate meeting management objectives.

INTRODUCTION

The Mount St. Helens elk herd is the largest of 10 formally recognized elk herds in Washington (Washington Department of Fish and Wildlife 2008). The herd occupies a large and diverse area of lowland and mid-elevation forest, interspersed with floodplains and valley bottoms in the southwestern part of the state. The herd name derives from the presence of the Mount St. Helens volcano, located near the center of the herd area. The volcanic eruption on May 18, 1980 devastated a large area occupied by elk, killing most elk in this impacted zone. Subsequently, as habitat recovery and restoration occurred, elk recolonized most of the area affected by the eruption (Merrill et al. 1987). This elk herd provides considerable elk-centered recreation, including elk hunting and wildlife-viewing. Because of the herd's history, because of the tourist appeal of the volcano, and because the herd area is bordered by developed corridors with sizable metropolitan populations, the Mount St. Helens elk herd is a high profile herd, featured often in local news media.

Over approximately the last 3 decades, elk habitat in areas affected by the 1980 eruption has evolved considerably, and the landscape carrying capacity for elk has been dynamic. Forage availability for elk appears to have peaked in the mid-to-late 1980s when early seral habitat was abundant and began to decline rapidly about the late 1990s as closed canopy forest conditions advanced. As habitat changed, indications that the elk herd was becoming increasingly food-limited became evident. Among the most dramatic indicators of the change in elk habitat quality, was the appearance of substantial episodic winter mortality events that began in the late 1990s and widespread evidence of strong herbivory effects on plant communities used by elk. The winter mortality events were most apparent on the floodplain of the North Fork of the Toutle River, an area that remains substantially impacted by the 1980 volcanic lahar.

For elk management to be appropriately responsive to dynamics in the availability and quality of elk habitat requires: defensible information on elk abundance, a fundamental understanding of basic elk vital rates (*i.e*., mortality and productivity) and how these are affected by habitat dynamics, and how systematic changes in habitat structure and composition affect the spatial and temporal availability of elk habitat components, especially forage. Historically, surveys of elk at Mount St. Helens were focused on generating ratio data (calves:100 cows and bulls:100 cows) to monitor juvenile recruitment and bull harvest effects. Previous efforts to use these data to model elk abundance were largely unsuccessful (Miller and McCorquodale 2006). Data on Mount St. Helens elk vital rates are available from the recolonization phase dating to the 1980s (Merrill et al. 1987), but more recent estimates of elk vital rates were lacking as of the mid-2000s. In light of these data limitations, we undertook a study in 2009 to: *1) develop a practical approach to monitoring Mount St. Helens' elk abundance; 2) generate defensible estimates (or indices) of recent and current elk abundance; and 3) evaluate physical condition and vital rates of a representative sample of elk from the population*.

Our efforts focused on a subarea of the core herd range where habitat dynamics have been the most dramatic in the last 3 decades and where periodic overwinter elk mortality has been prevalent. Our work did not directly focus on documenting habitat conditions, forage availability, or herbivory because concurrent work by the Weyerhaeuser Company, researchers with the National Council for Air and Stream Improvement, and a graduate student at the University of Alberta were concurrently researching these issues.

STUDY AREA AND BACKGROUND

The Mount St. Helens elk herd area covers much of southwest Washington, east of Interstate 5 (Fig. 1), and during our work, consisted of 14 Game Management Units (GMUs) defining 5 Population Management Units (PMUs). This large area ($\approx$ 4,710 mi^2) extends north to south from almost south Puget Sound to the Columbia River Gorge and west to east from I-5 to US Highway 97 (more than 40 miles east of the Cascade Crest). The scale of the defined herd area made it impractical to serve as a formal study area, so we selected a 5 GMU core area as our study area; the GMUs we selected were: Winston (GMU 520), Loowit (GMU 522), Margaret (GMU 524), Coweeman (GMU 550), and Toutle (GMU 556) (Fig. 1). These GMUs represent a large swath of the herd's core range, including an extensive area of industrial and state-

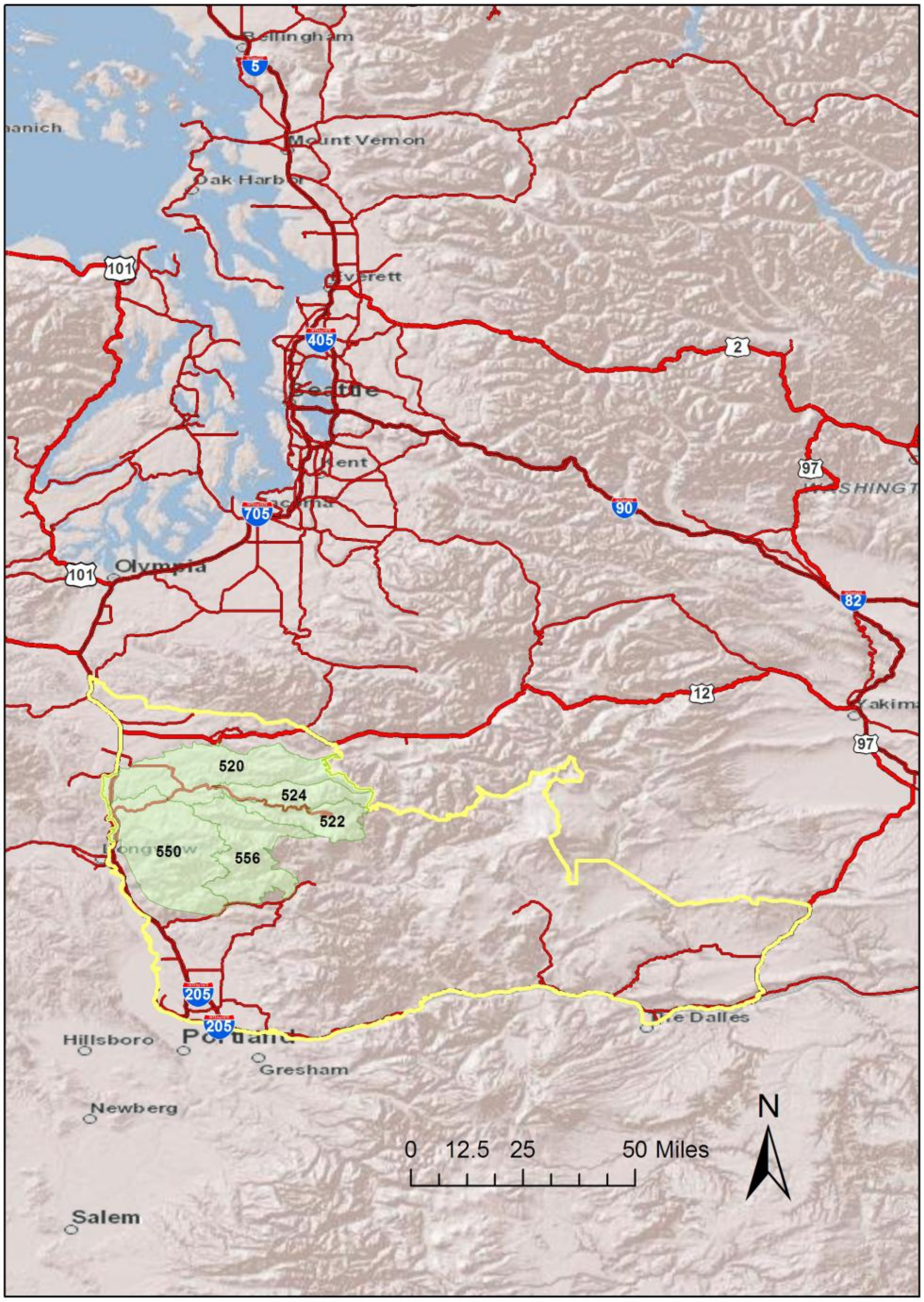


Figure 1. Map of the Mount St. Helens elk herd area (yellow outline) and the core study area (green shaded, with GMU numbers).

managed forest, as well as that part of the landscape still impacted by the 1980 eruption of the volcano (North Fork of the Toutle River and the Mount St. Helens National Volcanic Monument). This area has historically supported the highest elk density, much of the historic recreational elk hunting, and includes the area presenting the most complex management challenges (*e.g.*, hunter access, elk effects on industrial forestry and plant succession, and episodic winter elk mortality on the mudflow). The exception to this spatial extent for our work was for fall sampling of organs from hunter-killed elk (see Methods below); we solicited and analyzed organ samples from additional GMUs within the herd area boundary (*i.e.*, the Columbia Gorge and Cascade GMUs).

Physiographically, most of the herd area is within the Southern Washington Cascade Province, except for the western-most portion, which is within the Puget Trough Province (Franklin and Dyrness 1973). Elevations within the study area ranged from approximately 6 meters above mean sea level (AMSL) to 2,535 meters AMSL at the crest of the volcano. The western portion of the study area consisted of relatively flat and gently rolling terrain, whereas steep, rugged topography characterized the eastern portion. Historically, the area was covered by dense coniferous forests, but urban, suburban, and agricultural development has converted much of the lowland area into a relatively open landscape. Most of the upland foothills and mountainous terrain remain dominated by coniferous forest, much of it managed for commercial timber products. Three major forest zones occur in the study area: the western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), and mountain hemlock (*Tsuga mertensiana*) zones (Franklin and Dyrness 1973). Douglas-fir (*Pseudotsuga menziesii*) is a naturally occurring co-dominant tree in the western hemlock zone, and is typically promoted in second growth forests because of the high commercial value of this fast-growing conifer. Timber harvest on industrial lands and some state lands has historically been by clearcutting. Forest management has produced a distinctive and extensive mosaic of recent clearcuts and second growth stands of various ages.

The Mount St. Helens elk herd area was dramatically transformed by the May 18, 1980 volcanic eruption that impacted 600 km^2 of the area north, northeast, and northwest of the crater. The eruption killed an extensive area of conifer forest and resulted in extensive (c. 4 billion board feet) blow-down (Frenzen and Crisafulli 1990, Franklin et al. 1995). Ash, debris, and/or mudflow covered much of the blast zone initially, but vegetative recovery in less-impacted areas proceeded rapidly. However, natural recovery has been slow and incomplete in areas nearest the crater and along the North Fork of the Toutle River (Wood and Del Moral 1988, Del Moral and Wood 1988, Del Moral and Wood 1993, Del Moral 1998, Lawrence and Ripple 2000). The principal industrial forest landowner, Weyerhaeuser, was substantially impacted by the eruption due to widespread loss of high value timber. Subsequently, the company invested extensively in salvage logging and reforestation to restore its lands to production.

In the nearly 30 years between the eruption in 1980 and the beginning of our study in 2009, much of the impacted landscape has returned to the typical appearance of a western Washington managed forest landscape, with little evidence of the 1980 cataclysm. Much of this recovery was promoted by active forest management (Franklin et al. 1995). However, dramatic evidence of the eruption is still visible on the highly erosive North Fork of the Toutle River, where a large matrix of rock, gravel, and ash covers much of the floodplain, with patchy "islands" of meadow-like prairie and stands of pioneering red alder (*Alnus rubra*) interspersed. The headwaters of the North Fork, the pumice plain, and the flanks of the crater have remained largely untouched by post-eruption management and still bear evidence of the devastation that occurred in 1980. This area has been allowed to recover under natural processes, and in 1982, 445 km^2 were federally designated as the Mount St. Helens National Volcanic Monument, which is administered by the U. S. Forest Service. Some limited recreation occurs within the monument, but the natural character of the area is emphasized and protected as a management priority.

The climate of the study area is Pacific maritime, with cool, wet winters and relatively dry summers. Annual precipitation has typically ranged 160-400 cm (63-157 inches) in recent decades, with most of the annual precipitation falling between October and April. Winter snowfall is common, varies considerably across years, and at higher elevations persists for much of the winter (Fig. 2). During and just previous to our study, cumulative daily snow depth at the Spirit Lake SNOTEL site (1,067 meters; USDA Natural Resources Conservation Service) was greatest for December 2007 and December 2012, intermediate in December 2008 and 2010, and lowest in December 2009 and December 2011 (Fig. 3). By March, cumulative daily snow depth was greatest in 2008, intermediate in 2009, 2011, 2012, and 2013, and lowest in 2010. Winter 2009-2010 was very snow-free compared to the other winters at the Spirit Lake site (Fig. 3). At a lower elevation (648 m) SNOTEL site (Pepper Creek) just south of the study area, cumulative daily snow depth in December was greatest in December 2007 and 2008, intermediate in December 2010 and 2012, and lowest in December 2009 and 2011 (Fig. 3). By March, cumulative daily snow depth at this lower site was greatest in 2008, slightly lower in 2009, intermediate in 2011, 2012, and 2013, and lowest in 2010 (Fig. 3). At the Pepper Creek SNOTEL site, the winter of 2009-2010 had little accumulated snow, whereas the winter of 2007-2008 was severe relative to snowfall.

Figure 2. Winter snowfall was common in the study area and often persisted for several months in the higher elevation portions of the elk range each year.

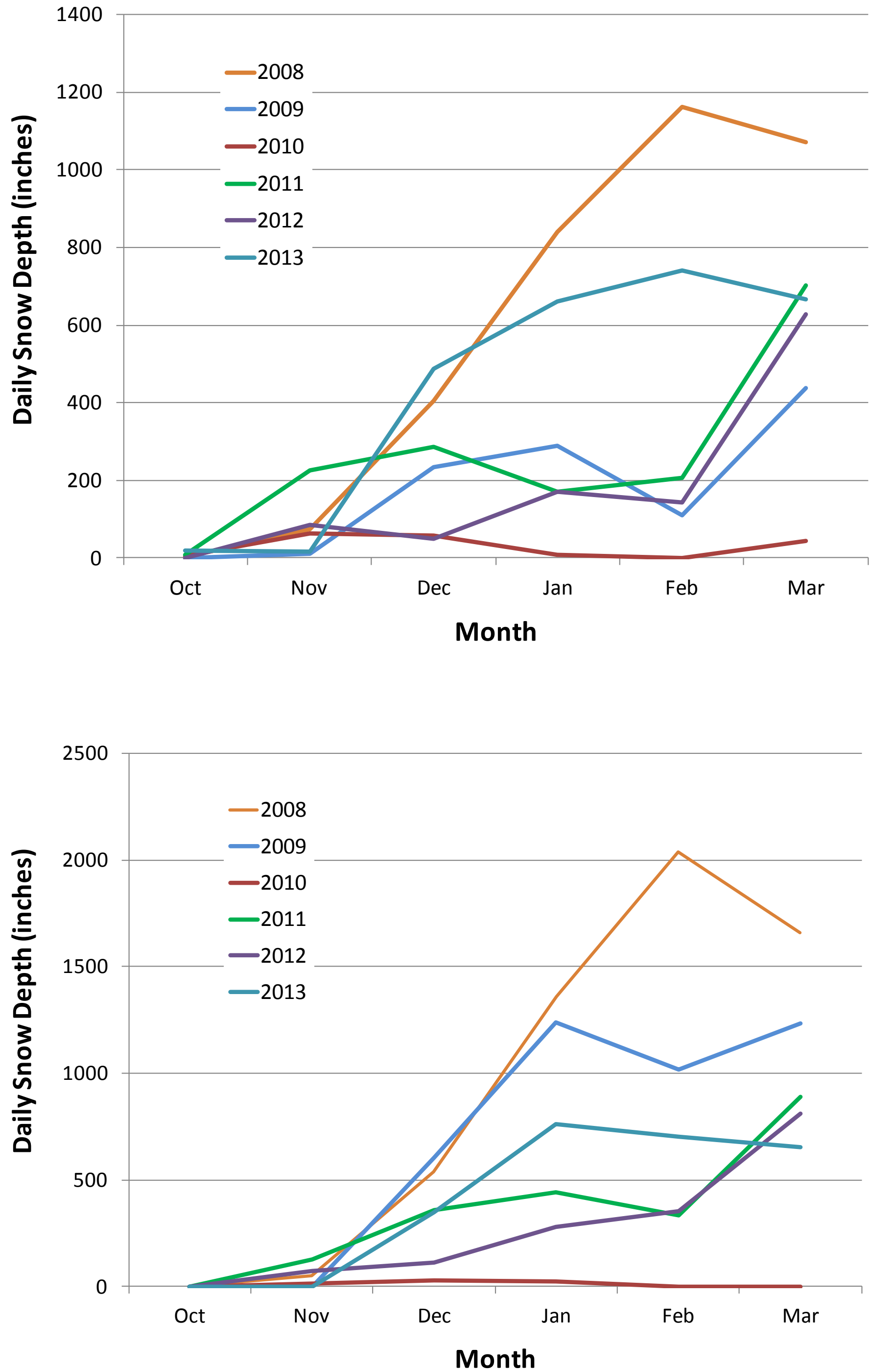


Figure 3. Cumulative daily snow depth (by month) for water years 2008-2013, from the Spirit Lake (upper panel; elevation = 1,067 m) and Pepper Creek (lower panel; elevation = 648 m) SNOTEL sites. A water year spans October 1 – September 30, and is labeled by the calendar year in which it ends.

Spring/summer/early fall precipitation, measured at the Spirit Lake SNOTEL site, was greatest in 2010 and 2012, lowest in 2007 (just prior to our study), and intermediate in all other years (Fig. 4). Early fall precipitation occurred in most years, but was largely absent in 2012 and minimal in 2011 (Fig. 4). Not only was 2010 the wettest summer, it was also the wettest fall, evidenced by the slope of the late August to mid-September cumulative precipitation line (Fig. 4).

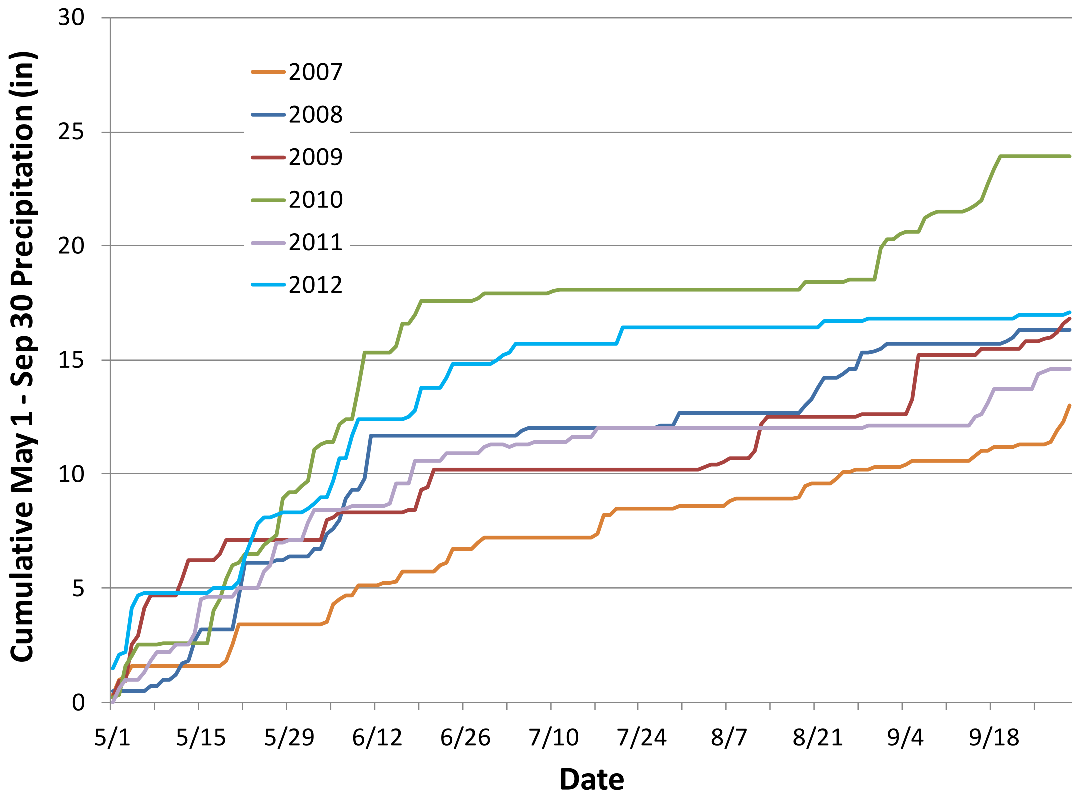


Figure 4. Cumulative spring-summer precipitation measured at the Spirit Lake SNOTEL site (elevation = 1,067 m), 2007-2012.

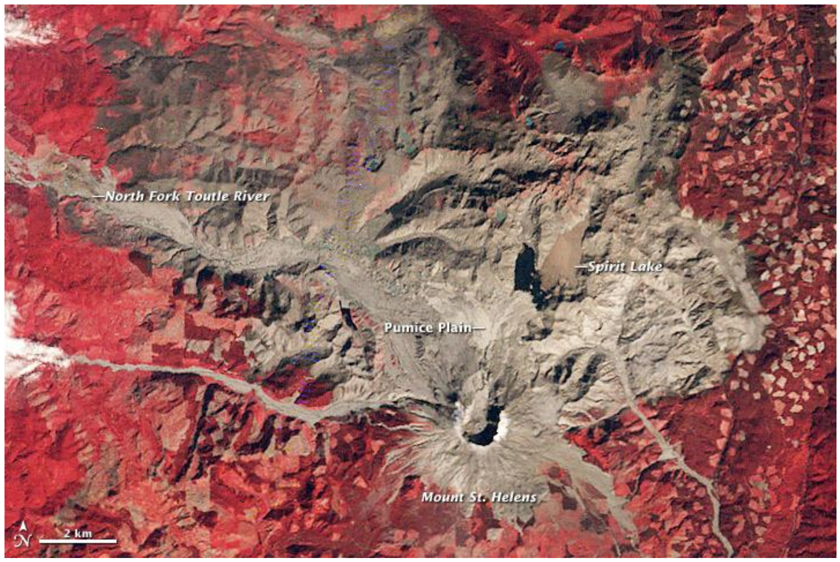
Land ownership in the Mount St. Helens elk herd area is relatively evenly split between public and private ownership (Miller and McCorquodale 2006). Much of the forested eastern portion of the area is federally managed as part of the Gifford Pinchot National Forest and includes several formally designated wilderness areas. WDFW and the Washington Department of Natural Resources (WDNR) also own and manage lands within the herd area. Large tracts of industrial forest dominate the western portion of the herd area occupied by elk; the Weyerhaeuser Company manages the largest area of corporate forest. The developed portions of the landscape (*e.g.*, valley floodplains, populated corridors along Interstate 5 and the Columbia Gorge, agricultural lands) are also in private ownership. Our core study area mostly encompassed corporate forest land, but included small tracts of WDFW and WDNR lands, as well as very small parcels of other private land. The only federal land within our core study area was the Mount St. Helens National Volcanic Monument tract.

Elk Habitat

Prior to the 1980 eruption, elk habitat in the western half of the Mount St. Helens elk herd area was typical of western Washington elk habitat. Early seral habitat, preferred by foraging elk, was maintained principally by clearcut logging on private, state, and federal forests (Witmer et al. 1985). Forest management created a diverse mosaic of stand ages that served to maintain quality elk habitat at both small and large scales throughout this region (Starkey et al. 1982, Witmer et al. 1985, Jenkins and Starkey 1996). Simulation modeling suggested forage availability for elk likely peaked in the 1960s region-wide and declined through the 1970s and 1980s based on forest harvest patterns (Jenkins and Starkey 1996), but forage availability for elk at the end of this time series was still likely higher than it had been in the first half of the 20th century.

The volcanic eruption altered the habitat mosaic for elk by killing vegetation in virtually all stands, regardless of age, and across habitats in about 600 km^2 of southwest Washington (Fig. 5). As previously described, in the 30 years between the eruption and the beginning of our study, the managed forest mosaic was largely recreated on the landscape (Fig. 5), albeit with a truncated distribution of stand ages in the original blast zone.

The regional dynamics of elk habitat values have also been strongly affected by forest management policy across ownerships in recent decades. An emphasis on conservation of older forest conditions on federal lands led to a dramatic decline in timber harvesting about 1991 on national forests in western Washington and Oregon, with a resultant decline in the availability of early seral stands important to elk on federal forests (Hett et al. 1978, Salwasser et al. 1993, Adams and Latta 2007). Since that time, the creation and maintenance of early seral elk habitat at larger scales has been largely limited to privately owned forests of the region (Adams and Latta 2007) (Fig. 6).



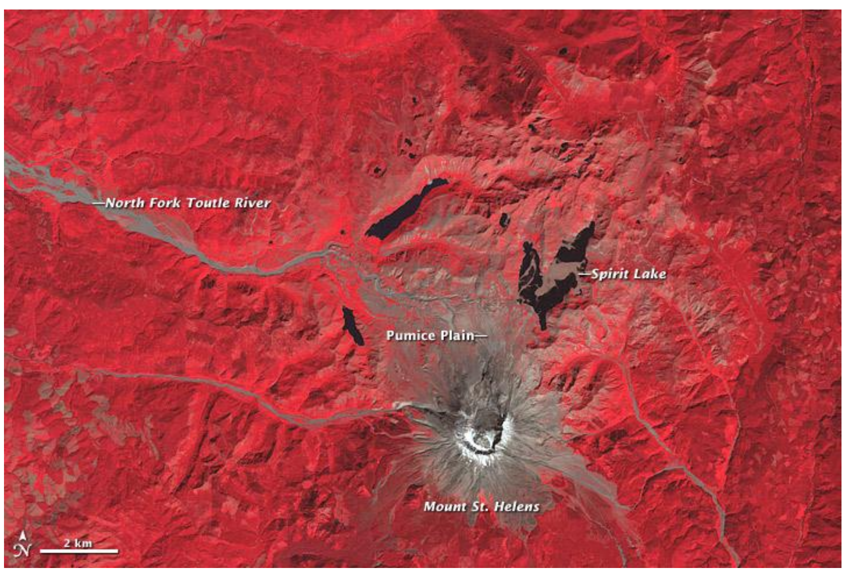


Figure 5. Infrared satellite images of the Mount St. Helens vicinity early post-eruption (top image, 1980), and nearly 30 years post-eruption (bottom image, 2009). In these images, vegetated areas (*e.g.*, forest, grassland, vegetated clearcuts) are red/pink, and bare ground, ash, mudflow, etc. are gray/brown (images courtesy of NASA's Earth Observatory Program).

Figure 6. Typical corporately managed elk habitat mosaic within the core study area (GMU 550 [left] and GMU 556 [right]).

Overwinter Elk Mortality

Since the spring of 1999, the Washington Department of Fish and Wildlife has conducted a winter elk mortality survey on about 4 km^2 of the floodplain of the North Fork of the Toutle River where substantial overwinter mortality has been periodically observed. This survey is conducted about late April each year and consists of a team of approximately 30-40 WDFW staff and volunteers walking transects through the entire sampling area, which consists mostly of the WDFW-owned Mount St. Helens Wildlife Area. The survey is used to provide an *index* of annual overwinter elk mortality, not an *estimate* of total overwinter mortality, given the limited spatial extent of the survey. During the survey, elk mortalities observed are examined for approximate death timing (recent [days old] vs. older [weeks to months old]), a femur is sectioned to document bone marrow condition (white and firm, red and runny, or desiccated), and GPS coordinates are taken to geospatially reference the site. The cumulative GPS dataset, as well as the presence or absence of cut femurs, is used to discriminate current year mortalities from those dating to a previous year.

The numbers of winterkilled elk observed during the annual transect survey has varied considerably across years (0-158) (Fig. 7). The highest count (*n* = 158) occurred at the end of the winter prior to our study (April 2008). During our study, winterkilled elk were detected each year; very few mortalities (*n* = 2) were tallied in spring 2010, but numerous dead elk were detected in most other years. In 2013, the 71 winterkilled elk detected was the third highest count observed since the surveys began in 1999.

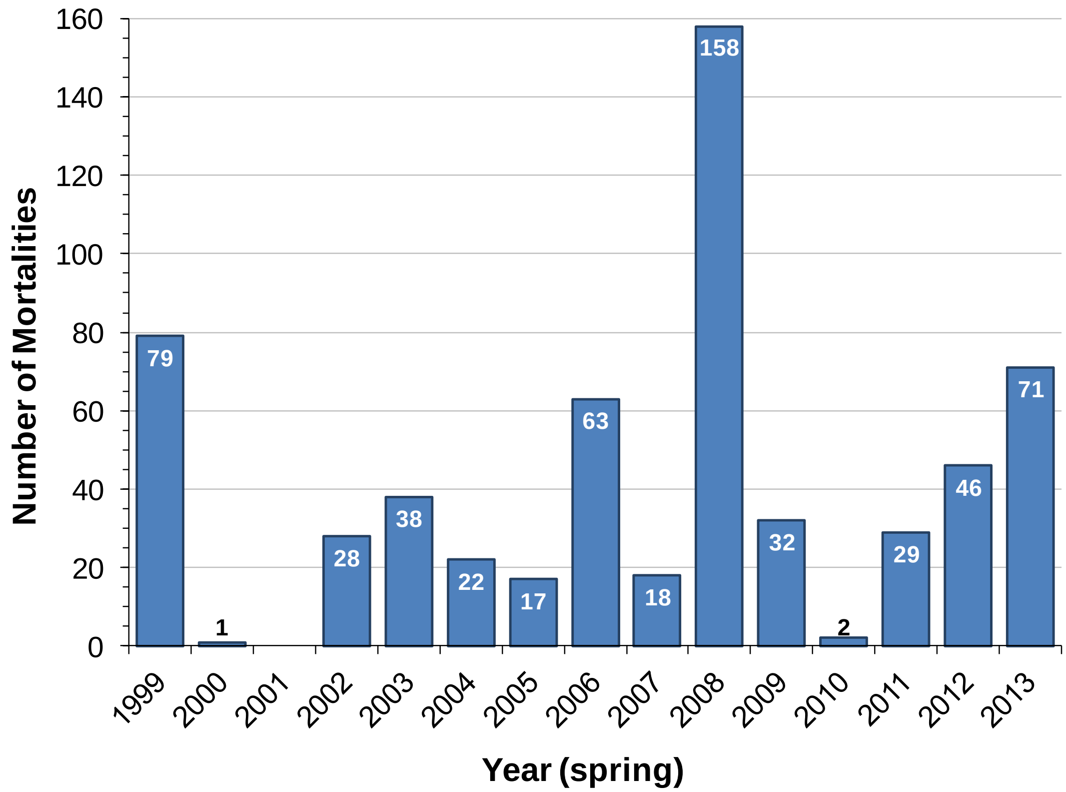


Figure 7. Number of current year overwinter elk mortalities tallied during the annual mortality survey on the Mount St. Helens Wildlife Area, April 1999-2013.

Elk Population Management

The management history for the Mount St. Helens elk herd has been documented in detail in the Mount St. Helens Elk Herd Plan (Miller and McCorquodale 2006), including season structures, season lengths, and hunter participation levels, by GMU, in recent decades. As is typical in elk management, most recreational hunting opportunity has historically been supported by bull elk general seasons in the Mount St. Helens elk herd area. A variety of season structures have been used to manage the general bull harvest, including any bull seasons, spike-only seasons, and ≥ 3-point seasons, across years and across GMUs. To support a diversity of hunting experiences, some GMUs in the Mount St. Helens herd area have been periodically designated as permit-only elk units with no general season elk hunting.

During our study, general bull seasons (≥ 3-point) were in place in GMUs 520 and 550. Permit only seasons governed bull elk hunting in GMUs 522, 524, and 556. Also during our study, all antlerless elk hunting was by permit only seasons across our study area GMUs, except that general antlerless elk seasons for archery hunters existed in GMUs 520 and 550. Density manipulation in elk populations is typically accomplished by varying the numbers of antlerless elk permits to achieve a desired cow elk harvest. During the period from the post-eruption, elk recolonization through the mid-2000s, antlerless elk hunting in the core GMUs of the Mount St. Helens herd was managed fairly conservatively to promote population stability and/or growth, outside of areas where elk damage issues existed. In response to the overwinter elk mortality issue, however, antlerless elk permits were liberalized in 2007, and even further liberalized in 2011 (Fig. 8), to reduce the local elk density and bring it into better balance with available habitat in the herd's core GMUs (Miller and McCorquodale 2006). The liberalization of antlerless elk permitting, 2007-2012, yielded the intended increase in antlerless elk harvest (Fig. 9). Qualitatively, the elk antlerless harvest, 2004-2012, has the same step-like appearance as the antlerless elk permit levels did during the same timeframe (Figs. 8, 9), with increased harvest of antlerless elk occurring each time permit levels increased.

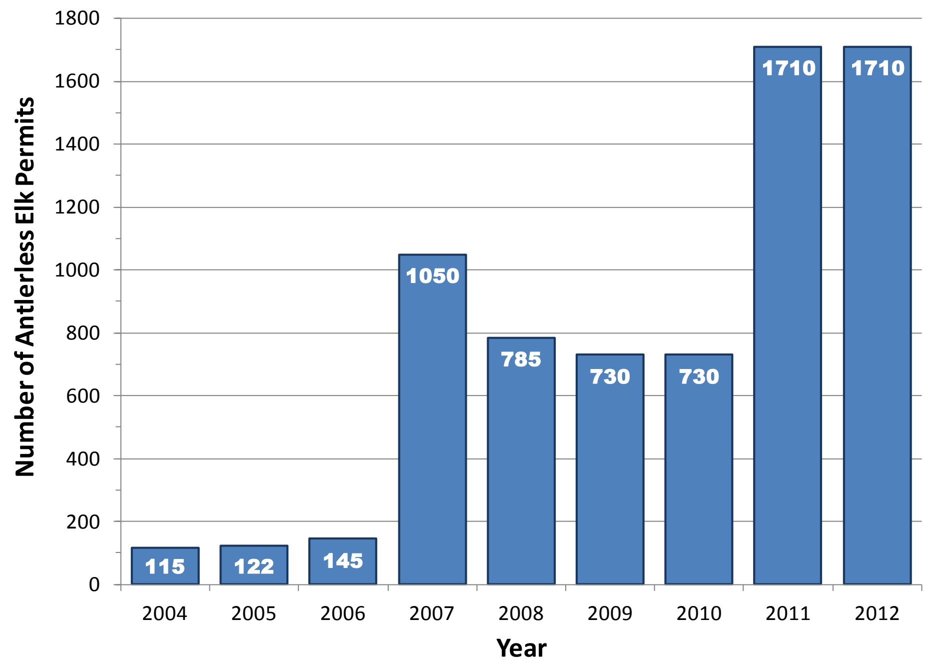


Figure 8. Numbers of antlerless elk permits issued, 2004-2012, for GMUs 520, 522, 524, 550, and 556, collectively.

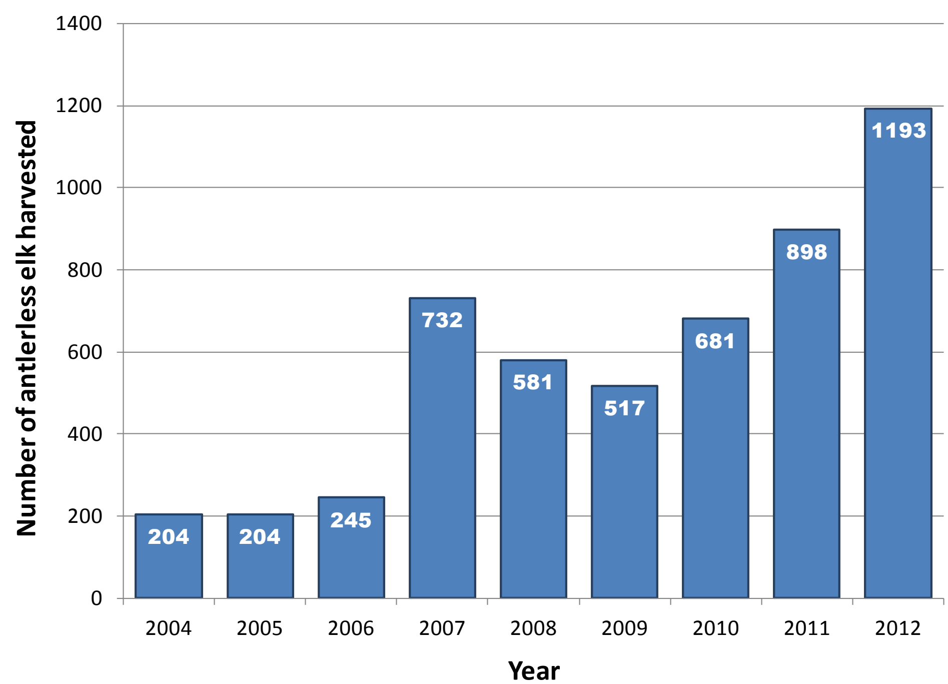


Figure 9. Numbers of antlerless elk killed, 2004-2012, in GMUs 520, 522, 524, 550, and 556, collectively.

METHODS

Marking and Handling

We captured adult and yearling cow elk and branch-antlered bull elk by darting them with a carfentanil citrate / xylazine hydrochloride mixture from a Bell 206 Jet Ranger helicopter. Captures occurred in February each year, 2009-2012. We ear-tagged elk we captured with colored and numbered plastic livestock tags. We fit most elk with 148-150 MHz, Very High Frequency (VHF) radiocollars (Telonics [Mesa, Arizona, USA]), but some received GPS-equipped radiocollars (Telonics or Lotek [Newmarket, Ontario, Canada]). All radiocollars had motion detectors that served as mortality beacons. We extracted a single vestigial upper canine from each elk to estimate age via cementum annuli analysis (Matson's Lab, Milltown, MT, USA), and we gave each elk a short-acting, prophylactic injection of penicillin, banamine, and an anti-clostridial to reduce risks of post-capture complications, such as dart wound infections. We also measured each elk's chest girth with a flexible tape measure to later estimate body mass. After handling, we reawakened immobilized elk via injections of the narcotic reversal, naltrexone hydrochloride and the xylazine reversal, yohimbine hydrochloride. After we administered reversal drugs, elk were generally alert and ambulatory within 1-7 minutes.

Body Condition and Reproduction

We estimated late winter (mid-February) ingesta-free body fat (IFBF) percentage from data we collected for adult cow elk during each capture event. We collected data and generated IFBF estimates following Cook et al. (2010). The basic data were: 1) body mass (kg; estimated via chest girth), 2) maximum subcutaneous rump fat depth (cm; measured using a portable ultrasound unit), and 3) a palpated body condition score (BCS = 0-5) measured at the rump (*i.e.*, prominence of sacral ridge and prominence of the sacro-sciatic ligament) (Cook et al. 2010). We also determined pregnancy status for each captured cow elk via ultrasound and visually examined and palpated each elk's udder to verify their lactation status: non-lactater (dry), true lactater (milk), or post-lactater (clear fluid).

We also quantified yearling and adult cow elk body condition during fall, 2009-2011, using modified Kistner subset scoring (Kistner et al. 1980, Cook et al. 2001*b*) applied to internal organs collected from hunter-killed elk. We visually scored (*i.e.*, 1-20) the extent of organ fat deposition associated with the heart, pericardium, and kidneys (Fig. 10) using standardized reference photos and calculated an estimated IFBF for each sampled cow elk using the equations of Cook et al. (2001*b*). We solicited these organs from antlerless-elk permit holders each year via mail requests and field contacts; hunters were asked to deposit organ samples at several collection stations we established each fall across our study area. Hunters were also asked to submit 2 middle incisors from their harvested elk for age determination via cementum annuli examination (Matson's Lab, Milltown, MT); they were also asked to report observed lactation status (*i.e.*, udder was dry, had milk, or had clear fluid). Organ samples were frozen promptly after field retrieval for subsequent scoring each winter at the Cowlitz Wildlife Area Headquarters. Scoring was done each year on a single day using a team-scoring approach to maximize scoring consistency within and across years.

Figure 10. Elk organs from hunter-harvested cow elk used to estimate fall body fat (%IFBF) for Mount St. Helens elk, 2009-2011 (left to right: pericardium, heart, kidneys).

Sightability-Correction Modeling

We developed and evaluated sightability correction models for late winter-early spring helicopter surveys in our 5-GMU core study area by collecting data from sighted and unsighted groups of radiomarked elk, Mar-Apr 2009-2011. We initially delineated 19 sampling units that were 16.8-62.7 (mean = 31.0) km^2 (Fig. 11). We selected sampling unit sizes such that a unit could generally be flown without having to refuel the helicopter, except for the mudflow unit (GMU 522). Two units never contained a radiomarked elk and also yielded very few unmarked elk observations, so we rarely flew these units because of a low benefit-to-cost ratio. For all other units, we flew each twice per winter during weeklong survey periods that were separated by 1-2 weeks, providing spatial and temporal replication.

We verified the distribution of radiomarked elk among our sampling units prior to a survey by flying just off the perimeter of each unit with the telemetry-equipped survey helicopter, being careful to not gain specific information about the location of elk within the units. Crews conducted initial visual surveys and telemetry-assisted follow-up in each sampling unit from a *Bell 206 Jet Ranger* helicopter. The crew of the survey helicopter generally had information on the distribution of radiomarked elk among counting units, but did not know the exact locations of these elk. We flew adjacent units consecutively where movement of elk across sampling unit boundaries was anticipated, based on previous telemetry data. The helicopter crew consisted of the pilot and 3

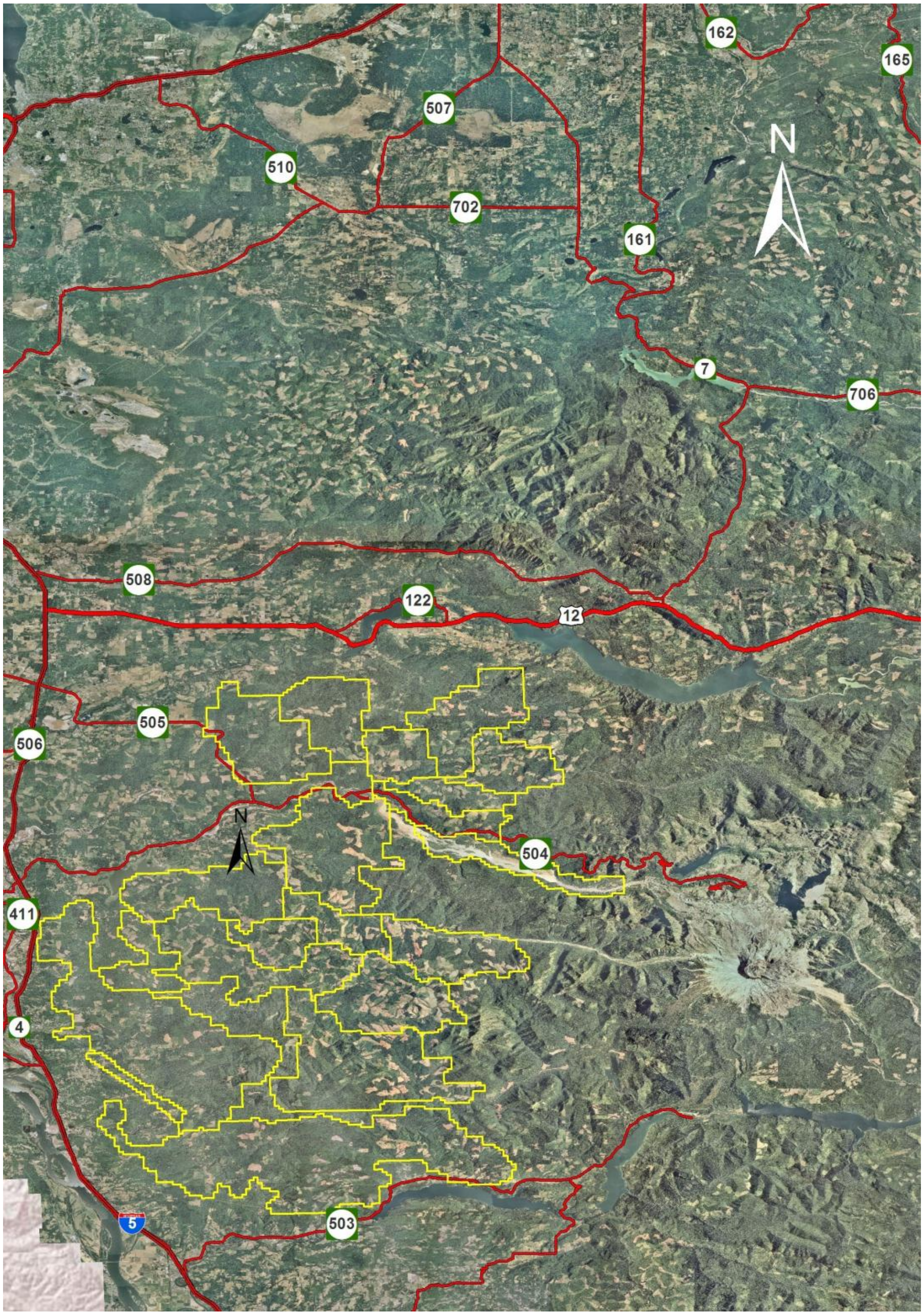


Figure 11. Initial delineation of counting units used for spring helicopter surveys and sightability modeling, 2009-2013, Mount St. Helens elk herd study area.

observers. The primary observer sat abreast the pilot and also recorded data; the 2 additional observers sat abreast, in the back seat of the aircraft. One backseat observer assisted in navigation and maintaining flight line protocols by following a GPS track log on a laptop computer. The helicopter was equipped with a single, forward-looking VHF telemetry antenna and a receiver that allowed radiomarked elk to be relocated and/or identified when needed during the data collection flights, as described below.

We conducted visual surveys of the counting units initially with the helicopter's telemetry system inactivated. We surveyed the counting units at an altitude of 40-70 m above-ground-level (AGL), flying at 80-120 km/hr. Because of the extensive size of the defined survey area, it was impractical to systematically survey the entire area with evenly spaced flight transects, as is typical for sightability surveys (Samuel et al. 1987, McCorquodale et al. 2013). Because a substantial part of the survey area was typified by habitat with predictably low elk sightability (*e.g*., high canopy closure regeneration stands and older conifer forest), our approach focused on flying a high proportion of the landscape where elk detection probabilities would be expected to be modest to high (*e.g*., clearcuts, young regeneration stands, leafless alder stands). In this way, we maximized efficiency by flying where we had some real chance of seeing elk and avoiding areas where sighting elk was very unlikely. This strategy was based on a fundamental goal of maximizing our ability to count as many elk as possible in the survey area, within the constraints of available time and financial resources.

The helicopter crew scanned for elk groups out of both sides of the helicopter. When a crewmember sighted an elk group, the pilot deviated from the flight line and circled the group while the crew collected the following covariate data: group size (GRP), activity of the first elk sighted (ACT: bedded, standing, or moving), percent canopy closure characterizing the area immediately around the group (CAN), percent snow cover (SNOW), cover type (COV) as a categorical variable (opening, clearcut, regenerating conifer stand, alder, conifer forest, or mixed hardwood/conifer forest), and lighting (LIGHT: flat vs. bright). The crew had graphical depictions of various canopy closure settings available for reference. We recorded CAN and SNOW as quantitative covariates, in increments of 5%. We also recorded GPS waypoints for all elk groups.

Crews also scrutinized sighted groups for the presence of radiomarked elk (Fig. 12) and recorded the composition of the groups (*i.e*., the numbers of adult cows, calves, yearling bulls, subadult bulls [raghorns = 2-3 yr-olds], and mature bulls [robust antlers ≥4 yr-olds]). If radiomarked elk were sighted in a group, the telemetry system was activated, and the crew identified all radiomarked elk present. We took digital photos of larger groups (≥ 30 elk) and later verified group size and composition from these photos. After we collected data for each sighted group, we deactivated the telemetry system if it had been used to identify collared elk, the pilot repositioned the helicopter back onto the original flight line, and we resumed the survey protocol.

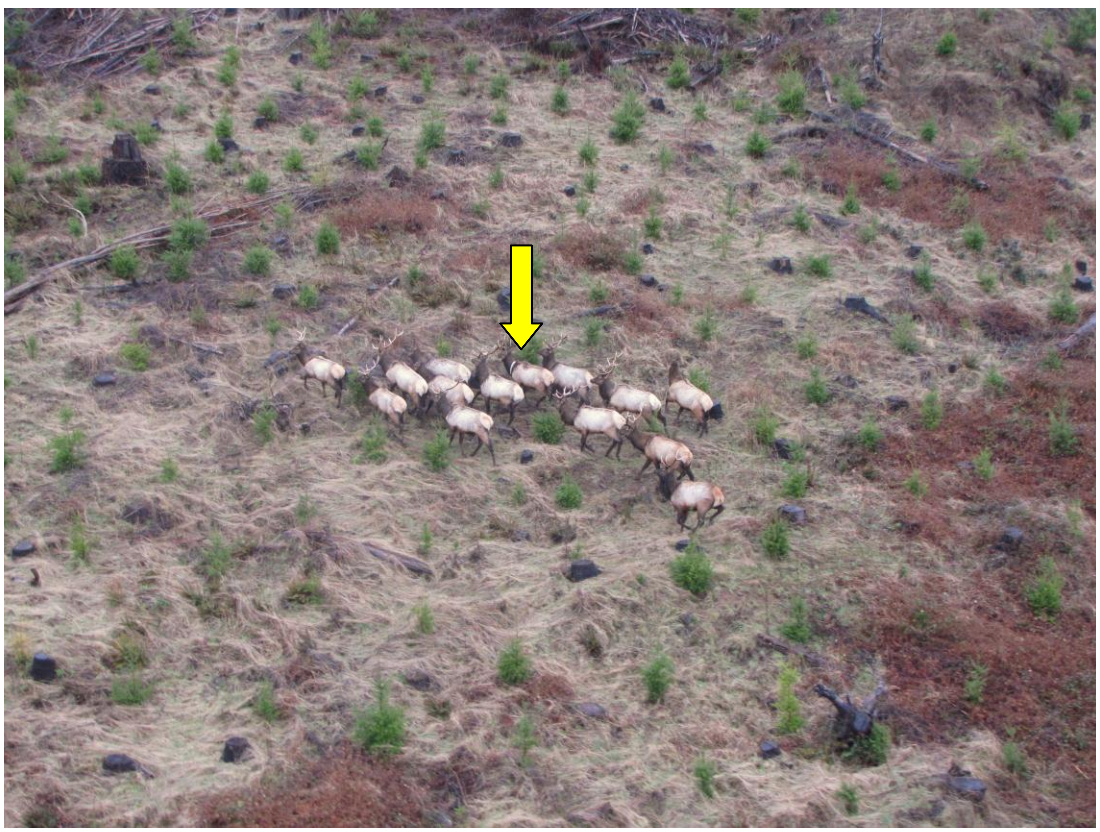


Figure 12. Bull elk group sighted during one of the helicopter surveys; yellow arrow indicates position of a radiomarked bull in the group.

When we had finished surveying a counting unit and had collected data for all sighted groups, we reactivated the telemetry system aboard the helicopter to facilitate locating elk groups containing radiomarked elk that we had missed during the visual survey. We located all missed radiomarked elk precisely via telemetry and collected the same data for these groups that we had collected for sighted groups. When these missed groups were located in heavy cover, the pilot homed to the radio signal and maneuvered the aircraft in low concentric circles over the radiomarked elk's location while the crew carefully watched for elk movement. Often, the pilot was able to haze these groups into sparser cover where the crew could enumerate and classify them. Sometimes, groups in the heaviest cover could not be completely counted or estimated with confidence, and these instances resulted in *missing data* for the GRP covariate. We also recorded GPS waypoints for all groups that had been missed, but were subsequently located via telemetry.

We modeled the sighting process as a binary response (*i.e*., 1 = sighted group, 0 = missed group) using logistic regression (Hosmer and Lemeshow 1989), employing group and environmental covariates as potential predictor variables. Modeling was based only on radiomarked groups (*i.e*., we recorded data from sighted groups that did not contain radiomarked elk, but did not use those data to model sightability). For groups that had missing values for the GRP covariate, we substituted the median group size from all groups we had confidently counted, but limited the data to groups missed in forested habitats (elk groups on the mudflow tended to be larger than groups observed in forested uplands). We also evaluated a transformed GRP covariate (LG2GRP = $\log_2$[GRP]) because we thought it was more reasonable for the effect (*i.e.*, odds ratio) of group size to be constant as group size doubled rather than as it increased by 1 elk across an array of group sizes. For modeling sightability, we also derived a covariate reflecting the dominant gender of the group (SEX). We initially used univariate logistic regression (*i.e*., models with only an intercept and a single predictor variable) to identify which predictors were systematically related to the sighting trial outcome (sighted vs. missed). We also tested for collinearity among predictors. We then brought forward those predictor variables that were related to sightability and conceptualized several alternative models of varying complexity reflecting logical combinations of covariates potentially affecting the sightability of elk groups during helicopter surveys. Where collinearity existed among covariates, we selected one covariate for inclusion in the multivariable models. We used Akaike's Information Criterion, adjusted for small samples (AIC_c) to assess model support and used model averaging to derive final coefficient estimates and their unconditional standard errors (Burnham and Anderson 2002).

In the spring of 2012 and again in 2013 we flew our surveys as we had done during 2009-2011, except that we ceased to relocate missed radiomarked elk, and we flew only 1 survey session in 2013; therefore, we did not use data from sighted groups in 2012 and 2013 as sightability modeling data because it was inappropriate to include data that could only come from sighted groups. We subsequently used the data collected for sighted groups only for all years, 2009-2013, to generate estimates of population size using the best-supported sightability model. These data included the data used to develop the sightability model (*i.e.*, 2009-2011) and non-model-building data (*i.e.*, 2012-2013). We derived abundance estimates and their 95% confidence intervals using the R (R Core Development Team 2008) package *Sightability Model*, following Fieberg (2012). We generated estimates of total elk abundance from each survey replicate, as well as separate estimates for adult cow abundance. We generated these estimates for both the full 5-GMU landscape and for each of the 5 GMUs separately. To estimate abundance, we used only data from the survey units we flew on every survey replicate (*i.e.*, we omitted data from the 2 units described above that were flown only occasionally).

Mark-Resight

Among available mark-resight estimators that are robust to heterogeneity of resighting probabilities across individuals within resighting occasions, we chose the maximum-likelihood based *logit-normal mixed effects* (LNME) model (McClintock et al. 2008). The likelihood for the LNME model formally estimated population size (N_j); it also generated MLEs for detection probability (p_{ij}) and the variance (σ_j^2) of a random individual heterogeneity effect, where the subscript *j* refers to primary occasions (year) and *i* to secondary occasions (survey) within a primary occasion (McClintock et al. 2008). In the absence of individual heterogeneity, the parameter p_{ij} is interpreted as the overall mean detection probability, but when heterogeneity > 0, overall mean detection probability is estimated under the LNME model as the derived parameter μ (McClintock 2008), which we report. The parameter μ is derived as a function of p_{ij}, σ_j^2, and ε_{ij} (number of marked animal encounters, where identity was not determined).

We implemented the LNME model in Program MARK (White and Burnham 1999), which allowed us to compare alternative model parameterizations that embodied hypotheses about sources of variability affecting LNME abundance estimates (McCorquodale et al. 2013). We coded 3 separate encounter history datasets for the LNME analysis: the first dataset was coded with a single marked animal group (*i.e.*, marked cows and bulls were pooled), the second dataset was coded such that marked cows and marked branch-antlered bulls were different groups, and the third dataset was coded with 7 groups: cow elk according to which of the 5 GMUs they occupied and bull elk relative to whether they occupied the mudflow or forested upland units. The single marked group dataset facilitated estimating total elk abundance, the 2-group dataset supported formal estimates of the subpopulations of the total number of adult cows and total number of branch-antlered bulls, and the 7-group dataset supported estimating GMU-specific abundance of cow elk and setting-specific abundance of branch-antlered bulls (mudflow vs. managed forest).

We developed a candidate model set for each analysis that consisted of 11 models for the 1-group dataset, 10 models for the 2-group dataset, and 15 models for the 7-group dataset. Alternative model parameterizations reflected different model constraints on detection probabilities and individual heterogeneity effects. Our models included possible temporal effects that we believed might be logically related to our survey results. For the recapture (resighting) probability (p_i), we contemplated models with no temporal variation (.), models wherein the first and second survey sessions across years were represented by a unique recapture probabilities, and models where we assumed various year-specific effects on recapture probabilities. These temporal effects models were based on potential influences of winter severity on detectability and on our experiences that generally suggested that detectability of elk was better the later into the spring that we flew. We used Akaike's Information Criterion, adjusted for small samples (AIC_c) and Akaike model weights (w_i) to make inference about the best supported models among our candidate models (Burnham and Anderson 2002), and we averaged across models to derive final abundance estimates.

The data collection described in the methodology for sightability-correction modeling (above) provided the essential data for our mark-resight analyses. The necessary data elements included the enumeration and sex/age classification of all elk within groups encountered during the visual portion of the experimental helicopter surveys and an accounting of the distribution of radiomarked elk among these groups (including identity of radiomarked elk). Our mark-resight analyses were based on 2 replicated surveys of the core study area each winter.

We compared sightability model estimates to LNME mark-resight estimates by estimating Pearson's product-moment correlation coefficient using GMU-specific annual abundance estimates from both approaches for adult cows.

Recruitment and Population Growth Rate

We assessed annual calf recruitment at the approximate end-of-winter by estimating the ratio of calves to 100 cows, a standard metric for juvenile recruitment. At the study area and GMU scales, we estimated the annual ratios and associated confidence intervals for years with 2 replicate surveys following Skalski et al. (2005) for sampling with replacement and following Skalski et al. (2005) for 2013 data (1 survey) for sampling without replacement. Fall antlerless elk harvest will affect calf:cow ratios estimated the following spring because animals have potentially been removed from both the numerator (calves) and denominator (cows). This is expected to be particularly problematic under liberal antlerless harvest, as was occurring during our study. Typically, most antlerless elk harvest consists of yearling and older cows (WDFW, unpublished data), and under this scenario, spring calf:cow ratios would tend towards overestimation, relative to the actual ratios that would be observed in the absence of harvest. We attempted to adjust our spring calf:cow ratios to account for this using estimated annual antlerless elk harvest and estimates of the ratio of calves to older elk in the harvest from hunter survey data. We consider the subsequent adjusted ratios as indices of spring calf:cow ratios rather than as formal estimates given compounded sampling error from each component (*i.e*., observed ratio, estimated harvest, estimated age-class distribution in the harvest).

We estimated the exponential population growth rate (*r*) as the slope of a weighted regression of the natural log transformed population estimates over years for both sightability model and LNME abundance estimates. We used the delta method (Casella and Berger 2002) to obtain the variance-covariance matrix of ln(*N*) from the variance-covariance matrix of (*N*). For LNME estimates, we obtained the variance-covariance matrix of abundance estimates from Program MARK (White and Burnham 1999). For the sightability model, because we obtained each estimate from independent data, all covariance terms were 0. We used function glm() in R (R Core Development Team 2008) to fit the weighted regression and used the inverse of the variance-covariance matrix of ln(*N*) as the weight-matrix. We constructed confidence intervals for *r* using the standard error for the slope from the weighted regression, assuming asymptotic normality.

Survival

We estimated annual survival rates for radiomarked elk during 2009-2010, 2010-2011, 2011-2012, and 2012-2013 (*i.e*., 4 survival years) using maximum-likelihood methods by invoking known fate models in Program MARK (White and Burnham 1999). For this analysis we coded encounter history data using 6 groupings: 5 GMU-specific groups for adult cows and a single pooled branch-antlered bull group. We estimated annual survival for a survival year defined as May 1-Apr 30 and estimated confidence intervals for annual survival using profile likelihoods. By using 15 alternative model parameterizations, we tested several hypotheses about Mount St. Helens elk survival during 2009-2012. Models varied in complexity from a simple 2 parameter model (survival differed only by sex, with no temporal or spatial variation) to a 24 parameter model (survival differed across groups and years). We compared models using

Akaike's Information Criterion, adjusted for small sample sizes (AIC_c) (Burnham and Anderson 2002).

We attempted to account for radiomarked elk mortalities by cause. Outside of the winter-spring season, when we conducted most of our annual population assessment fieldwork, our monitoring of radiomarked elk was infrequent, so sometimes we could not assign a definitive cause of death. We were, however, confident that we could reasonably discriminate most natural mortalities from hunting-related mortalities, based on timing of death, evidence at carcasses we located, or other corroborating evidence (*e.g.*, a cleanly cut collar with no carcass). A majority of the hunting-related mortalities were reported to us by hunters, according to directions embossed on one side of the ear tag each elk received when it was originally captured.

Elk Hoof Disease

During the late 1990s, elk in southwest Washington with an apparent hoof affliction were first reported. Initial reports came from lowland valleys where pastureland interfaced with more traditional elk habitat. These reports, ranging from limping elk to elk with elongated hoof sheaths and/or ulcerated hooves, were sporadically received over the next several years. At the time our study began, the condition was known to exist in segments of the Mount St. Helens elk herd, but appeared to be limited to the west-most portion of the herd area. Our research scope did not formally include evaluating the spatial extent, morbidity, or population dynamics implications of this condition. During our elk capture operations we attempted to avoid capturing elk that were clearly sick or injured, as these animals typically would have elevated risk of capture-related complications. However, during the course of our work we inadvertently captured a few elk with varying degrees of hoof disease; this occurred when the affliction was not obvious as the elk ran from the pursuing helicopter. We did radiocollar such elk, and they provided some limited information on near-term fates of elk with hoof disease. The sample size of radiomarked elk with hoof disease was not sufficient, however, to formally assess any contribution to annual mortality risk for elk, specific to hoof disease, nor would these elk be considered a random sample of affected elk.

Concurrent with the latter portion of our study, investigations were initiated to identify the etiology and better define the epidemiology of this condition. This work is being conducted by veterinary pathologists at several veterinary colleges around the world, in consult with the Washington Department of Fish and Wildlife's staff veterinarian. Results from the veterinary investigations are beyond the scope of this report and will be published elsewhere.

Environmental and Temporal Effects

In addition to the analytic methods previously described, we explored a variety of temporal (year), spatial (GMU or subareas), and weather variables for their effects on responses such as IFBF, pregnancy, recruitment, indexed overwinter mortality, etc. We used general linear models (GLM) when the potential predictor variables were categorical (*e.g*., year, GMUs, subareas) and/or the response was nominal (*e.g*., pregnant vs. non-pregnant), and we used ordinary least squares (OLS) regression when responses and potential predictors were interval data. We also estimated the product-moment correlation coefficient to evaluate collinearity between pairs of quantitative variables (*e.g*., annual recruitment and overwinter mortality indices).

To explore the potential effects of weather on calf recruitment and overwinter mortality, we used SNOTEL data from the Spirit Lake SNOTEL site as potential predictors and the annual calf recruitment index and overwinter mortality index as responses. From the SNOTEL data, we calculated: 1) total late summer/ early fall (Aug 1- Sep 30) precipitation, 2) total early summer (May 1 – July 31) precipitation, 3) total lactation season (May 1 – Sep 30) precipitation, 4) the linear slope (OLS) of accumulated late summer/early fall (Aug 1 – Sep 30) precipitation, 5) accumulated snow water equivalents (SWE) for early winter (Dec 1 – Jan 31), 6) SWE for late winter (Feb 1 – Mar 31), and 7) SWE for the full winter (Nov 1 – Mar 31). We used SWE to index winter severity because SNOTEL data on daily snow depth were not routinely collected at any SNOTEL site near our study area until shortly prior to our study, preventing us from characterizing longer-term winter severity. We calculated standard normal deviates (Z_i) for each weather metric, where $Z_i = X_i - \mu / \sigma$, and X_i = the observed value for year i, μ = the 1990-2005 mean for that metric, and σ = the standard deviation

(1990-2005) for that metric. This transformed observed annual weather metrics during our study into the number of standard deviations (+/-) relative to the long-term mean for a given metric. For example, a positive Z value for early summer precipitation would indicate a wetter than normal early summer and a negative Z value would indicate a drier than normal early summer. Spring-summer-fall drought was indicated by negative Z values, and severe winters were indicated by positive Z values. Our hypotheses were that spring calf recruitment would be potentially positively influenced by wet summer-fall weather in the birth year and/or potentially negatively influenced by higher winter severity in the calves' first winter. We hypothesized overwinter mortality would be higher in springs following droughty summer-falls and/or severe winters. To explore the cumulative effect of poor late summer-fall conditions combined with a subsequent harsh (snowy) winter, we changed the sign of the summer-fall precipitation Z-scores and then summed the summer-fall precipitation and winter SWE Z-scores. We did this so that for both seasonal weather severity indices, a positive Z-score reflected increased weather severity (relative to elk energy budgets) and negative Z-scores for weather severity reflected good environmental conditions for elk.

RESULTS

Capture and Marking

We captured 150 unique elk (110 F: 40 M) during 154 mid-winter capture events, 2009-2012. The ages of cow elk we captured ranged 1-16 years, with most cows in the prime-age class (ages 2-11 years) (Fig. 13). The ages of branch-antlered bull elk we captured ranged 2-9 years (Fig. 14). The median estimated age, based on cementum annuli, for both captured cows and captured bulls was 5 yrs. Yearling cows were very likely under-represented in our captured elk sample (relative to the population) due to size selection intended to prevent darting very large calves (*i.e.*, the sizes of very large calves and very small yearlings potentially overlapped). No elk died during handling; 1 cow elk died within a few days of capture, possibly due to post-capture complications.

We captured 26, 18, 12, 36, and 22 cows and 12, 11, 8, 5, and 4 branch-antlered bulls across GMUs 520, 522, 524, 550, and 556, respectively. Across years, 2009-2012, we captured and radiomarked 44, 27, 21, and 22 cow elk and 11, 11, 10, and 8 branch-antlered bulls, respectively. Effort across years maintained relatively consistent radiomarked elk sample sizes, 2009-2012, in the face of annual attrition due to mortalities and collar malfunction.

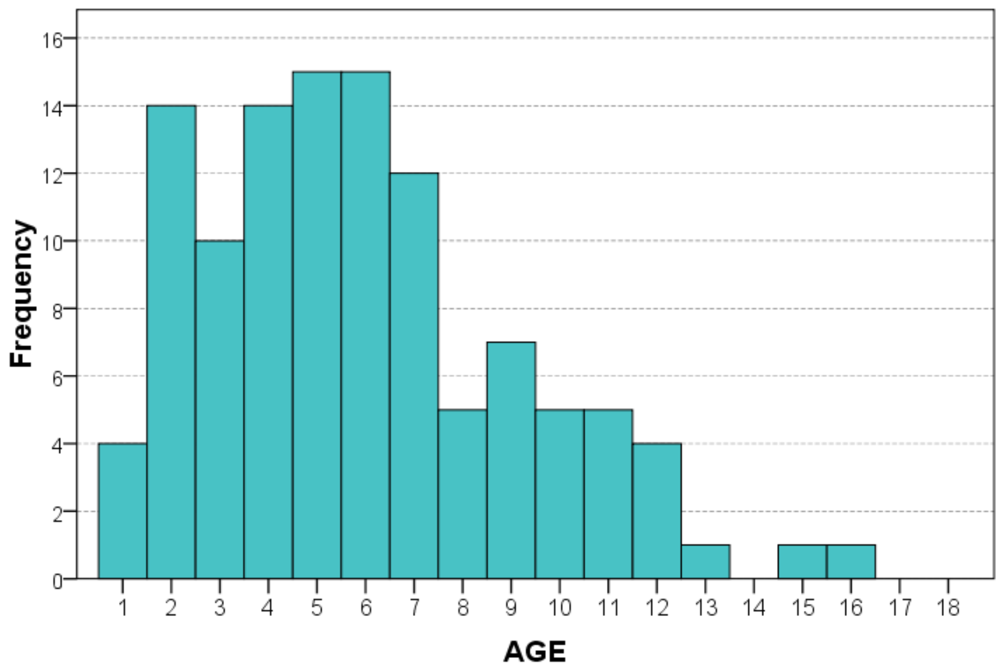


Figure 13. Distribution of ages for cow elk captured and radiomarked, Feb 2009-2012, Mount St. Helens, Washington.

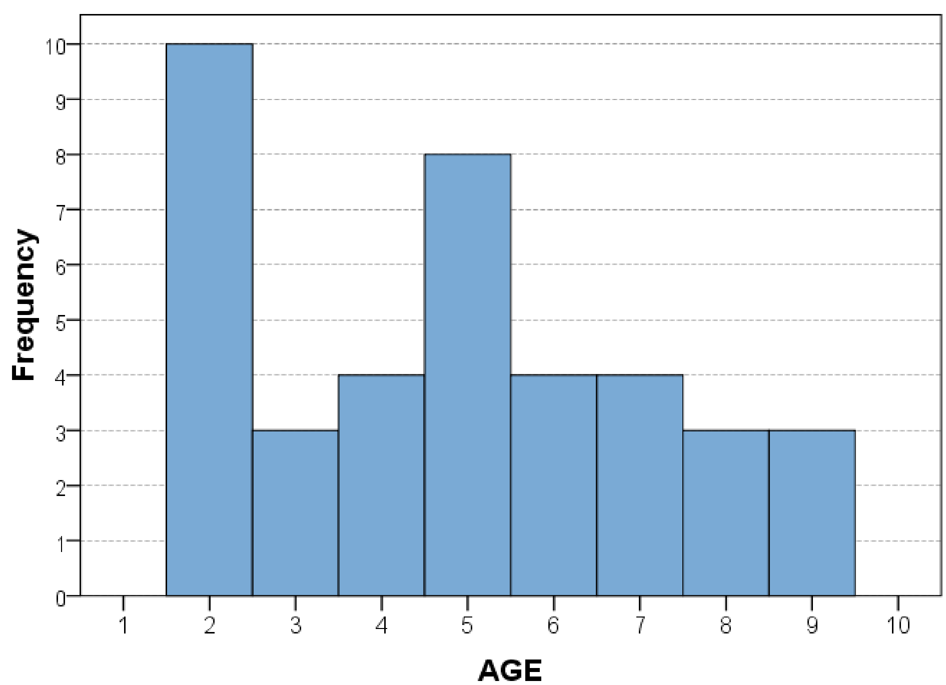


Figure 14. Distribution of ages for bull elk captured and radiomarked, Feb 2009-2012, Mount St. Helens, Washington.

Late-Winter Condition and Fertility

The mean body mass for cow elk handled in February was 218.2 kg (481.1 lbs) (95% CI = 214.9-221.4 kg; 473.9-488.2 lbs). For branch-antlered bulls, mean body mass was 246.3 kg (543.1 lbs) (95% CI = 239.7-253.0 kg; 528.5-557.9 lbs). Cow body mass generally increased with age until about age 5 (Fig. 15). Although body mass among cows we handled was highest at about age 10, age-specific estimates were based on small samples after about age 7. The heaviest cow we handled was 253.7 kg (559.4 lbs) and the heaviest bull was 287.01 kg (632.8 lbs). The numbers of branch-antlered bull elk we handled were insufficient to support inference about the mass vs. age relationship for bulls.

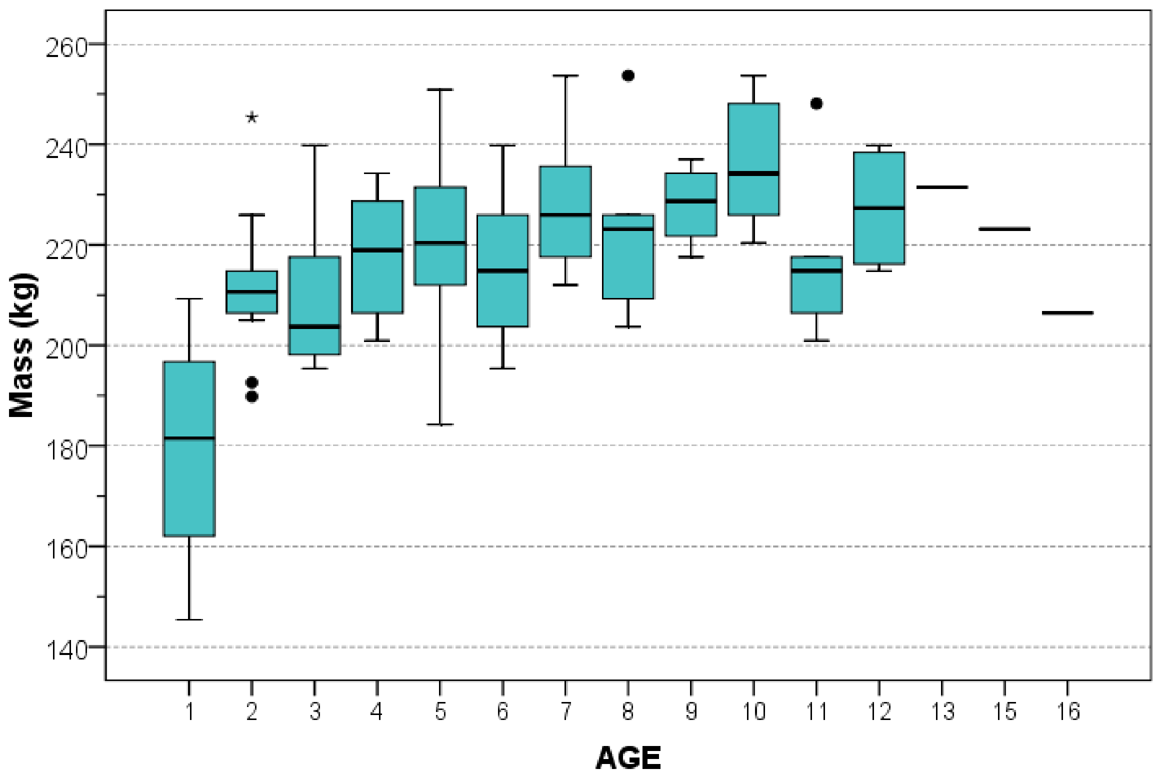


Figure 15. Boxplots of age-specific mass for cow elk captured and radiomarked, Feb 2009-2012, Mount St. Helens, Washington. Colored boxes represent the middle 50% of estimates within each age-class, and heavy horizontal lines represent median values. Only a single estimated mass was available for cows aged 13, 15, and 16.

Using a general linear model with fixed effects for year, GMU, pregnancy status, and lactation status, we did not detect any systematic effect of year (P = 0.32) on winter body fat (IFBF) for adult (≥2 yr-old) cow elk. GMU, lactation, and pregnancy did affect IFBF (P = 0.02, 0.07, 0.005, respectively). Lactaters were consistently leaner than non-lactating elk across years (Fig 16). Pregnant elk were fatter than non-pregnant elk (Fig. 17). Pooling years and GMUs, mean IFBF in February was 5.64% (95% CI = 5.08-6.21%) for non-lactating cow elk and was 3.26% (95% CI = 2.34-4.18%) for elk with evidence of late season lactation. Similarly, means for non-pregnant and pregnant adult cows were 3.38% (95% CI = 2.56-4.20) and 5.95% (95% CI = 5.38-6.52) IFBF.

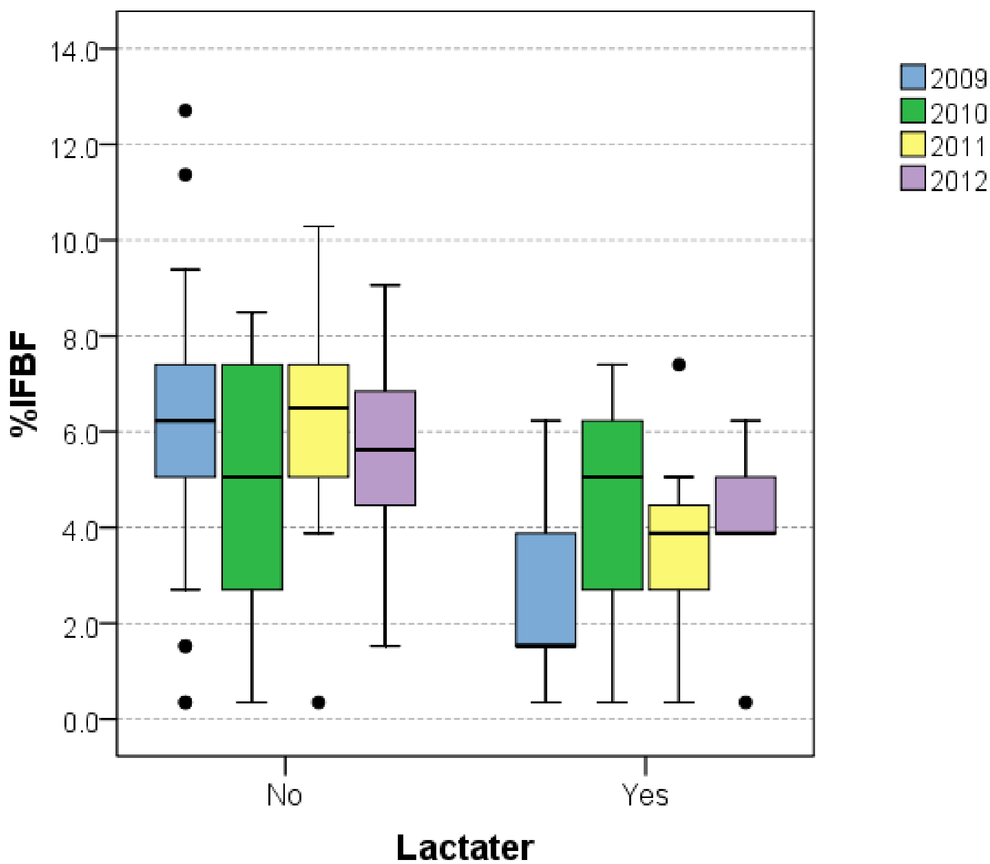


Figure 16. Boxplots for ingesta-free body fat (%IFBF) by lactation status for cow elk captured and radiomarked, Feb 2009-2012, Mount St. Helens, Washington. Colored boxes represent the middle 50% of estimates, and heavy horizontal lines represent median values.

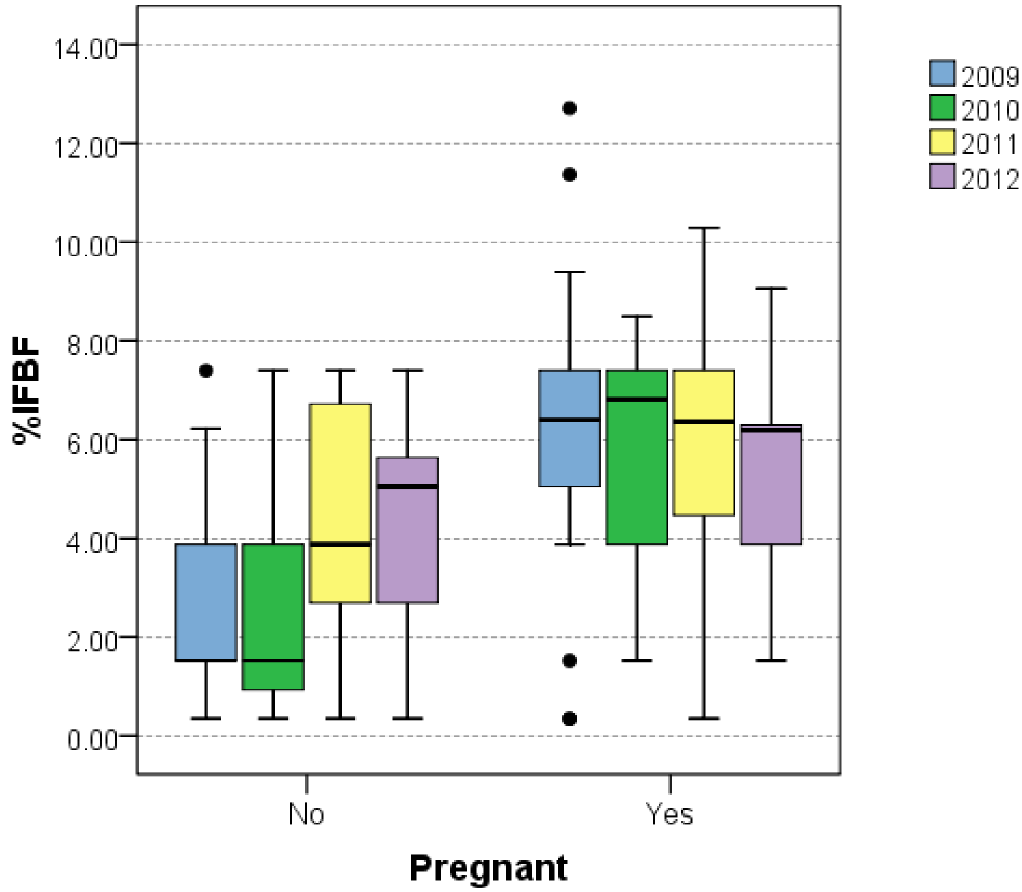


Figure 17. Boxplots for ingesta-free body fat (%IFBF) by pregnancy status for cow elk captured and radiomarked, Feb 2009-2012, Mount St. Helens, Washington. Colored boxes represent the middle 50% of estimates, and heavy horizontal lines represent median values.

Using a general linear model to control for the fixed effects of lactation and pregnancy status, which both were related to IFBF (see above), we found some differences among GMUs in mid-winter IFBF for adult (≥ 2 yr-old) cow elk that we handled, 2009-2012. Using $P \leq 0.05$ as the significance level, GMU 522 cow elk had higher IFBF levels than cow elk captured in GMUs 520 and 550 (Fig. 18); other GMU contrasts were not significantly different ($P > 0.05$).

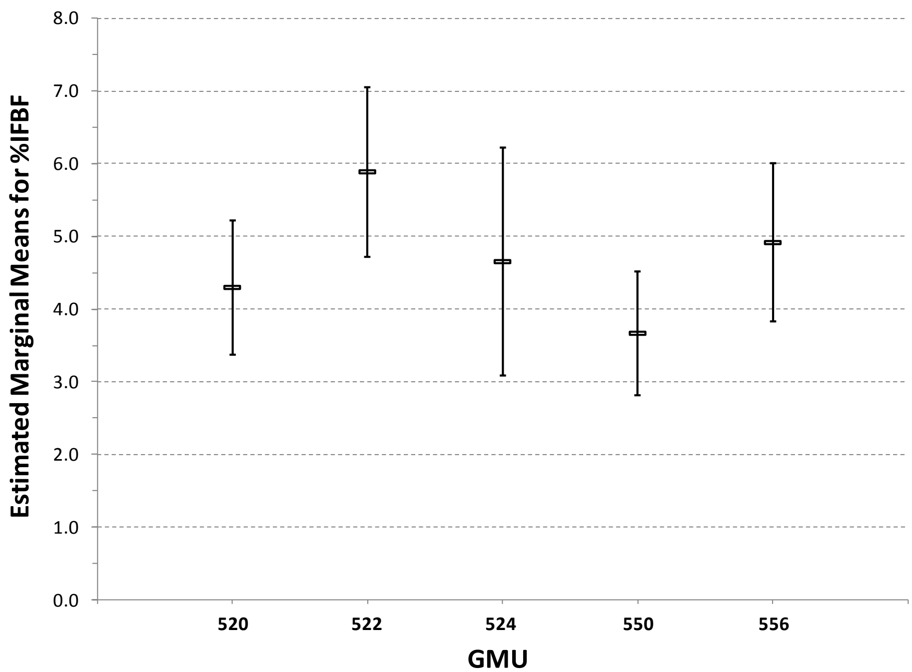


Figure 18. Plot of marginal means for %IFBF by GMU, controlling for pregnancy and lactation status, Mount St. Helens cow elk, 2009-2012.

Overall, 73 of 109 (67%) adult (≥ 2-yr-old) cow elk we handled in mid-winter, 2009-2012 were pregnant on ultrasound examination; none of 4 yearling cows were pregnant. We had limited data for very old cows, but among 3 cows older than 12 years, 2 (66.7%) were pregnant. Of 73 cows aged 4-10 years, 52 (71.2%) were pregnant in February. Across GMUs, the observed pregnancy rate among adult cows was 42.3% (n = 26) in GMU 520, 83.3% (n = 18) in GMU 522, 90.0% (n = 10) in GMU 524, 71.4% (n = 35) in GMU 550, and 65.0% (n = 20) in GMU 556. As above, there was a statistical association between cow elk condition and pregnancy; pregnant elk were fatter than non-pregnant elk. We did not detect an effect of year on pregnancy status. Evidence of recent lactation for cows handled in February was rare (4 of 73 pregnant cows; 3.5%).

Fall Body Condition

We collected hunter-contributed organ samples from 423 harvested elk during 2009-2011. These samples ranged from a single contributed organ (*e.g.*, a heart) to all of the requested organs (*i.e*., heart, pericardium, kidneys). Among the 423 samples, there were 226 complete organ sets. Overall, we received 360 heart, 285 pericardium, and 347 kidney samples. Cook et al. (2001*b*) identified Kistner subset scores based on the full organ sample complement as excellent predictors of IFBF; they also explored various 2- and 1-organ subsets for their predictive utility relative to IFBF (R. Cook, personal communication). IFBF was clearly related to all 2 organ component pairs (*e.g*., heart-pericardium, heart-kidney; $r^2 > 0.90$). Relationships of single organ scores to IFBF were less consistent ($r^2 = 0.64$, 0.82, and 0.88 for the heart pericardium, and kidneys respectively). We subsequently estimated IFBF using the full organ subsets and all 2-organ subsets available (2-organ predictive equations supplied by R. Cook). This allowed us to derive 364 usable estimates of fall IFBF for hunter-killed cow elk within the Mount St. Helens herd area, 2009-2011. Because yearling cow elk tend to be consistently lean (WDFW, unpublished data), we based further analyses on 323 fall IFBF estimates from cow elk older than 1 yr-old. Generally, the data were approximately normally distributed, with a few more very lean animals than expected (Fig. 19). IFBF estimates ranged 0.30-19.8% for cow elk older than yearlings.

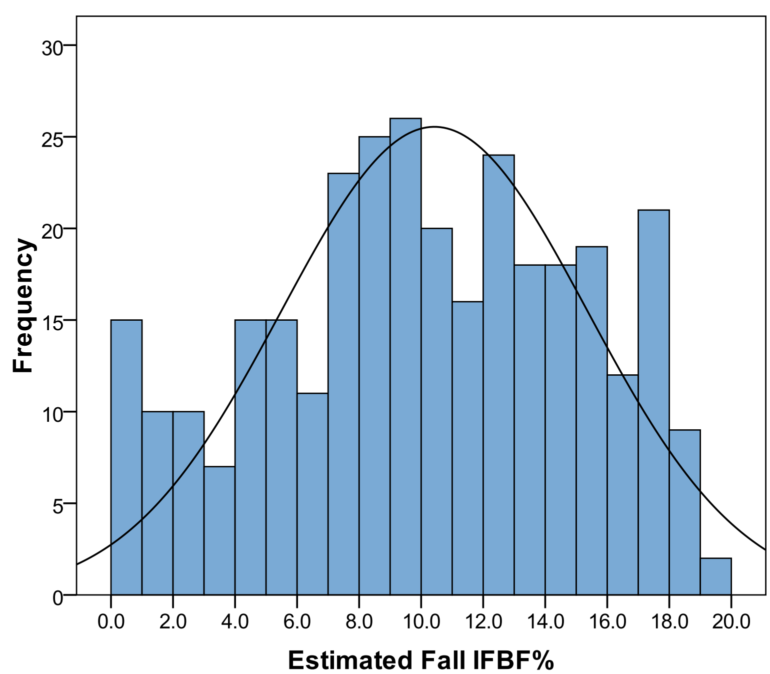


Figure 19. Frequency histogram (and normal curve) for fall IFBF estimates from hunter-killed cow elk, Mount St. Helens, WA, 2009-2011.

Sample sizes among some GMUs were small, so to explore potential spatial variation among fall IFBF estimates, we grouped the data into subareas (1 = the N. Fork of the Toutle River mudflow; 2 = the managed forest landscape of the core study area [GMUs 520, 524, 550, 556]; 3 = GMU 560; 4 = the Columbia Gorge GMUs). In a general linear model with fixed effects for year, subarea, and lactation status, and with cow age as a covariate, there were significant ($P \leq 0.05$) effects of subarea and lactation on IFBF; year and cow age did not affect IFBF. The marginal means by lactation status, controlling for other factors, were 12.51% IFBF for non-lactaters and 10.84% for lactaters. In the subarea contrasts, IFBF for cows from subarea 2 was lower (marginal mean = 9.20%) than for subarea 3 (marginal mean = 13.07%) and for subarea 4 (marginal mean = 12.38%) cows (Fig. 20). Estimates for mudflow cows (marginal mean = 12.07%) were qualitatively similar to estimates for subarea 3 and 4 cows and different than for subarea 2 cows, but because few mudflow cows were sampled (n = 9) the pair-wise contrasts involving mudflow cows were nonsignificant.

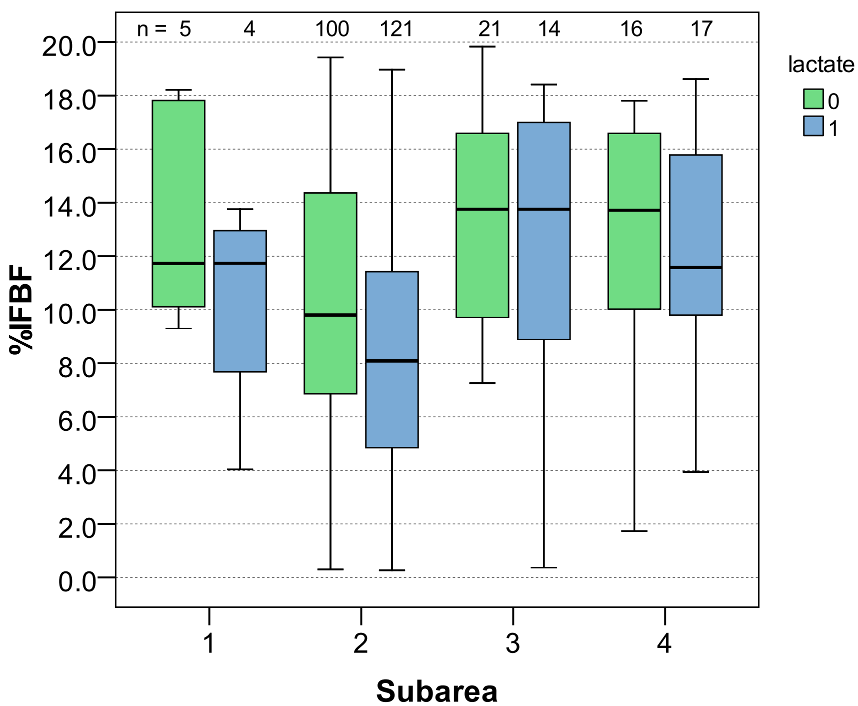


Figure 20. Boxplots for fall %IFBF from hunter-killed elk across subareas (1 = GMU 522, 2 = GMUs 520, 524, 550, 556, 3 = GMU 560, 4 = Columbia Gorge GMUs) by lactation status, Mount St. Helens, WA, 2009-2011.

Sightability Modeling

We collected sighting trial data for 331 groups containing at least 1 radiomarked elk during 2009-2011. Overall, we saw 174 groups (52.6%) without aid of telemetry and missed 157 groups (47.4%) that we later located via telemetry. We saw a higher proportion of radiomarked cow groups (146 of 261 groups; 55.9%) than of radiomarked bull groups (28 of 70 groups; 40.0%; Table 1). Elk were more easily seen when in larger groups, when active, and when in open (*i.e.*, low canopy cover) cover types (Table 1). Relative snow cover and light conditions, as we measured them, did not seem to systematically affect elk sightability on this landscape.

The covariates CAN, GRP, LG2GRP, and SEX were all related to the probability that an elk group was sighted in univariate tests (Table 2). Because one of the outcomes (*i.e.*, sighted or missed) was not observed for at least 1 level of the categorical covariates ACT and COV, MLEs did not exist for these covariates. We recoded ACT into a new covariate (ACT2) with 2 levels: 0 = bedded; 1 = active, and we recoded COV into a new covariate (COV2) with 4 levels: 1 = clearcut; 2 = regeneration stand, conifer, or alder; 3 = meadow, wetland, field, or mudflow. These new covariates were related to the probability that an elk group was sighted (Table 2).

Preliminary modeling indicated that LG2GRP was a better predictor of sightability than was the untransformed GRP covariate, so we subsequently used LG2GRP in all multivariate models. An analysis of variance (ANOVA) suggested that the covariate CAN (% canopy) was collinear with the recoded cover type covariate (COV2) (r^2 = 0.51), so we chose to use only the CAN covariate in subsequent multivariate logistic models. In a large number of cases where we missed a group and subsequently located it via telemetry we could not confidently determine the group's initial activity level, which resulted in a large number of missing values for ACT2. We were not comfortable attempting to impute data for all of these missing values, and to preclude eliminating a large number of cases from our multivariable models because of the missing activity data, we elected to drop the activity covariate from further consideration.

Table 1. Summary of univariate association of independent variable levels and sightability of elk groups during helicopter surveys, Mount St. Helens, 2009-2011.

Variable	Total Groups	Groups Seen	%Seen
Canopy (%)			
0-15	116	111	95.7
20-35	43	37	86.0
40-55	32	20	62.5
60-75	36	6	16.7
>75	101	0	0.0
Snow (%)			
< 50	278	150	54.0
≥ 50	50	24	48.0
Group Size			
1-2	68	21	30.9
3-4	20	13	65.0
5-6	23	15	65.2
7-8	28	19	67.9
9-10	81	15	18.5
>10	98	91	92.9
Group Type			
cow-calf	261	146	55.9
bull	70	28	22.0
Activity			
bedded	60	23	38.3
standing	150	142	94.7
moving	9	9	100.0
Cover Type			
clear cut	69	67	97.1
regeneration	91	52	57.1
conifer	67	2	3.0
alder	24	18	75.0
field/meadow/wetland	34	32	94.1
river or road	2	2	100.0
Light			
bright	55	31	56.4
flat	273	143	52.4

Table 2. Results of univariate significance tests (logistic regression) for predictor variables potentially affecting sightability of elk groups during spring helicopter surveys, Mount St. Helens, 2009-2011. Bold text delineates predictors significantly related to group sightability.

Variable	X^2	*P*-value
CAN	**296.44**	**<0.001**
SNOW	0.52	0.471
GRP	**62.28**	**<0.001**
LG2GRP	**40.69**	**<0.001**
SEX	**5.64**	**0.018**
ACT	***	***
ACT2	**79.16**	**<0.001**
COV	***	***
COV2	**131.67**	**<0.001**
LIGHT	0.29	0.589

*** model did not converge; MLE does not exist.

Among our candidate sightability models, 2 models accounted for 98% of the available model weight (Table 3). The best model had 3 predictor variables (LG2GRP, CAN, and SEX) and an intercept. The next best model, which was 1.70 AIC_c units from the best model, was similar except that it lacked the SEX variable. All of the remaining models were at least 7.36 AIC_c units from the best-supported model. Simple (*i.e.*, 1 predictor variable) models that predicted sightability based on group size (LG2GRP), canopy closure (CAN), or sex (SEX) alone had little support. The sign for the SEX covariate differed between the single variable model (*i.e.*, SEX was the only predictor) and the best multivariable model, the β_i for SEX was erratic across models and was poorly estimated (*i.e.*, large SE) (Table 4), the sign for SEX in the best multivariable model was illogical, and the Wald statistic for SEX in the best multivariable model was marginally nonsignificant (P = 0.06). Collectively, these results made us skeptical of inclusion of SEX in the multivariable context. So, we subsequently selected the second best model in Table 3 as our best model. This model predicted larger elk groups were more likely to be seen, as were elk in more open habitat (Table 4). This model fit the data (Hosmer-Lemeshow statistic = 9.26; P = 0.32) and correctly classified 91.4% of the model building observations; 163 of 179 groups predicted to be seen were seen (91.0% correct), and 125 or 136 groups predicted to be missed were missed (91.9% correct).

Table 3. Model selection results for models predicting the sightability of elk groups from a helicopter, Mount St. Helens Elk Herd Area, 2009-2011.

Model	K^a	$-2LL$	AIC_c	$\Delta AIC_c{}^b$	$w_i{}^c$
LG2GRP, CAN, SEX	4	145.59	153.72	0.00	0.69
LG2GRP, CAN	3	149.34	155.42	1.70	0.29
CAN	2	157.04	161.08	7.36	0.02
CAN, SEX	3	157.01	163.09	9.37	0.006
LG2GRP	2	397.32	401.35	247.63	0.00
LG2GRP, SEX	3	396.41	402.49	248.77	0.00
SEX	2	452.35	456.39	302.67	0.00

[a]Number of unique parameters in $model_i$.
[b]Difference in AIC_c units between $model_i$ and the best model.
[c]Relative model weight in $model_i$.

Table 4. Parameter estimates (β_i and standard errors = SE) for the fitted sightability models from Table 3, Mount St. Helens Elk Herd, 2009-2011.

Model	LG2GRP	SE(LG2GRP)	CAN	SE(CAN)	SEX	SE(SEX)
LG2GRP, CAN, SEX	0.63	0.20	-0.09	0.010	1.24	0.65
LG2GRP, CAN	0.42	0.17	-0.09	0.009	–	–
CAN	–	–	-0.09	0.009	–	–
CAN, SEX	–	–	-0.09	0.009	0.09	0.53
LG2GRP	0.54	0.09	–	–	–	–
LG2GRP, SEX	0.60	0.12	–	–	0.34	0.36
SEX	–	–	–	–	-0.64	0.27

Fitting the 2-predictor multivariable model with effects of group size and canopy on predicted sightabilities yielded the following model:

$$\boldsymbol{y = 2.85 + 0.42(\mathrm{LG2GRP}) - 0.09(\mathrm{CAN})}$$

Sightability-corrected estimates of total elk abundance and total cow elk abundance (2 estimates per year from replicated surveys), derived from the above sightability model, indicated relatively stable to slightly increasing numbers of elk within our 5-GMU study area from 2009 to 2011 and a subsequent substantial decline during 2012-2013 (Fig. 21). Peak point estimates for total elk and total cow elk were 5,132 elk and 2,803 cow elk in the spring of 2011; minimum point estimates were 2,717 elk and 1,608 cow elk in the spring of 2013.

GMU-specific estimates for total elk abundance, 2009-2013 (Figs. 22-26), indicated a relatively steady decline in elk abundance in GMUs 520 and 550, a modest decline in GMU 524, an initial increase followed by a substantial decline in GMU 556, and initially increasing then stabilizing numbers of elk in GMU 522.

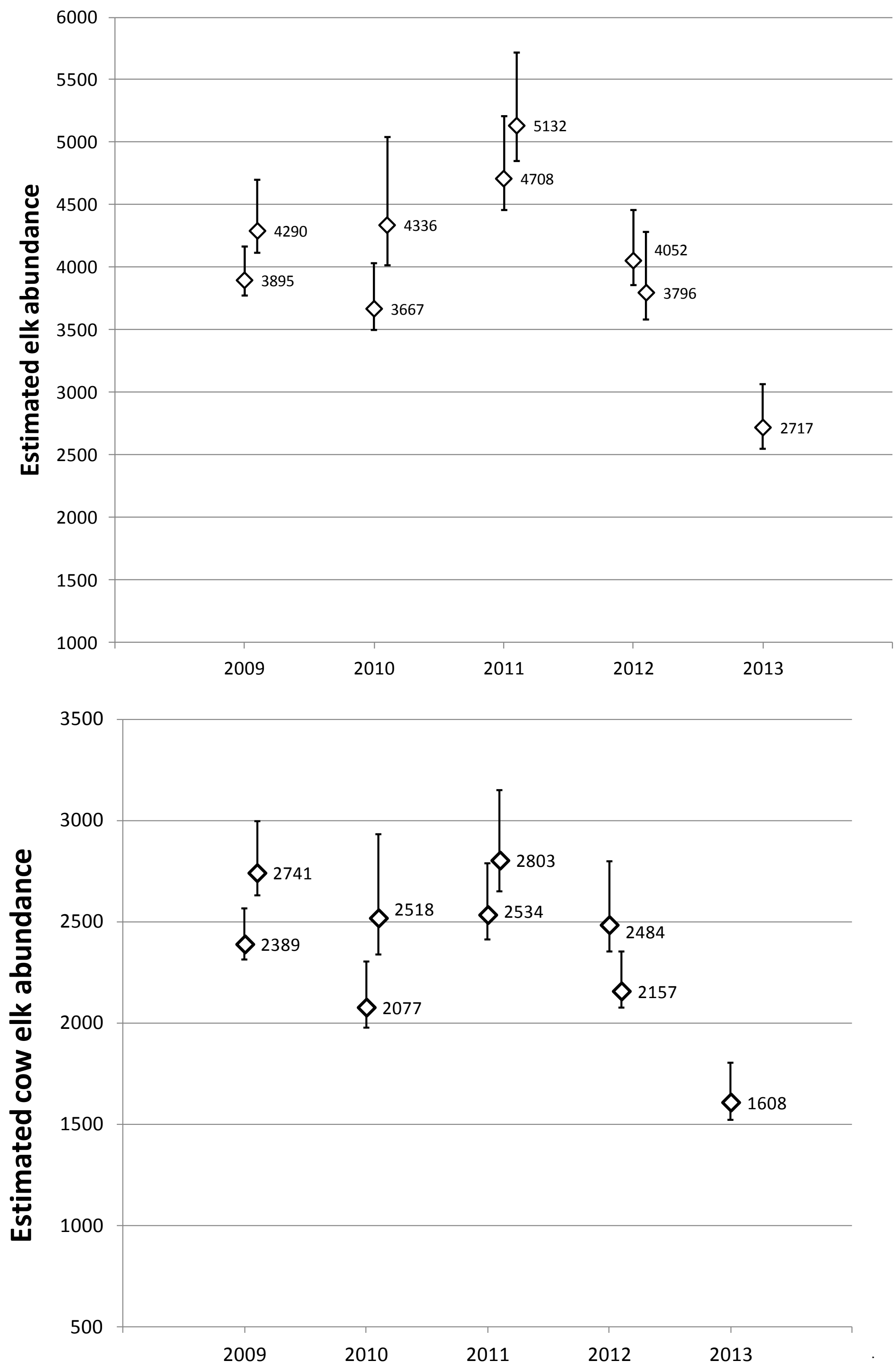


Figure 21. Sightability model estimates (± 95% CI) for total elk and total cow elk abundance in the study area, Mount St. Helens, 2009-2013.

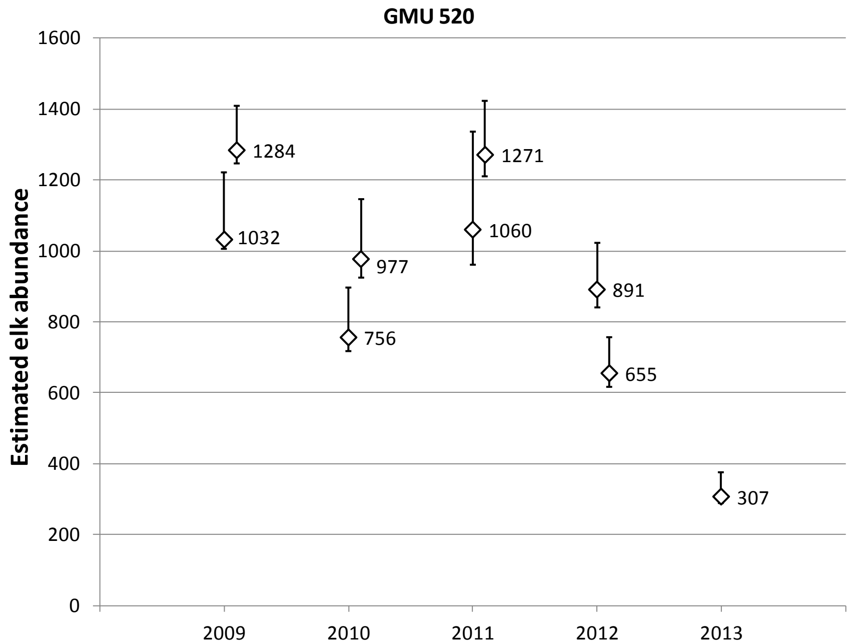


Figure 22. Sightability model estimates for total elk abundance (± 95% CI) in GMU 520, Mount St. Helens, 2009-2013.

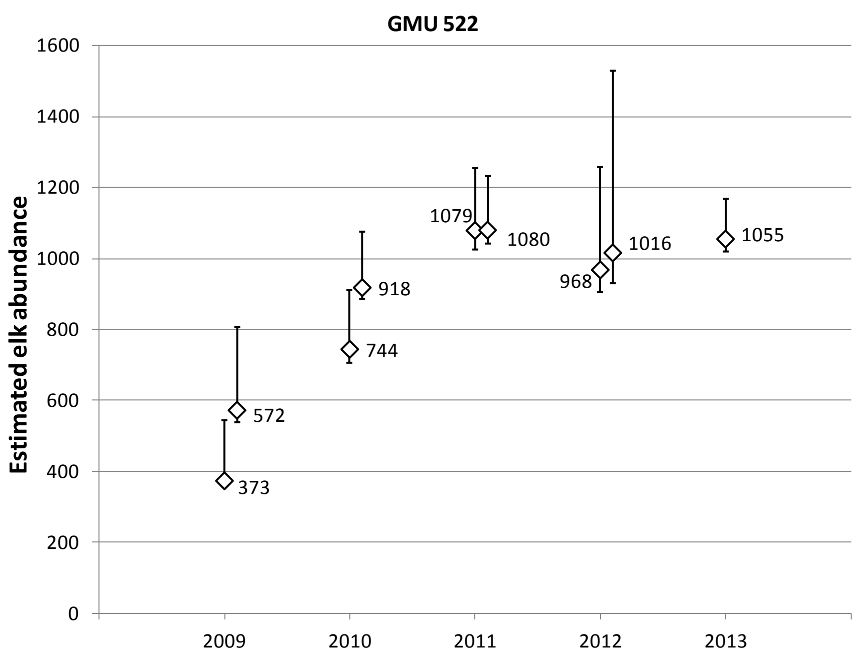


Figure 23. Sightability model estimates for total elk abundance (± 95% CI) in GMU 522, Mount St. Helens, 2009-2013.

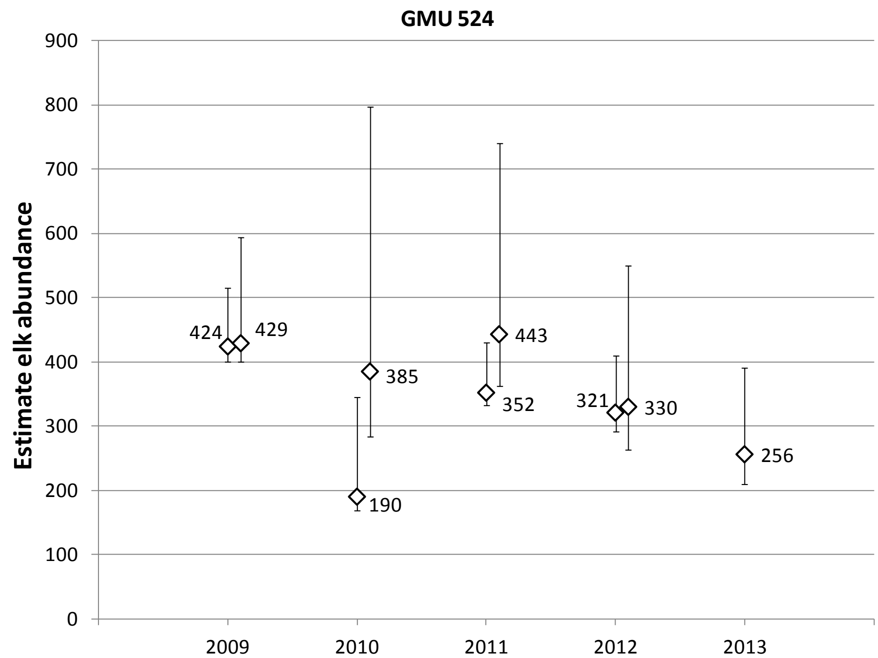


Figure 24. Sightability model estimates for total elk abundance (± 95% CI) in GMU 524, Mount St. Helens, 2009-2013.

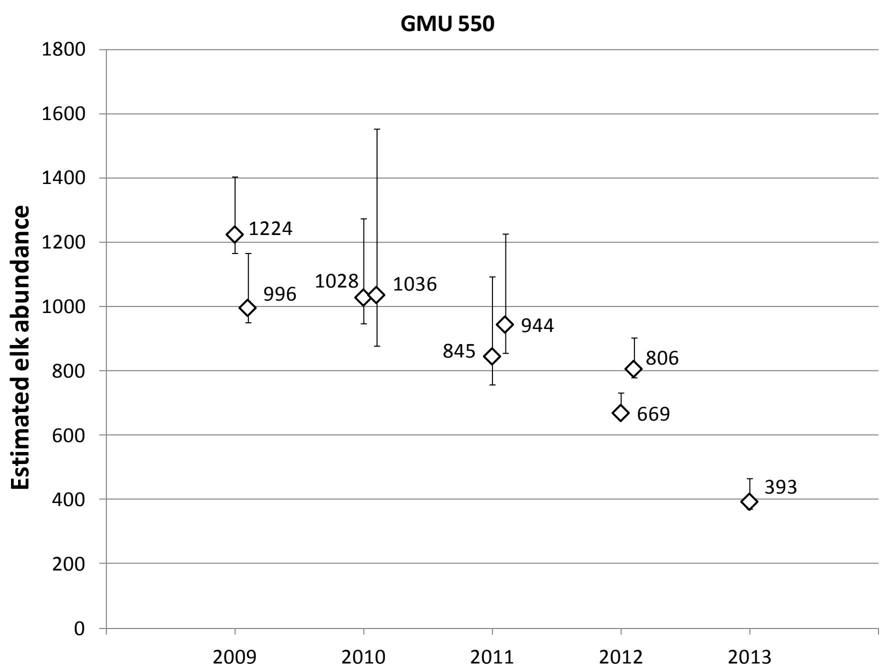


Figure 25. Sightability model estimates for total elk abundance (± 95% CI) in GMU 550, Mount St. Helens, 2009-2013.

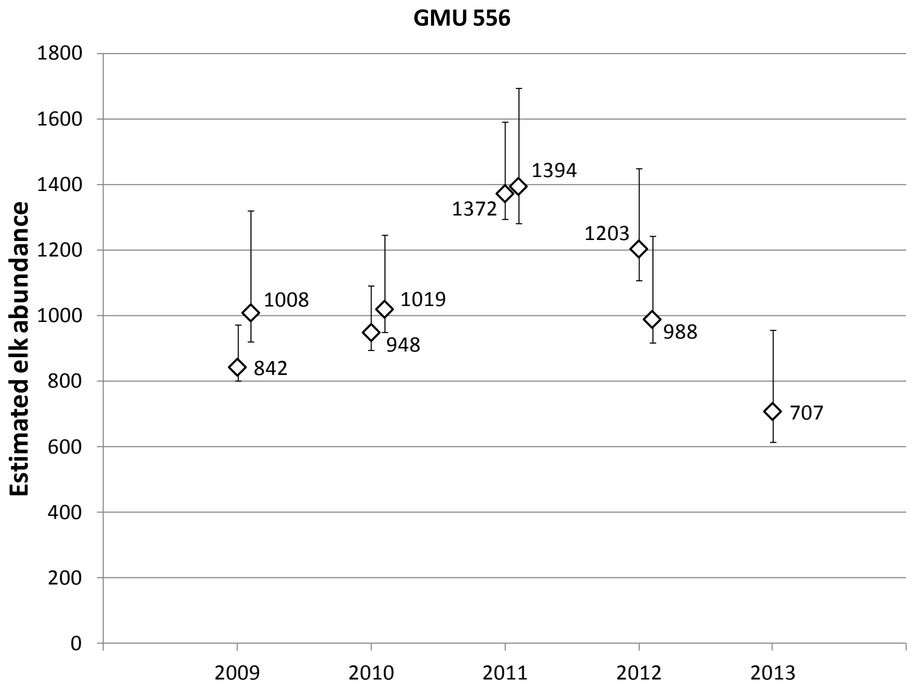


Figure 26. Sightability model estimates for total elk abundance (± 95% CI) in GMU 556, Mount St. Helens, 2009-2013.

GMU-specific estimates for total cow elk abundance, 2006-2013 (Figs. 27-31), also indicated a steady decline in the number of cow elk in GMUs 520 and 550, a modest decline in GMU 524, a slight increase followed by a decrease in GMU 556, and a relatively steady increase in cow numbers in GMU 522.

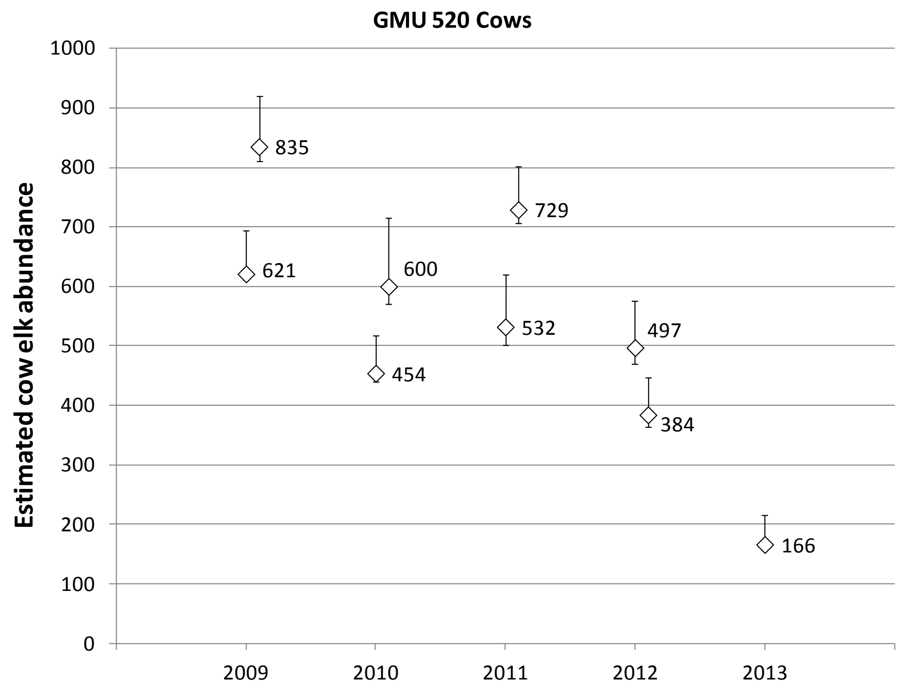


Figure 27. Sightability model estimates for cow elk abundance (± 95% CI) in GMU 520, Mount St. Helens, 2009-2013.

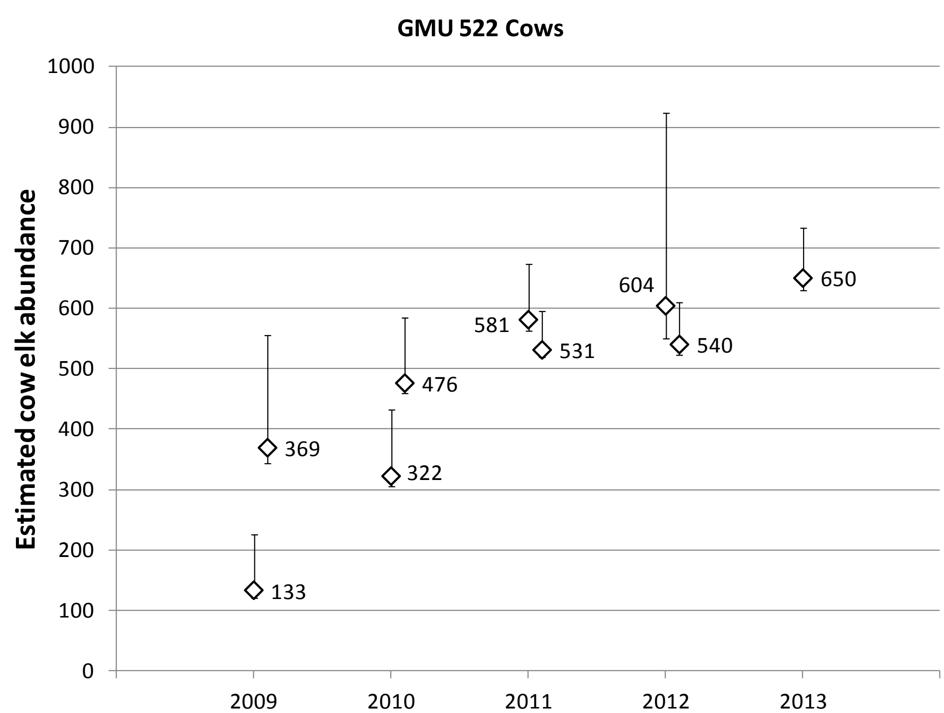


Figure 28. Sightability model estimates for cow elk abundance (± 95% CI) in GMU 522, Mount St. Helens, 2009-2013.

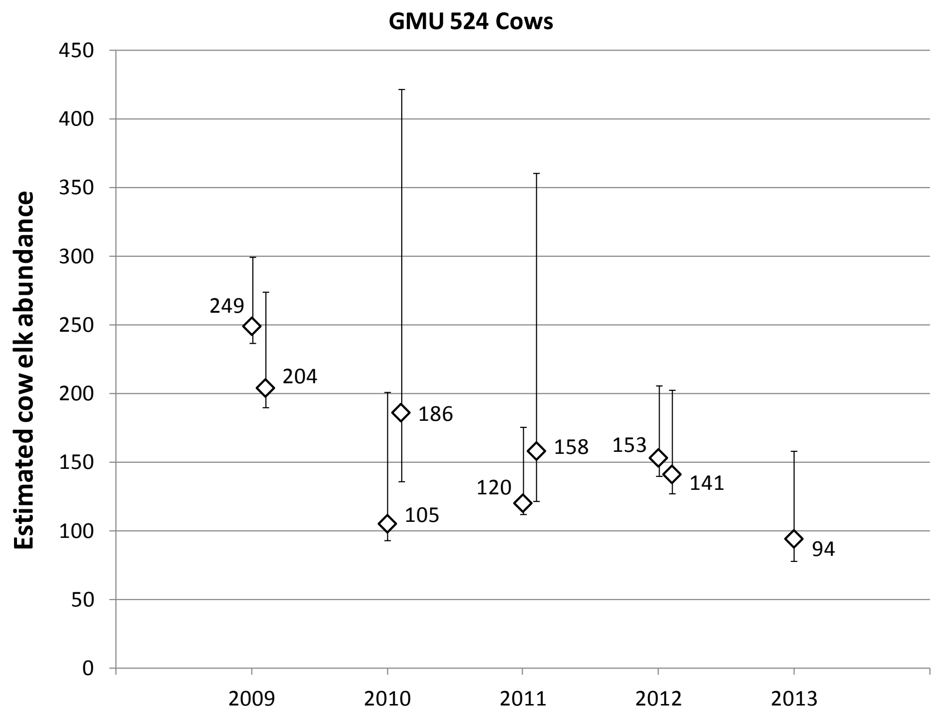


Figure 29. Sightability model estimates for cow elk abundance (± 95% CI) in GMU 524, Mount St. Helens, 2009-2013.

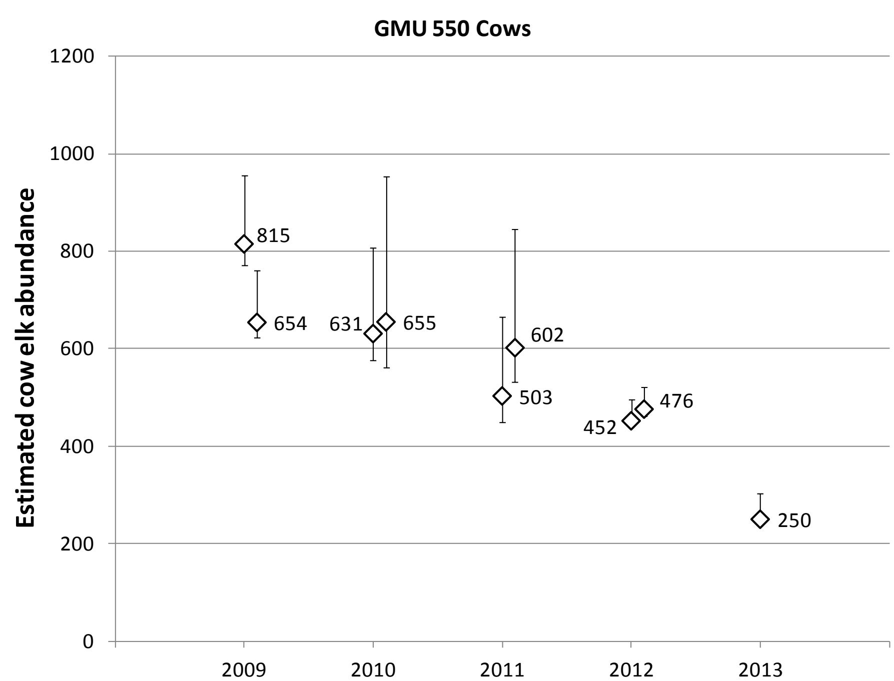


Figure 30. Sightability model estimates for cow elk abundance (± 95% CI) in GMU 550, Mount St. Helens, 2009-2013.

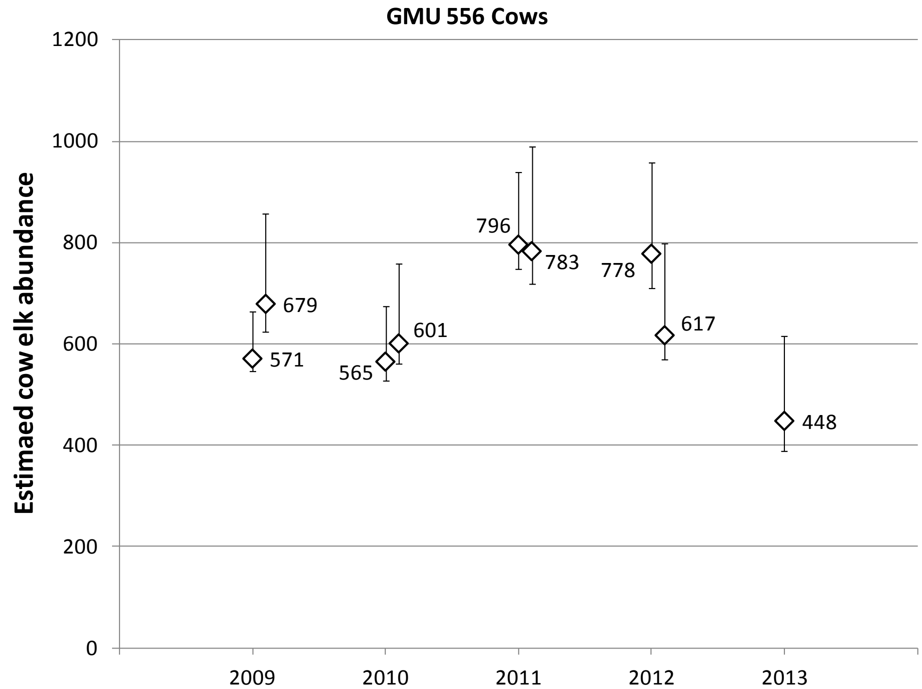


Figure 31. Sightability model estimates for cow elk abundance (± 95% CI) in GMU 556, Mount St. Helens, 2009-2013.

Mark-Resight

As per the Methods section (above), we generated mark-resight estimates 2009-2012 using the LNME model, a multi-sampling-occasion model, and using the Lincoln-Petersen (LP) model for 2013 (1 sampling occasion). Across the 11 LNME models for total elk in the area surveyed twice each year, 2009-2012, the best supported model had a constant detection parameter (p_i), 2 unique heterogeneity parameters (σ_i) (where 2009=2011 and 2010=2012), and annual variation in estimated total elk (Table 5). Two other models were within 2 AIC_c units of the best model. The second best-supported model had 2 unique detection parameters (1 for 2012 and 1 for all other years), a constant heterogeneity parameter, and annual variation in estimated total elk (Table 5). The last model within 2 AIC_c units of the best model was the simplest model, with a single estimated detection parameter across all sessions, a constant heterogeneity estimate, and annual variation in estimated total elk (Table 5). The remaining models had limited support.

Table 5. Model selection results for LNME mark-resight estimates of total number of elk in the 5-GMU study area, 2009-2012, Mount St. Helens, WA.

Model[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	Dev[f]
$p(.),\sigma^2(2009{=}2011{\neq}2010{=}2012),N(\mathrm{yr})$	7	829.28	0.00	0.32	814.88
$p(2012{\neq}\mathrm{else}),\sigma^2(.),N(\mathrm{yr})$	7	830.35	1.07	0.19	815.95
$p(.),\sigma^2(.),N(\mathrm{yr})$	6	830.72	1.43	0.16	818.41
$p(2011{\neq}\mathrm{else}),\sigma^2(.),N(\mathrm{yr})$	7	832.12	2.84	0.08	817.72
$p(2009{\neq}\mathrm{else}),\sigma^2(.),N(\mathrm{yr})$	7	832.50	3.22	0.06	818.10
$p(\mathrm{sess1}{\neq}\mathrm{sess2}),\sigma^2(.),N(\mathrm{yr})$	7	832.52	3.23	0.06	818.11
$p(.),\sigma^2(\mathrm{yr}),N(\mathrm{yr})$	9	833.35	4.06	0.04	814.70
$p(2010{\neq}\mathrm{else}),\sigma^2(.),N(\mathrm{yr})$	7	833.71	4.43	0.04	819.31
$p(\mathrm{yr}),\sigma^2(.),N(\mathrm{yr})$	9	834.46	5.18	0.02	815.81
$p(\mathrm{sess1}{\neq}\mathrm{sess2}^{g}),\sigma^2(\mathrm{yr}),N(\mathrm{yr})$	10	835.19	5.90	0.02	814.39
$p(\mathrm{full}),\sigma^2(\mathrm{yr}),N(\mathrm{yr})$	16	842.89	13.61	<0.001	808.87

[a] model structure (p = detection probability; σ^2 = heterogeneity parameter; N = abundance estimate).
[b] number of unique model parameters.
[c] Akaike's Information Criterion, adjusted for small samples.
[d] difference in AIC_c units between model$_i$ and the best model.
[e] Akaike model weight.
[f] model deviance.
[g] detection probability varied between first and second surveys, but no annual effect.

Model-averaged estimates of total elk abundance in the area we surveyed each year with replicated surveys, based on the LNME model weights in Table 5, suggested a modest decline in total elk during 2009-2012; using the LP estimate from the same area in 2013 suggested an overall substantial decline in total elk, 2009-2013 (Fig. 32).

Actual estimates ranged from a high of 8,238 elk in 2011 to a low of 4,987 in 2013. Estimates generally depicted a consistent pattern, except that the 2011 estimate was substantially higher than the estimates for the previous 2 years. We discuss possible explanations for this in the Discussion section, but note here that the 2009-2010 winter was by far the mildest winter of the study; the high estimate for the spring of 2011 occurred 1 year after the mild winter. The models in Table 5 and the estimates derived from those models in Fig. 32 also did not allow detection rates of cows and bulls to be sex-specific.

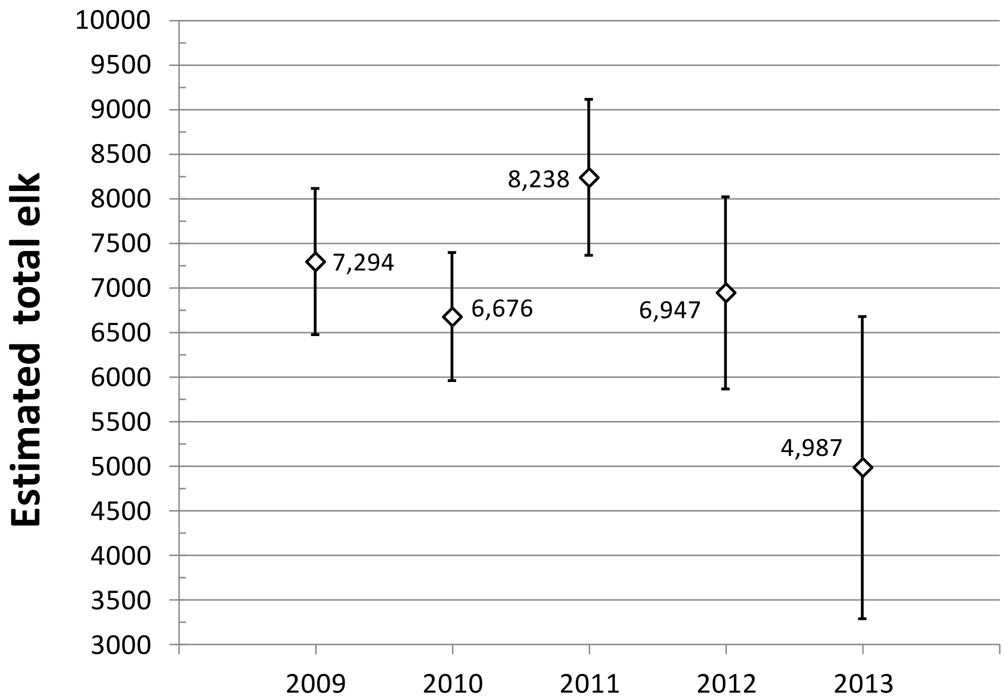


Figure 32. Mark-resight estimates (2009-2012 = LNME; 2013 = Lincoln-Petersen) for total elk (± 95% CI) in the 5-GMU study area, 2009-2013, Mount St. Helens, WA.

Among the 10 LNME models we evaluated for estimating the total number of cow elk and the total number of branch-antlered bull elk in the area we surveyed twice each year, 2009-2012, only 2 models were well-supported. Collectively, these 2 models accounted for 99% of the available model weight. The best model had 12 unique parameters: 2 year-invariant, but sex-specific detection parameters, 2 year-invariant, but sex-specific heterogeneity parameters, and sex and year-specific estimates of abundance (Table 6). The next best model was 0.81 AIC*c* units from the best model and differed from the best model only in that it had a single unique detection parameter that was equal for both sexes (Table 6). The remaining models in the candidate model set, including those with the least and most unique parameters were not supported.

Table 6. Model selection results for LNME mark-resight estimates of total number of cow elk and branch-antlered bull elk in the 5-GMU study area, 2009-2012, Mount St. Helens, WA.

Model[a]	k[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	Dev[f]
p(sex),σ^2(sex),N(sex × yr)	12	869.31	0.00	0.59	844.19
p(.),σ^2(sex),N(sex × yr)	11	870.11	0.81	0.40	847.17
p(sex × yr),σ^2(sex),N(sex × yr)	18	877.22	7.91	0.01	838.71
p(yr),σ^2(sex × yr),N(sex × yr)	24	885.94	16.63	<0.001	833.43
p(sex × yr),σ^2(sex × yr),N(sex × yr)	32	901.08	31.77	0.00	828.89
p(sex),σ^2(sex),N($F_{1=2\neq3\neq4}$[g], M[.])	8	980.79	111.48	0.00	964.28
p(.),σ^2(sex),N($F_{1=2=3\neq4}$, M[.])	7	1000.94	131.63	0.00	986.54
p(sex),σ^2(sex),N(sex)	6	1022.40	153.09	0.00	1010.10
p(sex),σ^2(sex),N($F_{1=2\neq3=4}$, M[.])	7	1023.15	153.84	0.00	1008.75
p(.),σ^2(.),N(sex × yr)	10	3596.29	2726.90	0.00	3575.51

[a] model structure (p = detection probability; σ^2 = heterogeneity parameter; N = abundance estimate).
[b] number of unique model parameters.
[c] Akaike's Information Criterion, adjusted for small samples.
[d] difference in AIC_c units between model$_i$ and the best model.
[e] Akaike model weight.
[f] model deviance.
[g] cow elk abundance constrained [number subscripts 1-4 = spring 2009-2012].

Model-averaged estimates of total cow elk abundance in the area we surveyed each year with replicated surveys, based on the LNME model weights in Table 6, suggested a pattern similar to the pattern for the total elk abundance estimates, 2009-2012 (Fig. 33). The LNME estimates for total cows declined from spring 2009 to spring 2010, increased again in spring 2011, and declined in spring 2012. Estimates ranged from a high of 4,444 cows in 2011 to a low of 3,758 cows in 2010. Including the LP estimate from the 2013 mark-resight survey, the overall pattern indicated a decline in the number of cow elk, 2009-2013 (Fig. 33). The LNME estimates for total branch-antlered bull abundance, 2009-2012, and the 2013 LP estimate for branch-antlered bull abundance in the area we surveyed each year suggested a relatively stable branch-antlered bull subpopulation, 2009-2013 (Fig. 34). Estimated bull numbers ranged from 647 (2009) to 797 (2013); confidence intervals for the 2013 cow and bull estimates were broad.

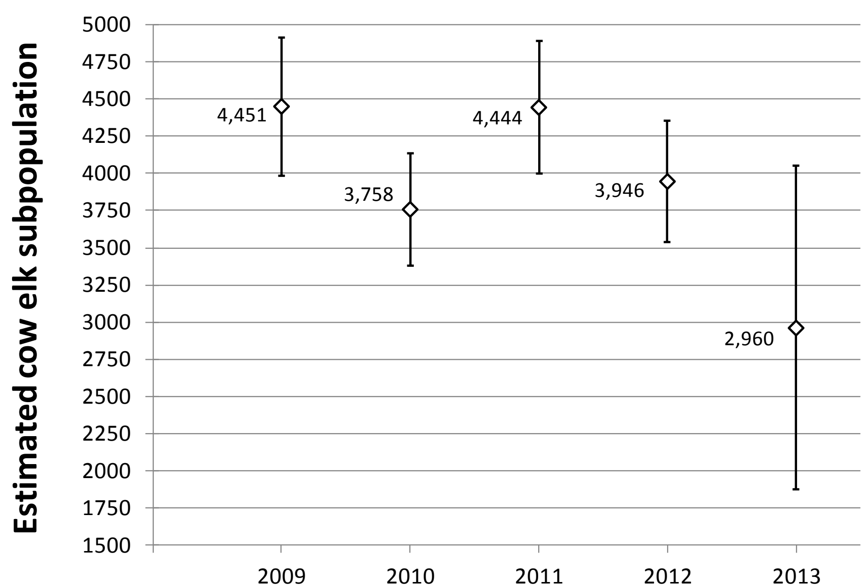


Figure 33. Mark-resight estimates (2009-2012 = LNME; 2013 = Lincoln-Petersen) for total cow elk (± 95% CI) in the 5-GMU study area, 2009-2013, Mount St. Helens, WA.

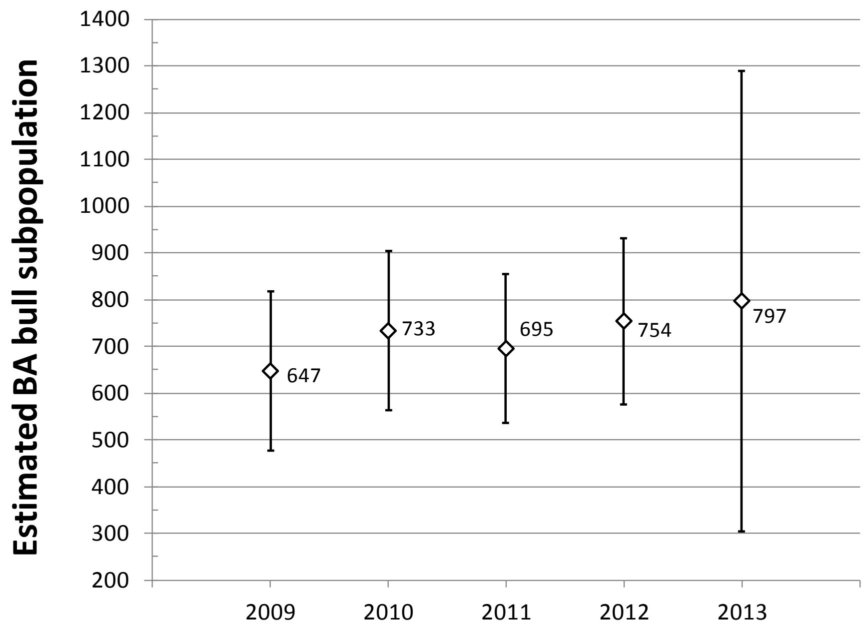


Figure 34. Mark-resight estimates (2009-2012 = LNME; 2013 = Lincoln-Petersen) for total branch-antlered bull elk (± 95% CI) in the 5-GMU study area, 2009-2013, Mount St. Helens, WA.

Detection rates for radiomarked elk, estimated as the derived parameter μ under the fully parameterized, sex-specific, LNME model (Table 6) were generally higher for radiomarked cows than for bulls (Table 7). Estimated detection for cows ranged 0.43-0.64 across surveys; 6 of 8 estimated detection rates for radiomarked cow elk were >0.50. Estimated detection for bulls ranged 0.28-0.56 across surveys; only 3 of 8 detection rate estimates for radiomarked bulls exceeded 0.50. Under the best sex-specific model, which had a single detection rate parameter for cows and a single parameter for bulls, μ = 0.54 (95% CI = 0.49-0.59) for radiomarked cows and μ = 0.44 (95% CI = 0.36-0.54) for radiomarked bulls.

Table 7. Estimated detection rates for radiomarked elk from the fully parameterized, sex-specific LNME mark-resight model, 2009-2012, Mount St. Helens, WA.

Year	Session	Sex	Estimated detection (μ_i)	95% CI_{low}	95% CI_{high}
2009	1	F	0.64	0.48	0.77
2009	2	F	0.56	0.41	0.71
2010	1	F	0.56	0.42	0.68
2010	2	F	0.52	0.39	0.65
2011	1	F	0.49	0.38	0.61
2011	2	F	0.60	0.48	0.71
2012	1	F	0.52	0.39	0.64
2012	2	F	0.43	0.32	0.56
2009	1	M	0.38	0.15	0.68
2009	2	M	0.28	0.09	0.60
2010	1	M	0.51	0.26	0.75
2010	2	M	0.44	0.21	0.69
2011	1	M	0.56	0.34	0.75
2011	2	M	0.51	0.30	0.71
2012	1	M	0.39	0.20	0.63
2012	2	M	0.39	0.20	0.63

Among the 15 models in the candidate model set for data coded to 7 groups (GMU-specific cows, branch-antlered bulls in GMU 522, branch-antlered bulls in the other 4 GMUs), 2 models garnered >80% of the model weight (Table 8). The best model had 4 detection parameters (*i.e.*, cows in GMU 522, all other cows, bulls in GMU 522, and bulls in all other GMUs), a single heterogeneity parameter that applied to all groups across all years, and group and sex-specific abundance parameters. The second best model was similar, except that heterogeneity was modeled as sex-specific (Table 8). All the remaining models were at least 3.52 AIC_c units from the best-supported model.

Table 8. Model selection results for LNME mark-resight estimates of group-specific cow elk (5 groups = GMU) and branch-antlered bull elk (2 groups = mudflow and non-mudflow bulls), 2009-2012, Mount St. Helens, WA.

Model[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	Dev[f]
pF(522[g]), *pM*(grp), σ^2(.),*N*(grp × yr)	33	1041.28	0.00	0.58	967.18
pF(522), *pM*(grp), σ^2(sex),*N*(grp × yr)	34	1043.10	1.82	0.23	966.48
pF(.), *pM*(grp), σ^2(.),*N*(grp × yr)	32	1044.80	3.52	0.10	973.20
pF(.), *pM*(grp), σ^2(sex),*N*(grp × yr)	33	1046.45	5.18	0.04	972.35
pF(grp), *pM*(grp), σ^2(sex),*N*(grp × yr)	37	1047.24	5.97	0.03	962.94
pF(522), *pM*(grp), σ^2(.),*N*(grp × yr, M'[h])	30	1048.31	7.03	0.02	981.66
pF(.), *pM*(grp), σ^2(.),*N*(grp × yr, M')	29	1051.76	10.48	0.003	987.56
pF(522), *pM*(.), σ^2(sex),*N*(grp × yr)	33	1055.57	14.30	<0.001	981.47
pF(.), *pM*(.), σ^2(sex),*N*(grp × yr)	32	1058.94	17.67	<0.001	987.35
pF(522), *pM*(grp), σ^2(sex),*N*(grp × yr, F'[i])	31	1127.33	86.06	0.000	1058.22
pF(.), *pM*(grp), σ^2(sex),*N*(grp × yr, F')	30	1135.67	94.39	0.000	1069.03
pF(522), *pM*(grp), σ^2(.),*N*(grp × yr, F''[j])	27	1262.98	221.70	0.000	1203.63
pF(.), *pM*(grp), σ^2(.),*N*(grp × yr, F'')	26	1278.86	237.58	0.000	1221.92
pF(522), *pM*(grp), σ^2(.),*N*(grp)	12	1898.10	856.82	0.000	1873.05
pF(.), *pM*(grp), σ^2(.),*N*(grp)	11	1904.74	863.47	0.000	1881.86

[a] model structure (*pF* = cow detection probability; *pM* = bull detection probability; σ^2 = heterogeneity parameter; *N* = abundance estimate).

[b] number of unique model parameters.

[c] Akaike's Information Criterion, adjusted for small samples.

[d] difference in AIC_c units between $model_i$ and the best model.

[e] Akaike model weight.

[f] model deviance.

[g] unique cow detection parameter for GMU 522 cows.

[h] abundance for non-GMU 522 bulls constant across years.

[i] abundance for GMU 556 cows constant across years.

[j] abundance for GMU 556 and GMU 524 cows constant across years.

Model-averaged LNME estimates of cow elk abundance in the area we surveyed each year with replicated surveys, based on the model weights in Table 8, suggested a substantial decline in GMU 520 and 550 during 2009-2012 (Figure 35). In GMU 520, point estimates indicated a decline of more than 40% between spring 2009 and spring 2012. In GMU 550, the indicated decline over the same period was about 1/3. During 2009-2012, cow elk abundance estimates in GMU 522 (the mudflow) increased, then stabilized (Fig. 35). In GMU 524, cow elk abundance estimates declined substantially between spring 2009 and spring 2010, and then became relatively stable (Fig. 35). Model-averaged LNME estimates for GMU 556 followed the same qualitative pattern as we had seen for total elk and total cow elk (Figs. 32, 33); estimates declined from 2009 to 2010, increased in 2011, and declined again in 2012 (Fig. 36). Overall, in GMU 556, estimated cow elk abundance was slightly higher in the last spring we conducted replicated surveys (2012) than it had been in the first 2 springs of our work (2009, 2010). We did not attempt to generate Lincoln-Petersen estimates of abundance at the GMU scale for the single 2013 survey because the numbers of marked elk per GMU were too small by spring 2013 to justify this approach.

Under the best LNME model derived for the 7-group dataset, the derived detection rate estimates (μ_i) for radiomarked elk were higher for both cow elk and for branch-antlered bull elk in GMU 522 (and the other portions of the North Fork of the Toutle R. mudflow) than for the rest of the study area (Table 9). Estimated detectability for bulls in the managed forest was relatively low and less than half that of mudflow bulls. LNME estimates for bull abundance were relatively stable 2009-2012 for both mudflow bulls and the forested subarea bulls (Fig. 37).

Table 9. Estimated detection rates for radiomarked elk from the best-supported, group-specific LNME mark-resight model, 2009-2012, Mount St. Helens, WA.

Group	Estimated detection (μ_i)	95% CI_{low}	95% CI_{high}
Cows (GMU≠522)	0.52	0.46	0.57
Cows (GMU=522)	0.67	0.56	0.77
BA bulls (GMU≠522)	0.33	0.24	0.44
BA bulls (GMU=522)	0.71	0.55	0.84

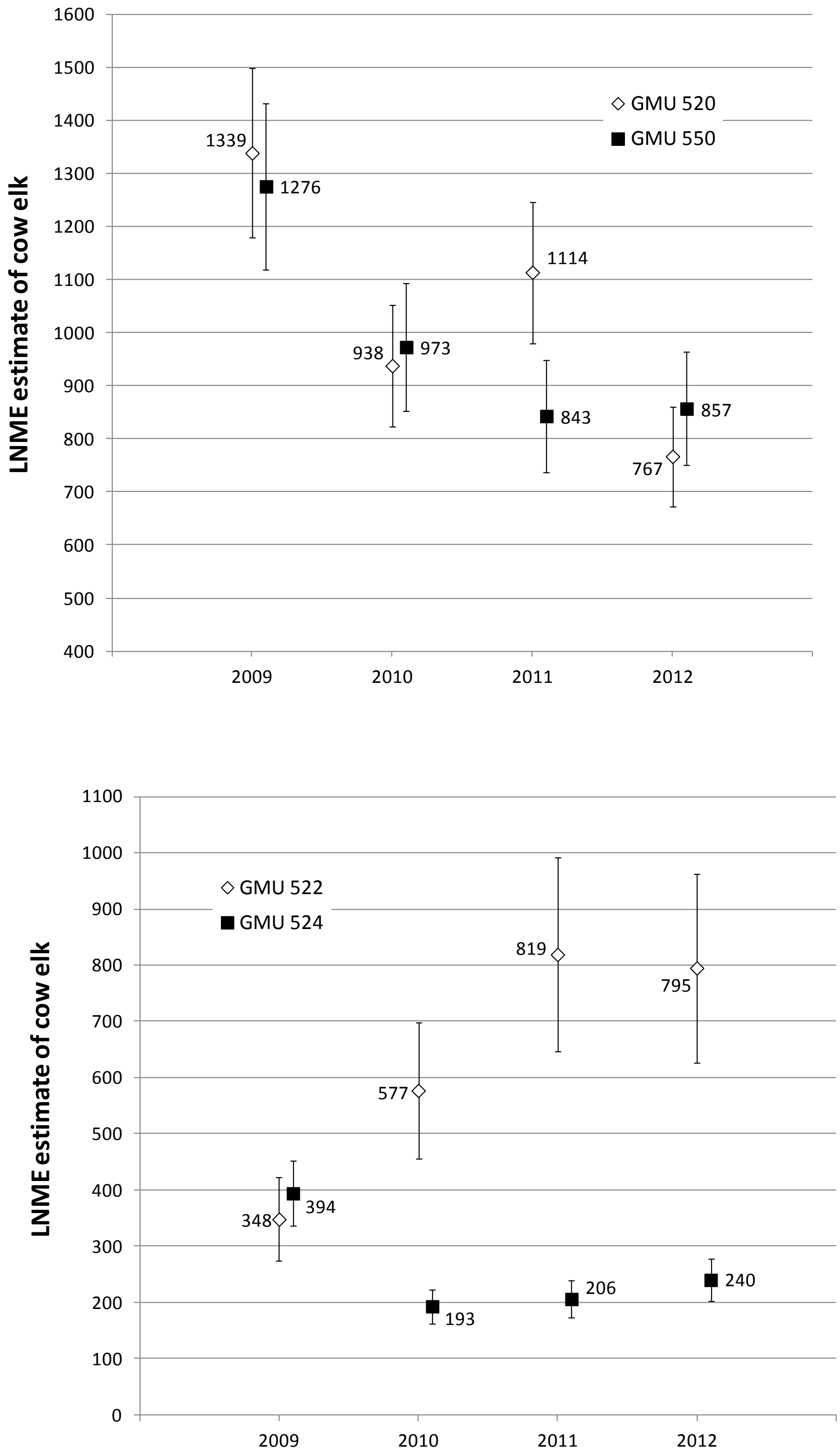


Figure 35. LNME Mark-resight estimates, 2009-2012, for total cow elk (± 95% CI) in GMUs 520 and 550 (top panel); 522 and 524 (bottom panel), Mount St. Helens, WA.

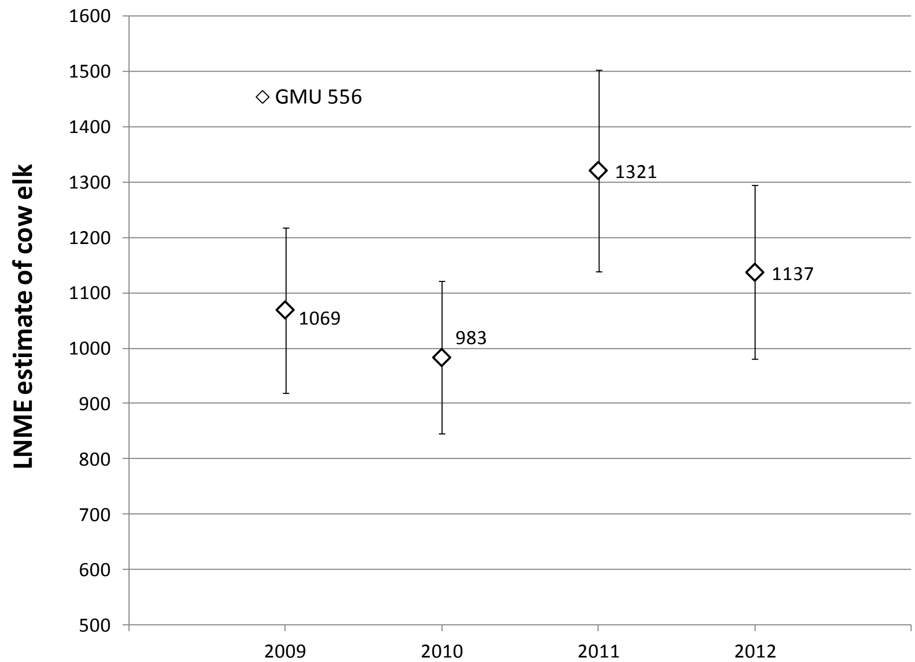


Figure 36. LNME Mark-resight estimates, 2009-2012, for total cow elk (± 95% CI) in GMU 556, Mount St. Helens, WA.

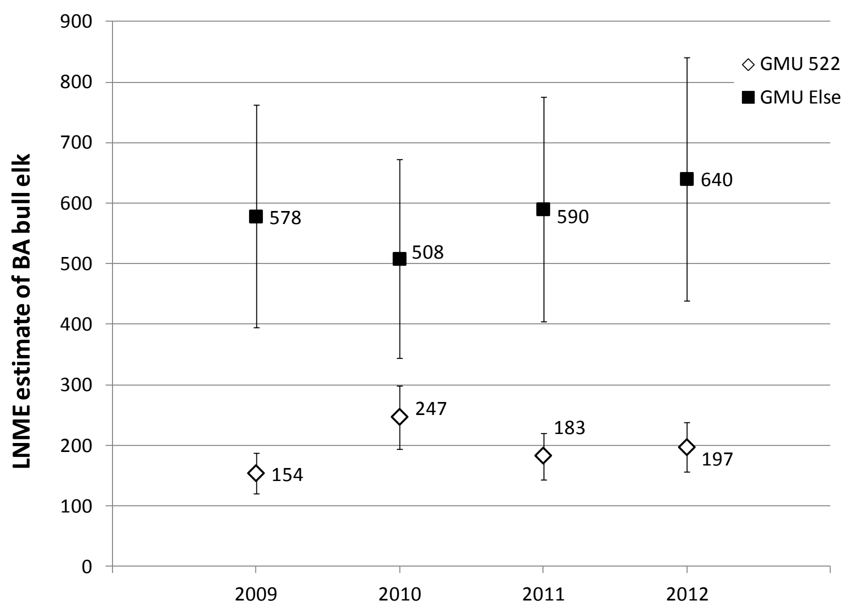


Figure 37. LNME Mark-resight estimates, 2009-2012, for total branch-antlered bull elk (± 95% CI), Mount St. Helens, WA.

Rate of Increase and Method Contrast

The series of annual estimates indicated a slight decline (negative rate of increase) for total elk abundance and total cow elk abundance using sightability model estimates, 2009-2013 (Table 10). By GMU, cow elk numbers declined substantially (≈ -20%) in GMUs 520, 524, and 550 using sightability model estimates. Cow elk abundance increased in GMU 522 and appeared relatively stable in GMU 556 using the sightability model estimates. For the mark-resight estimates, 2009-2012, total elk abundance trend was relatively flat and slightly negative for all cow elk (Table 10). For GMU 520, 524, and 550 cow elk, the mark-resight estimates indicated a substantive decline (≈-15%); the trend for GMU 522 mark-resight cow estimates was substantially positive and for GMU 556 cows was modestly positive (Table 10).

Table 10. Estimated group-specific, exponential rate of increase (r), Mount St. Helens, WA. Sightability model estimates (2009-2013); LNME mark-resight estimates (2009-2012).

Abundance	r	95% CI_{low}	95% CI_{high}
Sightability model			
All elk	-0.04	-0.13	0.04
All cow elk	-0.06	-0.13	0.01
GMU 520 cows	-0.21	-0.36	-0.05
GMU 522 cows	0.19	0.06	0.33
GMU 524 cows	-0.18	-0.28	-0.08
GMU 550 cows	-0.20	-0.27	-0.12
GMU 556 cows	0.01	-0.09	0.11
LNME mark-resight			
All elk	0.01	-0.09	0.12
All cow elk	-0.02	-0.11	0.07
All cow elk (2009-2013)	-0.08	-0.21	0.06
GMU 520 cows	-0.15	-0.30	-0.001
GMU 522 cows	0.28	0.11	0.45
GMU 524 cows	-0.15	-0.43	0.14
GMU 550 cows	-0.13	-0.22	-0.05
GMU 556 cows	0.05	-0.07	0.16

The mark-resight estimates for GMU-specific cow abundance across years, 2009-2012, were highly correlated (Pearson's $r \geq 0.94$; $P < 0.001$) with sightability model estimates (from first and second session replicates, and means of the 2) (Fig. 38).

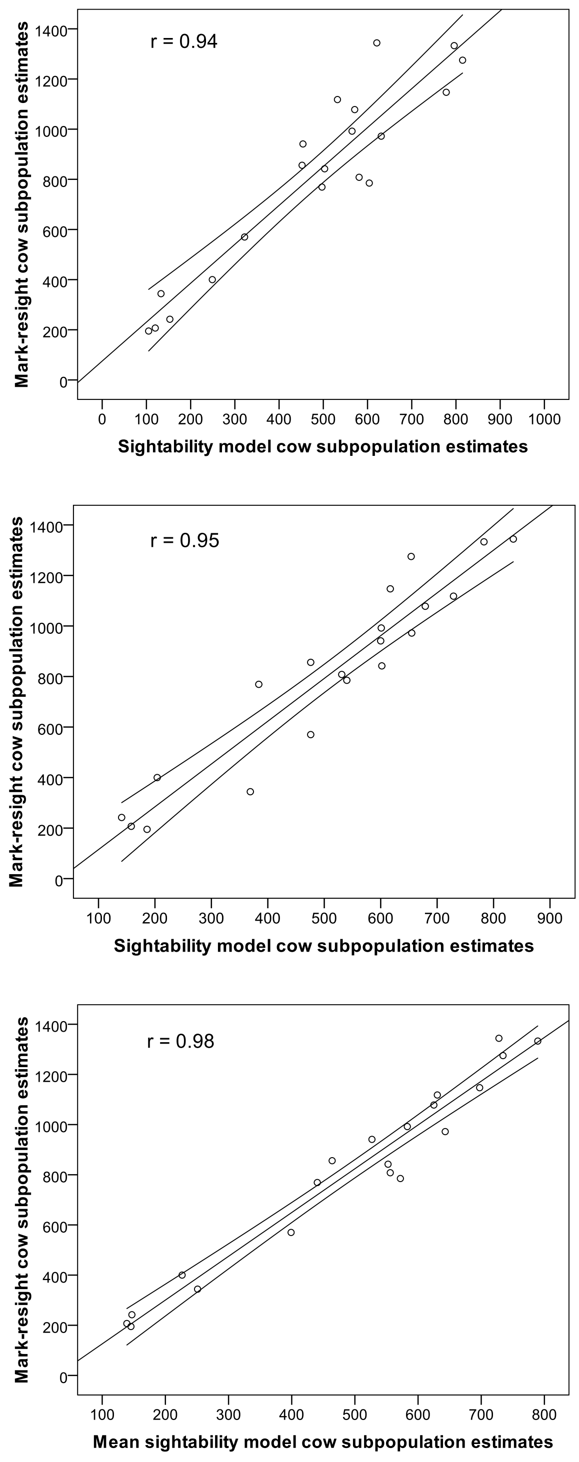


Figure 38. Correlation between Sightability Model (SM) estimates and LNME mark-resight estimates for cow elk abundance, 2009-2012 (panels are, top to bottom: for first survey replicate SM estimate, second survey SM estimate, and the means of the 2 annual SM estimates).

Recruitment

Annual observed spring calf recruitment across the entire 5-GMU study area varied considerably during 2009-2013, with estimates exceeding 40 calves per 100 cows in 2010 and 2011 and an estimate < 25 calves per 100 cows in 2013 (Fig. 39).

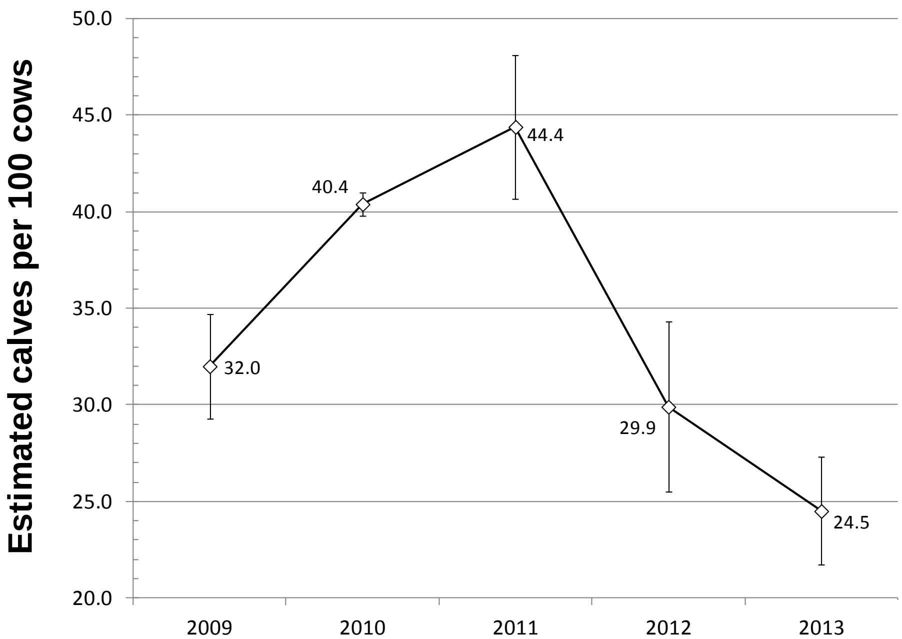


Figure 39. Elk calf-cow spring ratio estimates (plus 95% CI), 2009-2013, for the 5-GMU survey area, from aerial surveys, Mount St. Helens, WA.

In most of the 5 GMUs, the observed pattern was qualitatively similar to the landscape-level pattern. In 2011, the highest calf ratio estimates across the time series occurred in GMUs 520, 522, 524, and 550 (Fig. 40). The highest estimate in GMU 556 occurred in 2010. In all GMUs except 520, the observed ratios were relatively high in 2010 and 2011 and relatively low in 2009, 2012, and 2013 (Fig. 40). After adjusting the observed GMU-specific spring calf ratios for antlerless elk harvest the previous fall, the derived calf recruitment indices followed a relatively consistent pattern across all 5 GMUs (Fig. 41). Adjusting for antlerless harvest mostly had the effect of aligning the GMU 520 pattern to those of the other 4 GMUs, and aligning the indices for 2012 and 2013 across GMUs.

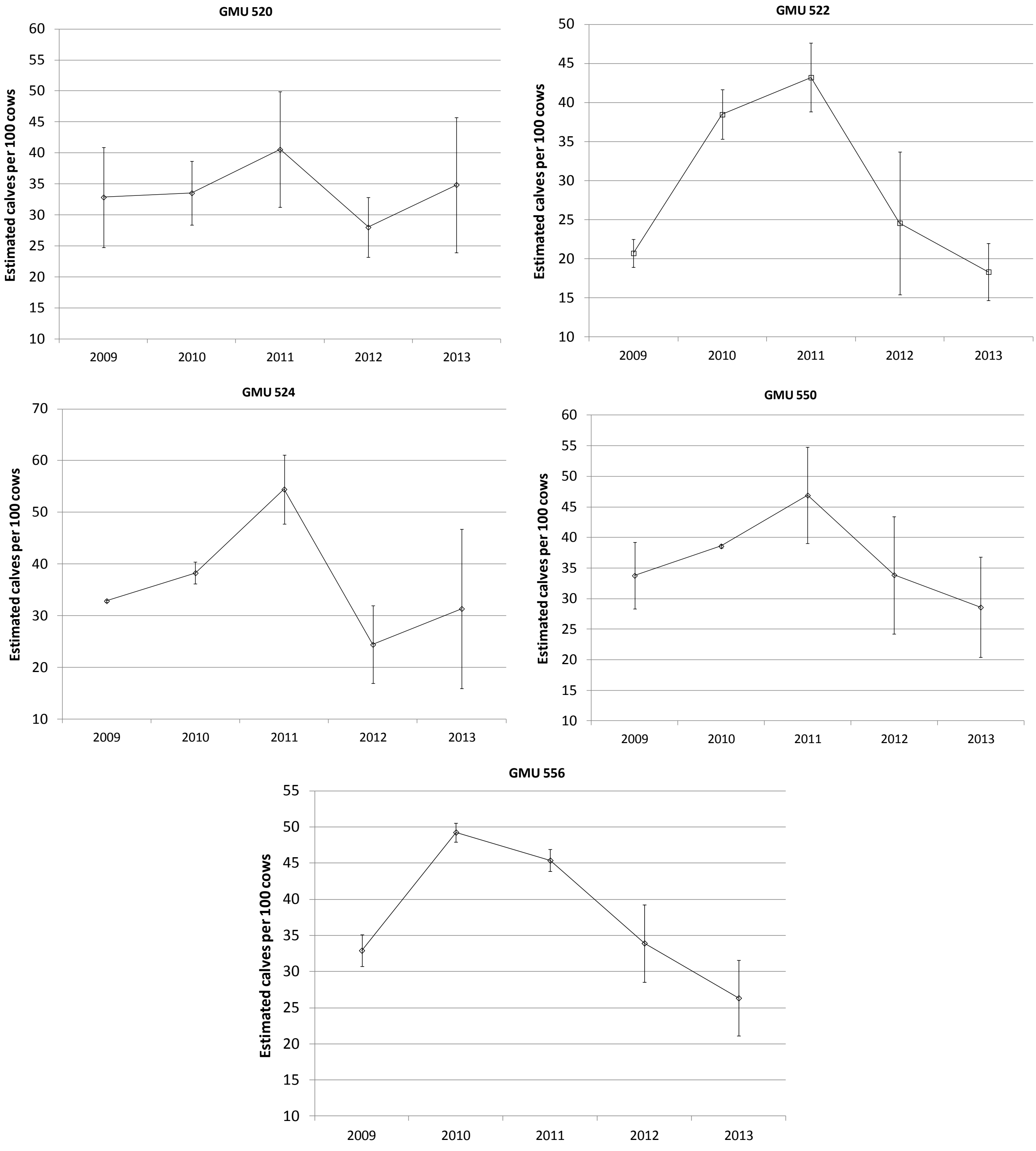


Figure 40. GMU-specific elk calf-cow spring ratio estimates (plus 95% CI), 2009-2013, from aerial surveys, Mount St. Helens, WA.

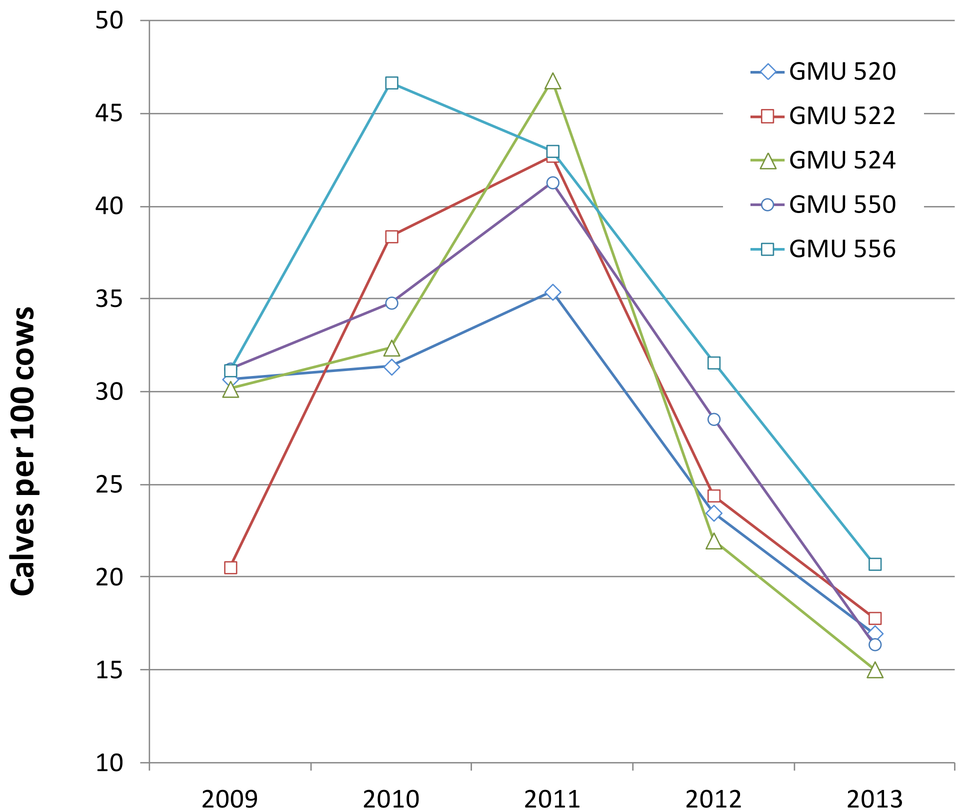


Figure 41. GMU-specific elk calf-cow spring ratio index (observed ratio adjusted for fall antlerless harvest), 2009-2013, Mount St. Helens, WA.

Survival

Over the course of the study, the sample sizes of elk at risk were relatively similar during the last 3 survival years; the sample of radiomarked elk was smaller in the first survival year in our analysis. We documented the deaths of 79 radiomarked elk (Fig. 42). Deaths per year ranged from 14 (2009-2010) to 31 (2012-2013). The numbers of elk killed by hunters were relatively stable (n = 9-13) across years, but the number of elk dying of natural causes was much higher in the last year of the study than in the first 3 years (Fig. 42). The results suggested that the final survival year (2012-2013) was typified by a particularly high loss of radiomarked elk, relative to other years. The natural mortalities during 2012-2013 were spread across all 5 GMUs (*i.e.*, were not limited to mudflow elk).

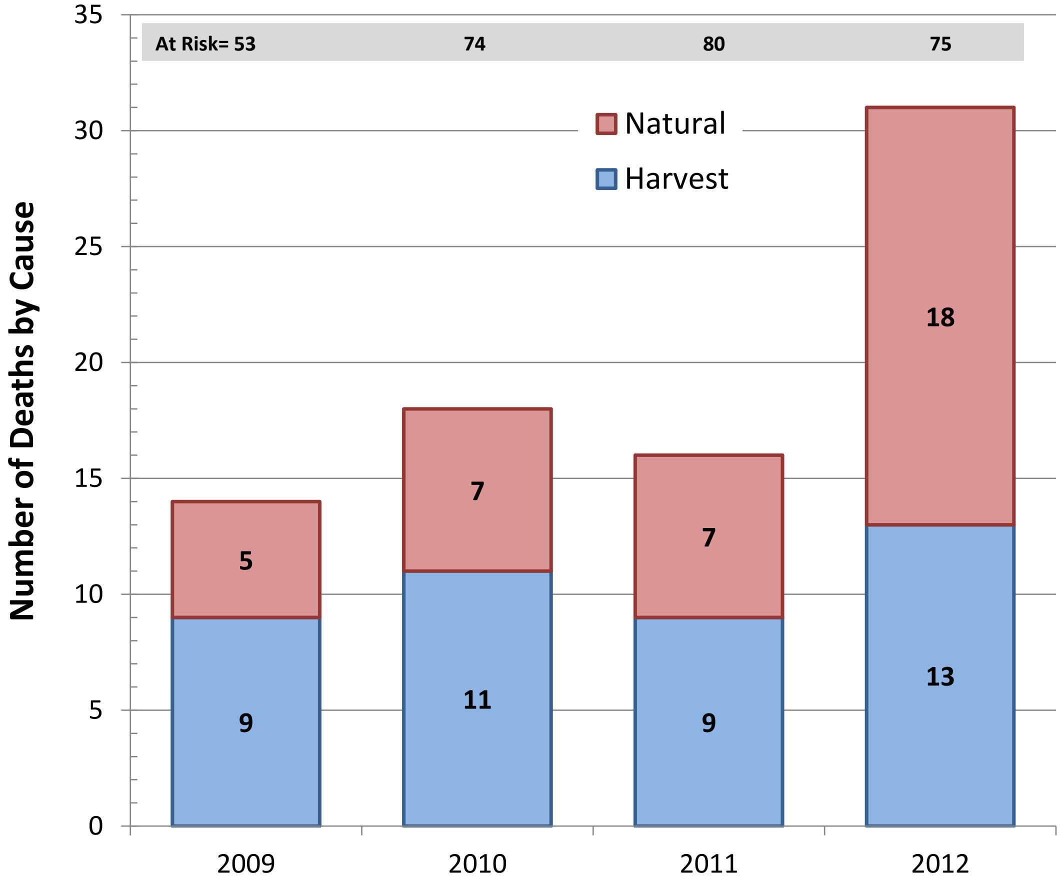


Figure 42. Total radiomarked elk deaths by cause, Mount St. Helens, Washington, survival years 2009-2012. Sample size of collared elk at risk at the beginning of each survival year is shown at the top of the panel.

Among the candidate models in our survival model set, 2 models accounted for 68% of the available model weight; the best model accounted for 50% of the weight and the next best model garnered 18% of the model weight (Table 11). The best model had a common cow survival parameter for GMUs 520, 522, 524, and 556 that was constant during 2009-2011, a common cow survival parameter for all GMUs during the last survival year (2012), a unique survival parameter for GMU 550 cows during 2009-2011, and constant bull survival across years. The second-best model differed only in that it had a unique 2012 survival parameter for GMU 550 cows. All of the remaining models were at least 2.88 AIC*c* units from the best supported model and were not competitive with the best-supported model.

Table 11. Model selection results for radiomarked elk survival, Mount St. Helens, 2009-2013.

Model	k^a	$\Delta AIC_c{}^b$	$w_i{}^c$	Deviance
Ad F (year,GMU $model_1{}^d$), Ad M (.)	4	0.00	0.50	26.63
Ad F (year,GMU $model_2{}^e$), Ad M (.)	5	2.07	0.18	26.61
Ad F (year,GMU $model_3{}^f$), Ad M (.)	7	2.88	0.12	23.22
Ad F (year,GMU $model_2$), Ad M (2012≠else)	6	4.10	0.06	26.55
Ad F (year,GMU $model_3$), Ad M (2012≠else)	8	4.95	0.04	23.16
Ad F (2012≠else), Ad M (.)	3	4.96	0.04	33.66
Ad F (year,GMU $model_4{}^g$), Ad M (.)	5	6.02	0.02	30.57
Ad F (2012≠else), Ad M (2012≠else)	4	6.96	0.02	33.59
Ad F (year,GMU $model_5{}^h$), Ad M (.)	4	7.01	0.01	33.64
Ad F (year,GMU $model_6{}^i$), Ad M (.)	5	8.21	0.01	32.76
Ad F (year), Ad M (year)	8	13.80	0.001	32.01
Ad F (year,GMU $model_7{}^j$), Ad M (.)	5	14.87	<0.001	39.42
Ad F (.), Ad M (.)	2	17.65	<0.001	48.39
Ad F (GMU), Ad M (.)	6	20.65	<0.001	43.10
Ad F (year,GMU), Ad M (year)	24	27.32	<0.001	08.96

[a]Number of unique parameters in model.

[b]AIC_c difference between best model and $model_i$.

[c]Akaike model weight.

[d]GMU_{all} 2012≠$GMU_{520,522,524,556}$ 2009-2011≠GMU_{550} 2009-2011.

[e]GMU_{550} 2012≠GMU_{else} 2012≠$GMU_{520,522,524,556}$ 2009-2011≠GMU_{550} 2009-2011.

[f]GMU_{550} 2009≠2012≠2010=2011≠GMU_{else} 2009≠2012≠2010=2011.

[g]GMU_{520} 2012≠GMU_{else} 2012≠$GMU_{522,524,550,556}$ 2009-2011≠GMU_{520} 2009-2011.

[h]GMU_{550} 2012≠GMU_{else} 2012≠GMU_{all} 2009-2011.

[i]$GMU_{520,550}$ 2012≠ GMU_{else} 2012≠$GMU_{520,550}$ 2009-2011≠GMU_{else} 2009-2011.

[j]GMU_{550} 2011=2012≠ GMU_{else} 2011=2012≠GMU_{550} 2009-2011≠GMU_{else} 2009-2011.

Model-averaged annual survival estimates were modest (0.84-0.86) for adult cows in GMUs 520, 522, 524, and 556 for the 3 survival years beginning in 2009-2011 (Table 12). Estimated cow survival was substantially lower (0.52) across those GMUs in the survival year beginning in 2012, and was relatively low (0.51- 0.66) in all 4 years for GMU 550 cows (Table 12). Estimated annual survival for branch-antlered bulls was 0.55-0.56 across years. Most survival estimates were relatively precise, but estimated cow survival for the last survival year and estimates across years for GMU 550 cows had relatively wide confidence intervals. Under the best supported model from Table 11, annual cow survival was estimated to be 0.85 (95% CI = 0.78-0.91) during 2009-2011 in GMUs 520, 522, 524, and 556. During the same years, cow survival was estimated at 0.64 (95% CI = 0.48-0.78) in GMU 550. Under the best model, cow survival in the final survival year (2012-2013) was estimated to be 0.52 (95% CI = 0.38-0.65) across all 5 GMUs. Branch-antlered bull survival under the best model was estimated to be 0.56 (95% CI = 0.43-0.67) across years.

Table 12. Model-averaged annual survival estimates (*S*-hat) and associated unconditional 95% confidence intervals for radiomarked Mount St. Helens elk for 4 survival years using the models and Akaike model weights from Table 11. All estimates are for radiomarked adult cow elk, unless specified otherwise.

Year	GMU	*S*-hat	95% CI for *S*-hat
2009	520	0.86	0.73-0.93
2010	520	0.84	0.75-0.91
2011	520	0.84	0.75-0.91
2012	520	0.52	0.38-0.66
2009	522	0.86	0.73-0.93
2010	522	0.84	0.75-0.90
2011	522	0.84	0.75-0.90
2012	522	0.52	0.38-0.66
2009	524	0.86	0.73-0.93
2010	524	0.84	0.75-0.90
2011	524	0.84	0.75-0.90
2012	524	0.52	0.38-0.66
2009	550	0.64	0.41-0.82
2010	550	0.66	0.47-0.82
2011	550	0.66	0.47-0.82
2012	550	0.51	0.28-0.74
2009	556	0.86	0.73-0.93
2010	556	0.84	0.75-0.90
2011	556	0.84	0.75-0.90
2012	556	0.52	0.38-0.66
2009	BA bulls[a]	0.56	0.43-0.68
2010	BA bulls	0.56	0.43-0.68
2011	BA bulls	0.56	0.43-0.68
2012	BA bulls	0.55	0.41-0.69

[a] Branch-antlered bulls.

Hoof Disease Observations

Although elk hoof disease remains an extremely important management issue in southwest Washington, our study's scope did not include evaluating the condition's etiology, prevalence, or distribution. As described in the Methods section, the elk marking and monitoring design also was not intended to quantify the condition's specific effects on elk population dynamics nor its long-term implications for elk management. Limited information, however, was obtained regarding the short-term fates of elk that had various presentations of hoof pathology when we captured them for radiomarking (inadvertently). During 2009-2012, we handled 16 elk with some hoof irregularity (Table 13). The hoof issues we observed ranged from minor overgrowth of the keratinized portion of the hoof (often colloquially called "elf slipper" or "scissor hooves") to substantial ulceration (typically between the toes). Most of the elk we handled with hoof issues did not die in the very near-term, typically surviving for at least a year or more; several survived for the duration of the study or the duration of the time we were able to monitor their fates (*i.e.*, until collar drop for GPS-instrumented elk) (Table 13).

Because of increasing concerns about the prevalence of hoof disease during the latter portion of our study and because we detected a substantial number of previously unreported mortalities of radiomarked elk just prior to our last surveys associated with this study (spring 2013), we attempted to locate the carcasses of all radiomarked elk transmitting mortality signals as of April 2013, following our survey flights. Of the 19 elk transmitting mortality signals, 1 was located at a residence (*i.e.*, unreported harvest) and 6 had been dead too long to reliably determine cause of death (*e.g.*, could not rule out wounding loss from fall 2012 hunting seasons). Of the remaining 12, a minimum of 9 showed physical evidence of malnutrition, and malnutrition was suspected as the cause of death for the other 3 based on time-of-death and location; 3 of the 9 elk known to have succumbed to malnutrition had moderate-to-severe hoof disease (2 had 2 foot involvement, 1 had a single affected hoof), and 2 had a minor hoof deformity on 1 foot. Thus, among the mortalities of radiomarked elk we investigated in April 2013, most appeared to be linked to malnutrition. A small number of these instances may have involved hoof disease as a contributing factor, but most apparently were unrelated to any hoof affliction.

Table 13. Fates of elk with any visible hoof issue at capture among those elk radiomarked 2009-2012, Mount St. Helens, WA.

Marked	Condition	Fate
Feb 2009	Moderate hoof disease	Hunter-kill fall 2009
Feb 2009	Moderate hoof disease	Survived winter ‘09-‘10; dead by spring 2011
Feb 2009	Scissor hooves	Survived until winter ’12-‘13
Feb 2009	Scissor hooves	Contact lost winter ’11-’12; alive until then
Feb 2009	Scissor hooves	Still alive as of spring 2013
Feb 2009	Scissor hooves	Hunter-kill fall 2009
Feb 2009	Scissor hoof	Hunter-kill fall 2009
Feb 2009	Clubbed hoof	Hunter-kill fall 2009
Feb 2009	Scissor hoof	Hunter-kill fall 2010
Feb 2011	Moderate hoof disease	Alive at GPS collar drop May 2012
Feb 2011	Moderate hoof disease	Alive at GPS collar drop May 2012
Feb 2011	Moderate hoof disease	Alive at GPS collar drop May 2012
Feb 2012	Severe hoof disease	Still alive as of spring 2013
Feb 2012	Moderate hoof disease	Still alive as of spring 2013
Feb 2012	Moderate hoof disease	Still alive as of spring 2013
Feb 2012	Severe hoof disease	Survived winter ’11-’12; missing by spring 2013

Environmental Effects

Among potential response variables, we found significant correlations between observed calf ratio and the harvest-corrected calf ratio index (r = 0.99, P = 0.001), between the overwinter mortality index and both the observed calf ratio (r = -0.81, P = 0.10) and the calf ratio index (r = -0.82, P = 0.09), and between fall IFBF estimated from harvested cow elk organ sets and both the observed calf ratio (r = 1.0, P = 0.001) and the calf ratio index (r = 1.0, P = 0.03). We did not find significant correlations between the overwinter mortality index and either fall IFBF from the organ sets (*r* = -0.60, *P* = 0.59) or mid-winter IFBF estimated for live-captured elk (*r* = 0.62, *P* = 0.38); mid-winter IFBF for live elk was also not correlated with observed calf ratios (*r* = -0.03, *P* = 0.97), the corrected calf ratio index (*r* = 0.03, *P* = 0.98), or the fall IFBF estimates from harvested elk organs (*r* = 0.25, *P* = 0.84). Among these response variables, the organ-based fall estimates of IFBF represented only 3 data years, so the correlations involving those data derived from only 3 bivariate data points.

Live elk IFBF estimates were not significantly correlated with any of the spring-summer-fall precipitation metrics (*r* = -0.35-0.68, *P* = 0.33-0.96). Live elk IFBF, was also not correlated with early winter SWEs (*r* = 0.80, *P* = 0.20) and the sign of this nonsignificant correlation coefficient for the relationship was nonsensical (*i.e*., as early winter snowfall increased, mid-winter body fat estimates increased). Based on only 3 data points (*i.e*., years), fall IFBF derived from harvested elk organ sets was correlated with the slope of a fitted regression line to late summer-fall precipitation (*r* = 1.0, *P* = 0.07, and the sign of the relationship was sensible), but was not significantly correlated with early summer precipitation (*r* = 0.62, *P* = 0.58), total late summer-fall precipitation (*r* = 0.90, *P* = 0.29), or total spring-summer-fall precipitation (*r* = 0.85, *P* = 0.35).

The observed calf ratios and the calf recruitment indices were strongly related to late summer-fall precipitation; annual calf recruitment was higher in springs with greater precipitation (and the rate of daily precipitation accumulation) occurring during the previous late summer and early fall (Fig. 43). More than 90% of the variation in the annual calf recruitment indices was explained by the late summer-fall precipitation metrics. The spring calf recruitment metrics were not correlated with early summer precipitation (*r* = 0.21-0.25, *P* = 0.69-0.74) or with total spring-summer-fall precipitation (*r* = 0.65-0.69, *P* = 0.20-0.23). Likewise, calf recruitment was weakly correlated with SWEs for the early winter (*r* = -0.33 to -0.37, *P* = 0.54-0.59), late winter (*r* = -0.37 to -0.43, *P* = 0.47-0.54), and full winter periods (*r* = -0.33 to -0.38, *P* = 0.52-0.59).

The overwinter mortality index was poorly correlated with the previous early summer (*r* = -0.49, *P* = 0.33), late-summer fall (*r* = -0.30, *P* = 0.57) and total spring-summer-fall precipitation (*r* = -0.53, *P* = 0.28). Overwinter mortality was, however, correlated with late winter and full winter SWEs (r = 0.87, 0.81; P = 0.02, 0.05). Overwinter mortality was not as strongly correlated with early winter SWEs (r = 0.66, P = 0.16). Overwinter mortality appeared to be related (P = 0.03) to late winter snowfall nonlinearly (Fig. 44), although a linear fit was also significant (r^2 = 0.86, P = 0.008).

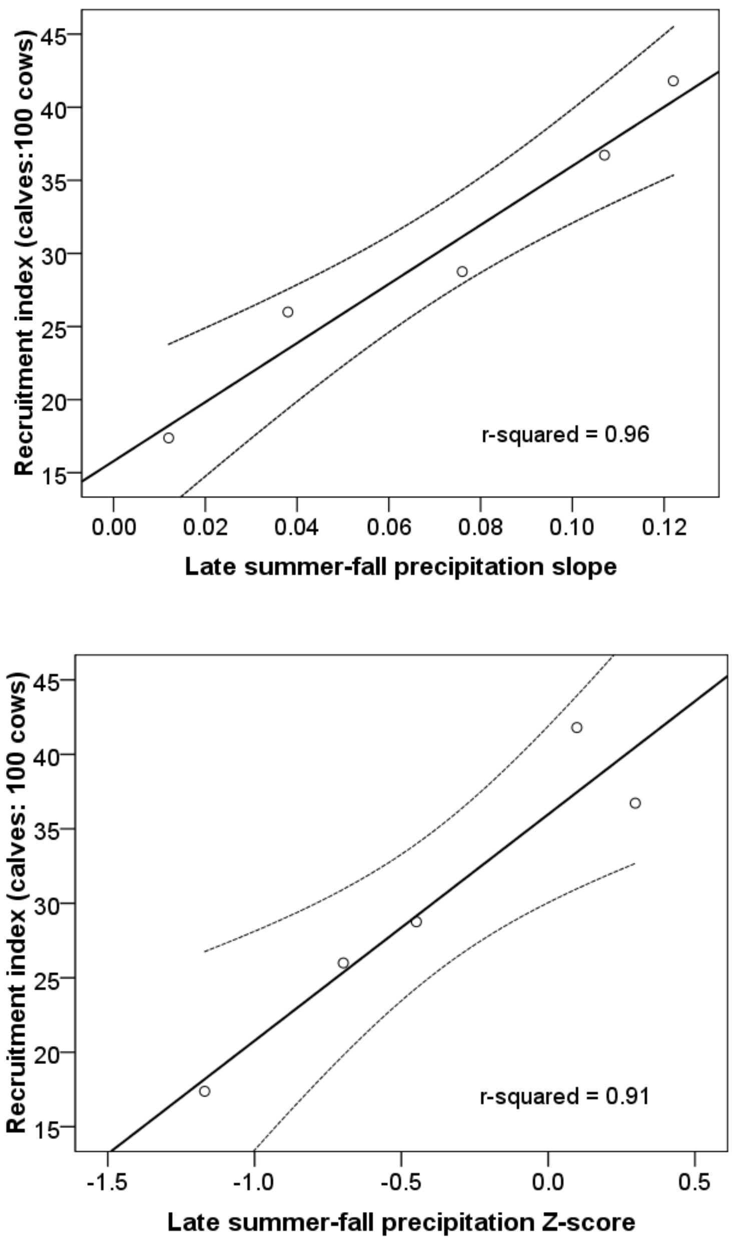


Figure 43. Linear fits of indexed spring calf-cow ratio to late summer-fall precipitation metrics, Mount St. Helens elk herd, 2009-2013.

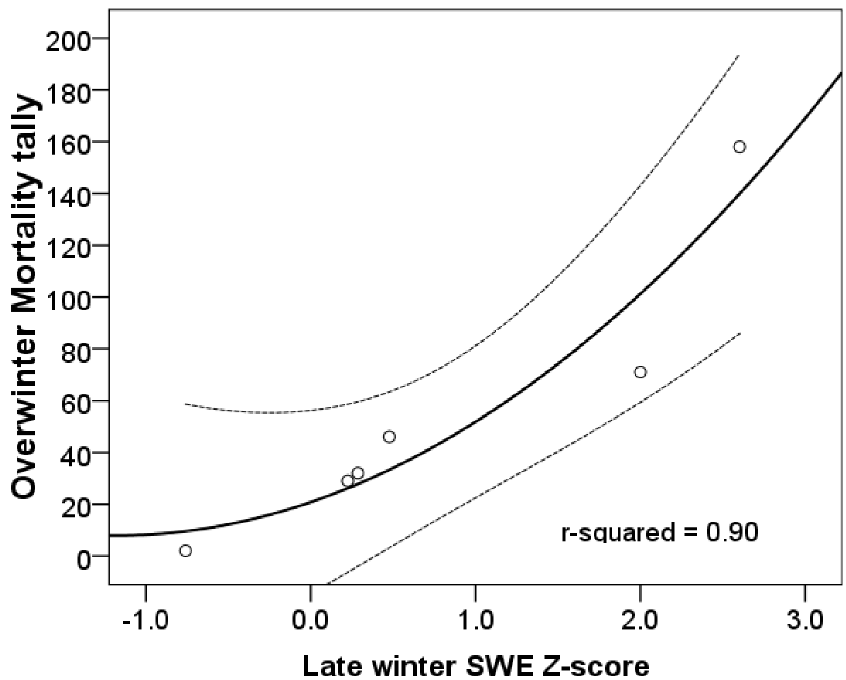
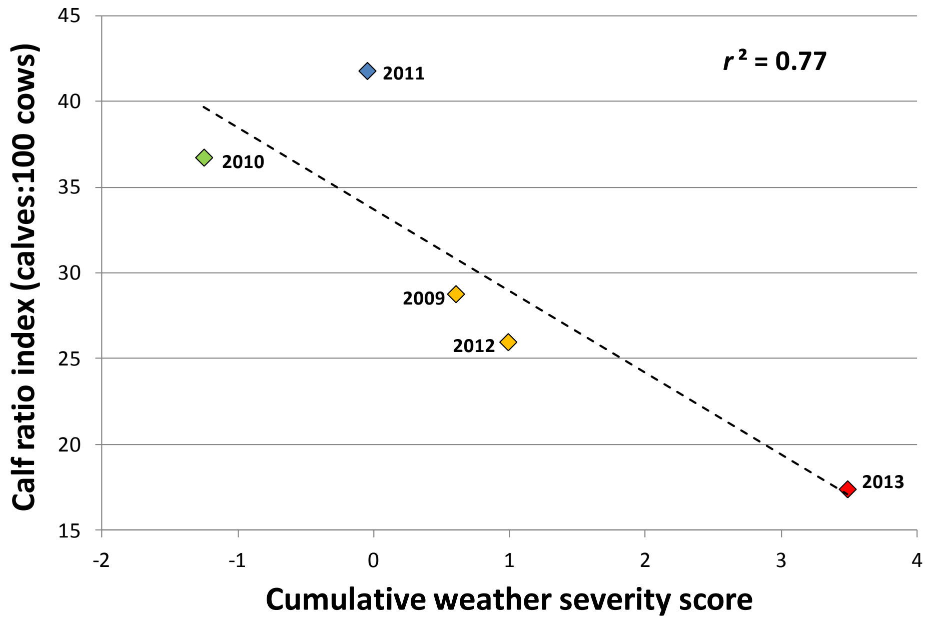


Figure 44. Non-linear fit of a spring overwinter mortality index to Z-scores for late winter snow water equivalents (SWE) measured at Spirit Lake, 2008-2013.

Combining the Z-scores for winter and previous late summer-fall weather severity (*i.e.*, relative winter snowfall and late summer-fall droughtiness) into a cumulative weather severity index did not improve the fit (*i.e.*, did not increase the r^2) to spring calf recruitment or overwinter mortality indexed in the spring (Fig. 45). Assuming the linear model, the residuals for the calf ratio index in 2011 and the mortality indices in 2008 and 2013 were larger than expected (Fig. 45). Because spring calf:cow ratios were unavailable prior to survey modifications made under this study, no data were available prior to the spring of 2009. The overwinter mortality survey predated our study, so an additional year of data (*i.e.*, spring 2008) was available for overwinter mortality relative to calf recruitment (Fig. 45).



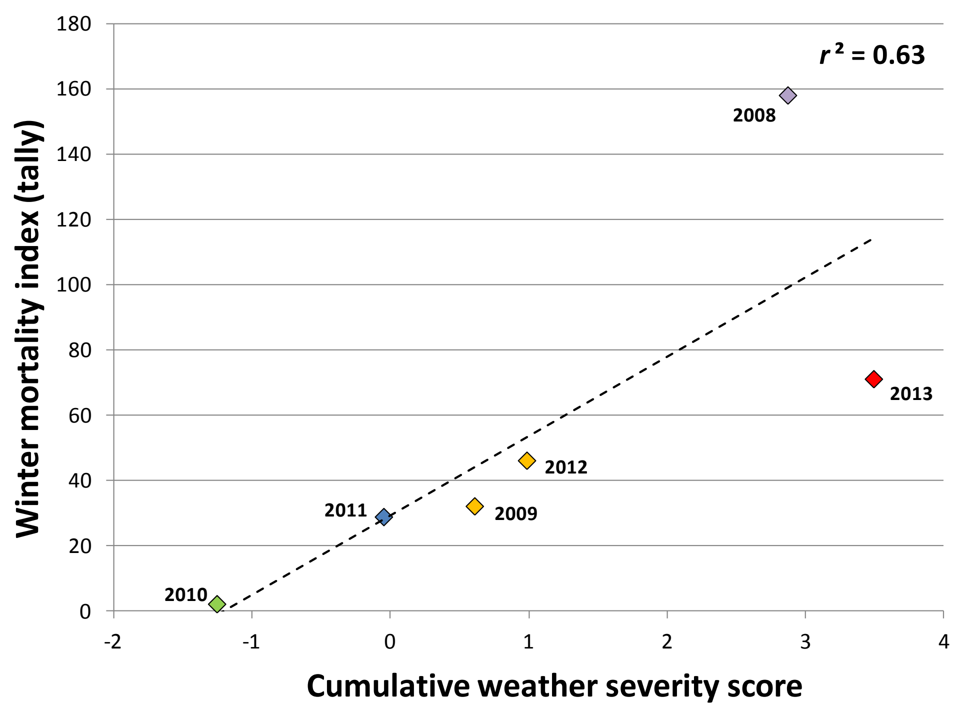


Figure 45. Linear fit of spring calf recruitment and overwinter mortality tallies to a combined index of current winter and previous late summer-fall weather severity. Marker colors: green = mild winter following normal summer; blue = normal winter and summer; yellow = normal winter and wet summer; purple = severe winter and normal summer; red = severe winter and droughty summer.

DISCUSSION

Our work was initially motivated by a need to better quantify elk abundance and demographics in the Mount St. Helens elk herd. Prior to our work, abundance estimates were attempted using the Sex-Age-Kill (SAK) model, a population reconstruction approach originally derived for white-tailed deer (*Odocoileus virginianus*) monitoring in the upper mid-west decades ago. The SAK model employs harvest data and additional demographic information (*e.g*., sex and age ratios) to reconstruct pre-harvest population size (Bender and Spencer 1999). Unfortunately, model outputs are very sensitive to assumption violations and parameter inputs that are rarely estimated well (*e.g*., the bull harvest mortality rate), often resulting in erratic performance and poor precision in the final abundance estimates (Millspaugh et al. 2009). Attempts to use the SAK model to estimate elk abundance at Mount St. Helens frequently produced biologically implausible results, and its use was eventually abandoned. (P. Miller, WDFW, personal communication).

As we initiated our work, it was apparent that the scale of the herd area made it infeasible to attempt to estimate total elk population size for the herd. Because these elk share a contiguous distribution with other elk in southwest Washington (*e.g*., Willapa Hills and South Rainier elk), the absence of a clearly defined biological population also rendered estimating total population size for the Mount St. Helens elk herd an indefensible goal. Therefore, we selected a 5-GMU subarea as our focal study area, with the intent of deriving estimates of population size or relative population size (*i.e*., an index) for this area. The 5-GMU study area represented an important core area for the Mount St. Helens elk herd that geographically captured most of the important elk management challenges for this herd (*e.g*., overwinter mortality, potentially excessive elk density, elk herbivory impacts, hoof disease). Despite that our study area was a limited subarea of the overall herd range, it was still a very large area that presented substantial challenges for quantifying elk abundance and for developing a long-term monitoring strategy.

In selecting a limited core subarea of the overall herd range, we recognized that estimates across years would be subject not only to demographic processes (*i.e*., natality and survival), but also movement (see Kendall 1999). Elk that were alive and present outside of our surveyed area in one year, might well be within the surveyed area boundary on a different year (see also Gould et al. 2005). Given that we surveyed elk each year in late winter / early spring, we expected movement to potentially influence our sampling year-to-year to some degree based on winter severity. This potentially added additional complexity to making inference about elk population trend, but alternatives were untenable. However, we believe the relatively large size of the area we sampled each winter reduced the effects of year-to-year movement and distribution on abundance inference, but did not eliminate these effects (see more on this below).

It was impractical, both fiscally and from the perspective of getting enough consecutive flyable weather days, to survey the entire study area with tightly spaced linear transects to obtain full, uniform coverage. Such an approach would have wasted a lot of resources flying large, heavily forested tracts where elk would be almost impossible to detect and where elk densities would be predictably very low (Starkey at al. 1982, Witmer et al. 1985, Jenkins and Starkey 1996). So, we adopted an approach wherein we attempted to fly most of the winter-occupied habitat with predictably moderate to high elk use and where elk would be at least modestly detectable. The use of an in-flight computer-based mapping system that allowed us to keep track of where we had flown and where the targeted habitat patches (*e.g.*, clearcuts, meadows/wetlands, young second-growth, hardwood stands) were located allowed us to effectively move through our counting units with good coverage of areas that met our criteria. Clearly, we missed elk that were in densely forested conifer stands, but such stands far from more open habitat with high elk forage values were presumed to harbor low numbers of elk. Conifer stands that were in close proximity to more open habitats would also hide elk, but our assumption was that these elk regularly used nearby openings for foraging (confirmed by our radio-tracking data; see also Hanley 1983); on any given set of flights, these elk were assumed to have real, non-zero probabilities of being detectable in the open habitat components adjacent to the heavier cover patches.

We explored monitoring approaches that were oriented towards large extent surveys (*i.e.*, data-based) rather than modeling approaches with less emphasis on actual field sampling (see Schwarz and Seber 1999 for a good general discussion of alternative designs). Both approaches we used—sightability-correction modeling and mark-resight—assumed elk groups often had detection rates <1.0. Imperfect detectability is common in aerial surveys of wildlife, including those of elk (Caughley 1974, Bartmann et al. 1986, Pollock and Kendall 1987, Samuel et al. 1987, Steinhorst and Samuel 1989, Gould et al. 2005, Barker 2008). Ignoring detectability predictably leads to biased estimates of abundance and other demographics, and good population monitoring programs must address the detection problem (Gardner and Mangel 1996, Pollock et al. 2002, Barker 2008, Tracey et al. 2008). Both sightability-correction and mark-resight models (an adaptation of mark-recapture methods; see White et al. 1982, Pollock et al. 1990) have been used previously in conjunction with aerial surveys of large ungulates (Samuel and Pollock 1981, Bartmann et al. 1987, Bear et al. 1989, Neal et al. 1993, Bowden and Kufeld 1995, Bleich et al. 2001, White and Shenk 2001, McCorquodale et al. 2013).

Regression-based sightability correction models are appealing because they require marked animals only during model development and usually require only slight modifications to data collection methods used in traditional composition surveys. The sightability correction model we derived is structurally similar to several other previously published models for elk (Samuel et al. 1987, Anderson et al. 1998, McCorquodale 2001, Gilbert and Moeller 2008, Jarding 2010, McCorquodale et al. 2013), wherein group size positively affected detectability of elk groups and canopy cover negatively influenced detectability. These are intuitive effects and suggest elk groups are missed more often when they are small and/or are shielded from view by trees and other concealing vegetation. Previous work in western Washington indicated that sightability model estimates were substantially lower than LNME mark-resight estimates (McCorquodale et al. 2013), and we had the same result at Mount St. Helens. Underestimation seems to be a predictable result with sightability models (Freddy 1998, Barker 2008), and appears to stem from the effect of low sightability groups; the method does not account effectively for such groups (McCorquodale et al. 2013), but sightability models have validated well where most elk have reasonably high detection probabilities (Unsworth et al. 1990).

Mark-resight modeling represents a fundamentally different approach to imperfect detectability and is based on a well-developed body of literature (Otis et al. 1978, White et al. 1982, Pollock et al. 1990, Schwarz and Seber 1999, Barker 2008). Traditional sightability models assume the probability of detecting a group is constant over time (under specific levels of predictor variables) and the probability of sighting is estimated once, during model development; whereas, in mark-resight models, the probability of detection is potentially re-estimated during each resighting occasion. Mark-resight has proven to be a relatively robust and useful method for estimating abundance of large ungulate herbivores (Gardner and Mangel 1996, White and Shenk 2001,Gould 2005, McCorquodale et al. 2013), and the LNME model has been shown to well-suited for applications such as aerial elk surveys. However, at large spatial scales, models such as the LNME tend to be very impractical. The LNME model requires replicated surveys, physically marked animals (such as radiomarked individuals) perpetually, and the effort to individually identify marked animals observed during surveys. We believe the LNME model provided reasonable estimates of elk abundance during our work, and the detection rates we estimated were sufficient to expect a mark-resight application to perform acceptably (Neal et al. 1993). We do not believe, however, that mark-resight is a practical alternative for long-term monitoring of elk abundance on this landscape for the aforementioned reasons.

Our aerial survey data and abundance estimates derived from those data (both sightability model and mark-resight estimates) suggested a decline in total elk and total cow elk abundance during our 2009-2013 study. Trends appeared to vary spatially across our study landscape. Estimated abundance clearly declined substantially for GMUs 520 and 550, the west-most GMUs in our study area. Raw counts within counting units in GMUs 520 and 550 also suggested declines in total elk and total cow elk abundance within these GMUs were most pronounced in counting units furthest west. A declining trend was also suggested by counts and abundance estimates for

GMU 524. Across these units, declining abundance was most pronounced the last 2 years of the study, and data from spring 2013 were very important in defining the trend for several estimates. Estimated rates-of-increase were more strongly negative for GMUs 520, 524, and 550 using sightability model abundance estimates relative to mark-resight estimates, but this was largely because GMU-specific mark-resight estimates were only available for 2009-2012. By the spring of 2013, attrition of radiomarked elk left too few collared individuals available to support GMU-specific mark-resight estimates; the last collaring effort had been in February 2012.

Our data did not clearly indicate a decline in elk abundance, 2009-2013, in GMU 556, although raw counts and the sightability model point estimates for total elk and total cow elk abundance in the spring of 2013 were the lowest we observed for this GMU across the years of our study. Estimated rates-of-increase for total elk and total cow elk in GMU 556 were slightly above zero, and confidence intervals on these estimates included positive values, which would not support a conclusion that elk in GMU 556 had declined during our study. In GMU 556, estimated elk abundance rose in spring 2011 and 2012 relative to 2009 and 2010, then it declined in 2013. In fitting the rate-of-increase estimate to the data, the increase in 2011 from 2010 was largely responsible for the non-negative indicated trend. Raw counts for counting units west-most in GMU 556 suggested declines across the years of our study, whereas in the other counting units within GMU 556, only 2013 data suggested a decline.

Our data implied elk abundance was stable-to-increasing in GMU 522 during our study, in contrast to other parts of the landscape. Our 2009 estimates in GMU 522 were likely artificially low relative to 2010-2013 estimates because we adjusted the boundaries of our counting unit to include areas further upstream on the North Fork of the Toutle River between the 2009 and 2010 surveys. We consistently counted slightly less or more than 1,000 elk in GMU 522, during 2010-2013. In most winters, we observed elk groups upstream on the North Fork of the Toutle River all the way to the edge of the pumice plain near the volcano. Elk were typically fewer this far upstream, but they were consistently there, even during moderate-to-severe winters. Radiomarked elk movements did indicate some elk moved into GMU 522 from adjacent

GMUs, particularly from GMUs 524 and 556, to winter on the mudflow. It was apparent that our late winter counts of elk in GMU 522 were likely more affected by immigration of elk from other GMUs, than were counts in other GMUs. Nonetheless, we had no indication that wintering elk density in GMU 522 declined during our 5-year study.

Overall, our results suggested a substantive decline in elk abundance in our 5-GMU study area, 2009-2013. However, it was apparent that most of this decline occurred on the western half of the study area (particularly GMU 550 and the western 1/2 of GMU 520). For virtually every geographic scale of abundance estimates for total elk and total cow elk, the 2013 point estimate was the lowest estimate obtained 2009-2013, except for GMU 522 estimates. For total elk and total cow elk across the 4-GMU landscape (excluding GMU 522), 2013 estimated abundance was on the order of 30-35% lower than the 2009 estimates. GMU-specific sightability model estimates of total elk and total cow elk abundance were on the order of 60-70% lower in 2013 than in 2009 for GMUs 520 and 550, were ~40-60% lower for GMU 524, and were ~20-25% lower for GMU 556.

Relative to estimating absolute abundance, it was apparent that our sightability model routinely underestimated the numbers of elk at all geographic scales, compared to mark-resight estimates. Our sightability model estimates generally were about 50-70% of comparable mark-resight estimates. It was, however, encouraging to see that estimates from both methods supported very similar inference regarding trend. There was a very high correlation between corresponding sightability model and mark-resight estimates. There were data common to both estimates in the correlation analysis, although mark-resight estimates were a function of data from both replicate surveys and sightability model estimates were replicate-specific (*i.e.*, half of the data reflected in the mark-resight estimates were missing from each sightability model estimate). The way detectability was modeled in each method was also fundamentally independent; mark-resight modeled the detectability of individuals and mark-resight modeled detectability of elk groups as a function of what caused some groups to be missed. Mark-resight modeled detectability apart from any causative factor. Also, rate of increase estimates were reasonably congruent between the 2 methods when the data times series were the same.

All of this suggested that although sightability model estimates were consistently underestimates of *absolute* abundance, the estimates supported apparently reliable trend inference. Essentially, sightability model estimates appeared to be a good index of *relative* abundance. It seems unlikely that management decisions based on a sightability model-derived index of abundance would be much different than decisions based on mark-resight estimates of absolute abundance, based on our data and analyses. Previously, sightability modeling appeared to perform erratically in northwestern Washington and was judged inferior to mark-resight (McCorquodale et al. 2013). However, the Nooksack elk population—the population that was the focus of the McCorquodale et al. (2013) work—was very small compared to the Mount St. Helens herd, and annual surveys of the Nooksack herd were characterized by only a few groups (<40 typically) being observed. When few groups are observed, the occasional detection of a group or 2 with low predicted sighting probabilities (*i.e*., supporting large model corrections) dramatically affects overall estimates of abundance derived from a sightability correction model. At Mount St. Helens, a large number of elk groups (an order of magnitude more groups than typical of Nooksack herd surveys) are observed during each survey replicate, and this reduces the influence of a small number of low sightability groups being seen, should that occasionally occur. That is, the contribution of what are essentially *outlier* groups to the overall abundance estimates are dampened when many groups are typically observed.

Estimated annual survival rates for cow elk on our study area from our best-supported survival model and model-averaged GMU- and year-specific rates across the full model set were relatively high (c. $\hat{S}$ = 0.84-0.86) except for the last survival year (2012-2013) for all GMUs and cow elk in GMU 550 in all years. Annual adult cow survival of roughly $\hat{S}$ = 0.85 would potentially support a stable to increasing population if annual recruitment of calves to yearlings was at least 30 calves per 100 cows, assuming 50% of the recruited calves were females. In a previous study (1988-1993), annual survival for radiomarked cow elk at Mount St. Helens was estimated at $\hat{S}$ = 0.82

(Smith et al. 1994). During the same study, radiomarked cow elk survival was estimated at $\hat{S}$ = 0.86 on an Olympic peninsula study area. These rates are all lower than the $\hat{S}$ = 0.93 annual survival estimated for radiomarked cow elk in northwest Washington (McCorquodale et al. 2013) for an increasing population with limited antlerless harvest and lower than estimates of $\hat{S}$ = 0.89-0.96 for Roosevelt elk in western Oregon (Cole et al. 1997). Brodie et al. (2013) explored annual survival in a meta-analysis of 2,746 radiomarked Rocky Mountain elk (*C. e. nelsoni*) across 45 populations in western North America and derived estimates ranging $\hat{S}$ = 0.85-0.91, depending on the richness of carnivore assemblages across landscapes.

Our best-supported survival models indicated substantially lower annual survival among radiomarked adult cows in GMU 550 in all years and in all GMUs during 2012-2013. These rates ($\hat{S}$ = 0.51-0.66) would be associated with a declining population under even the best calf recruitment scenarios. This analysis indicated that during the last year of our study (2012-2013), adult cow mortality was high across the entire landscape. That this effect was likely real was further evidenced by the results of the spring overwinter mortality survey; the 2013 tally was the second highest in the last decade. The low survival estimate during 2012-2013 was also congruent with declines in raw elk counts and estimates of abundance stemming from the annual aerial survey in the spring of 2013. The last year of our study (2012-2013) was associated with a relatively high snowfall winter, a droughty summer-fall prior to winter, and a relatively high antlerless elk harvest in the fall of 2012.

Our tally of losses of radiomarked elk to non-hunting mortality was much higher the last year of our study relative to other years. This was congruent with the relatively high tally of unmarked elk deaths documented during the annual mortality survey and observations of a number of recently dead unmarked elk across the larger landscape during the aerial survey in spring 2013. As noted above, the environmental conditions—poor for both summer-fall and winter conditions—were predisposing for a challenging energetics scenario for elk. Based on post-mortem examinations of both radiomarked and unmarked elk, almost all of the winter-spring deaths were due to malnutrition. Some of these elk had clinical hoof disease of varying severity, but most did not. Our data were not suitable for definitively addressing whether the presence of hoof disease substantively raises the risk of overwinter mortality for affected elk or not; our study design was not intended to address this question. Clearly, some elk are severely debilitated by the condition—others less so—leading to a seemingly logical assumption that some additional mortality risk is likely associated with advanced disease. The only information we have, however, derived from the fates of radiomarked elk, indicated that most of the small number of these elk known to have a hoof affliction survived for an extended time.

Annual survival among branch-antlered bulls, estimated from our models, was $\hat{S}$ = 0.56. This rate was similar to an annual survival estimate ($\hat{S}$ = 0.59) for bull elk managed under *limited entry* regulations in western Washington, a harvest strategy designed to yield modest bull mortality (Bender and Miller 1999) and was higher than bull elk survival estimated during a previous telemetry study at Mount St. Helens ($\hat{S}$ = 0.49) (Smith et al. 1994). In a western Oregon study, bull survival was estimated at 0.54-0.58—very similar to our estimated survival rate—under point-restricted and any bull general season hunting regulations across 3 GMUs (Biederbeck et al. 2001). In that study, most bulls were killed before their 4th birthday. During our study, branch-antlered bull abundance appeared relatively stable across years; bull harvest regulations and permit levels were relatively static during our study, in contrast with antlerless elk permitting that was increased substantially to reduce the density of antlerless elk.

IFBF levels in late fall, estimated from hunter-harvested elk, were about 8.0% body fat for lactating elk and about 10% for non-lactating elk for most of our study area. Elk on high quality diets are capable of much higher fat accretion (Cook et al. 2004a, Bender et al. 2006, Piasecke and Bender 2009, Cook et al. 2013). On high quality summer-fall diets, even lactating elk are capable of IFBF levels in the 15-18% range in fall (Cook et al. 2004a). However, elk in western Washington and Oregon—presumably mostly Roosevelt elk or a mixed lineage of Roosevelt elk/ Rocky Mountain elk—are often strongly nutritionally limited (Bender et al. 2008, Cook et al. 2013). Among the *west-slope* elk populations for which condition data have been collected, elk at Mount

St. Helens appear to be relatively typical, based on our data from hunter-harvested elk and data in Cook et al. (2013) derived from live elk sampling via ultrasound in the fall. Fall data for live Mount St. Helens elk included in Cook et al.'s (2013) work indicate a bit lower condition than what we estimated from harvested elk, but derive from sampling only elk on the mudflow of the North Fork of the Toutle River in 2003 and 2005. In comparison to our fall estimates of ~8.0% and ~10.0% IFBF for lactaters and non-lactaters, Trainer's (1971) elk condition data, based on kidney fat indices (KFI) for a large sample of hunter-harvested elk in western Oregon, suggested mean values of about 8.50% and 13.50% IFBF (converting KFI to IFBF using the transformation in Cook et al. [2001a]). Similarly, earlier work by Merrill et al. (1985) at Mount St. Helens early in the elk recolonization phase, post-eruption indicated fall IFBF levels of ~8.0% and ~10.5% derived from KFI data for lactaters and non-lactaters. These estimates are very similar to our fall estimates, the methodological differences notwithstanding. Note, however, that Cook et al. (2001a, 2001b) have demonstrated that condition assessments derived only from KFI can be problematic because of a strongly nonlinear relationship between KFI and actual IFBF. KFI estimates appear to work reasonably well at moderate levels of IFBF, but are less reliable as an index to IFBF at both high and low IFBF levels (Cook et al. 2001b). Our mean IFBF estimates for fall, derived from hunter-harvested elk, suggested modest, but not poor condition typified elk on our study area. However, the interquartile range for fall IFBF estimates included values of ~7.0% and ~5.0% for nonlactaters and lactaters, indicating strong nutritional limitation for a substantive number of elk within our samples.

Our late winter (Feb) estimates of IFBF from live-handled elk indicated mean body fat levels of a little less than 5.0% to a little more than 6.0% for nonlactaters and a little less than 3.0% to a little more than 4.0% for lactaters. Using mean IFBF values from the fall-harvested elk and the late winter live-handled elk would suggest that Mount St. Helens elk on our study area lose about half of their fall fat stores by the end of winter. By late winter, these elk are quite lean. Based on the data from Cook et al. (2013) for wild elk populations across the western U.S., nonlactating Mount St. Helens elk are fairly typical, condition-wise, of western Washington and western Oregon elk; elk with evidence of late-season lactation at Mount St. Helens were among the leanest relative to other coastal and west-slope elk, but sample sizes for late-season lactaters at Mount St. Helens were small (Cook et al. 2013).

We estimated the overall pregnancy rate among elk we handled in Feb, 2009-2012, at just under 70%. That is clearly a suboptimal rate for elk on a good nutritional plane (Cook et al. 2004a). Prime-aged elk with access to quality forage during summer-fall typically have pregnancy rates in the mid-to-high 90% range (Cook et al. 2001c, Cook et al. 2004a, 2013). However, coastal and west-slope elk populations in Washington and Oregon are often nutritionally limited and display suboptimal pregnancy rates. Using a large sample of reproductive tracts from harvested Roosevelt elk in western Oregon in the 1960s, Trainer (1971) estimated the pregnancy rate across cow age classes at 50%, with the highest rate (59%) for prime-aged cows (ages 4-10 yrs.). Later, Harper (1985) reported a pregnancy rate of 57% for a larger sample of reproductive tracts from western Oregon elk (included the data from Trainer 1971) ≥ 2-yrs-old and a rate of 63% for prime-aged (ages 4-10 yrs.) elk. Collectively, the data in Harper (1985) represented sampling spanning 3 decades (1960-1980s) in western Oregon. Using reproductive tracts from elk harvested in southwest Washington (Willapa Hills) during the early 1970s, Kuttel (1975) estimated a pregnancy rate of 70.3% across all cows ≥1 year-old, and a rate of 74.1% if yearling cows were excluded. Smith et al. (1980) measured pregnancy rates from harvested cow elk on Washington's Olympic peninsula and reported rates of 61.3% excluding yearlings and 53.5% across all age classes for data collected in the late 1970s. Cook et al. (2013), using ultrasound data from live-captured elk, documented pregnancy rates of 68.6-100.0% across 4 coastal elk herds in Washington and 76.9-100.0% for 8 west-slope Cascades herds in Washington and Oregon. Merrill et al. (1987) previously measured pregnancy rates for Mount St. Helens cow elk during 1982-1985 from a mixed sample of harvested and live-captured elk and reported a rate of 69% for 2-yr-olds and 87% for cows aged ≥3-yrs-old. In context, our pregnancy rate data for 2009-2012 indicated productivity on par—if not slightly better—with historic western Oregon and Washington elk data, but slightly lower than recent data for most western Washington and western Oregon Cascades elk herds. Our data also indicated slightly depressed productivity for cow elk at Mount St. Helens in recent history, relative to the lower density elk population on the same landscape during the post-eruption, elk recolonization phase in the early to mid-1980s.

Spring calf recruitment during 2009-2013 was highly variable, according to our survey-based estimates. Calf recruitment—standardized by the abundance of adult cows—is the result of 2 demographic processes: cow elk fecundity (productivity) and 1st year calf survival. Large herbivore populations, including elk populations, are typically characterized by relatively high and consistent adult survival, but substantial annual variation in juvenile survival (Coughenour and Singer 1996, Gaillard et al. 1998, 2000, Bonenfant et al. 2002, Lubow et al. 2002, Garrott et al. 2003). Demographically, population change is most affected by adult female survival in theory, but because of relative stability in adult female survival rates, realized population fluctuations are usually associated with dynamic juvenile survival (Coughenour and Singer 1996, Lubow and Smith 2004, Raithel et al. 2007, Harris et al. 2008). Eberhardt (1977) hypothesized that declining per capita resource availability (driven either by environmental fluctuation or increasing animal density) would affect demographics of large mammal populations following a predictable pattern: 1) declining juvenile survival, 2) increasing age of primiparity (female sexual maturity), 3) declining reproductive rates of adult females, and lastly 4) declining survival of adults. This ordering reflects the expected relative sensitivity of each demographic parameter to increasing food limitation, and empirical data have largely supported this hypothesis for large herbivores (Gaillard et al. 1998, Bonenfant et al. 2002).

Our data indicated very good recruitment in the spring of 2010 and 2011, even after attempting to correct for antlerless elk harvest. During these years, we commonly estimated recruitment exceeding 35 calves per 100 cows, and for some GMU-specific estimates during 2010-2011, >40:100. Calf recruitment this high—under the pregnancy rates we documented for radiomarked cow elk—seems exceptional. During our work, we consistently tried to guard against misclassification of calves and yearlings. When large herbivores are food limited, early body growth is typically impacted (Albon et al. 1987, Loison and Langvatn 1998, Mysterud et al. 2001, Cook et al. 2004a). Variation in calf birth mass, calf gender, maternal nutrition, and first-year growth effects combine to yield a range of calf sizes by later winter. This and nutritional effects that carry over to yearling body sizes can result in substantial overlap in the sizes of large calves and small yearlings. We attempted to avoid misclassification of calves by continually trying to calibrate our perception of yearling cow size using the sizes of yearling bulls present in the elk groups we observed. We believe we were fairly conservative to avoid overestimating the numbers of calves, but it is still likely that some misclassification error occurred. That said, post-season calf:cow ratios exceeding 35:100 have also been previously documented for other western Washington and western Oregon elk populations that had pregnancy rates ≤70% (Kuttel 1975, Smith 1980, Raedeke et al. 1982, Harper 1985). Early in the post-eruption, elk recolonization phase, Merrill et al. (1987) estimated Aug-Oct calf recruitment in the range of 40-57 calves per 100 cows at Mount St. Helens when corresponding pregnancy rates were 31% for yearlings, 69% for 2-yr-olds, and 87% for ≥3 yr-olds.

The high calf recruitment we estimated for spring 2010 and 2011 was associated with favorable annual conditions. The winter of 2009-2010 was extremely mild, nearly snow-free, and the winter of 2010-2011 was modest relative to snowfall and mild relative to early snowfall. The summer-fall of 2010 was the wettest among all of our study years, with substantial late-summer, fall precipitation. The summer-fall of 2009 was not as wet overall, but had significant late-summer, fall moisture. Thus, our highest estimates of recruitment did occur under conditions that intuitively would favor good summer foraging conditions and minimal overwinter mortality, presumably conditions favoring higher than average calf recruitment.

In contrast with the 2010 and 2011 estimates, elk calf recruitment was lower in the spring of 2009 and much lower in 2012, 2013. Overall, observed estimates were in the 25-30:100 range for the study area and in the 25-35:100 range for all GMU-specific estimates except for GMU 522 during these years. Estimates for GMU 522 during these years were slightly lower than for the other GMUs. After attempting to correct the observed ratios for removals of antlerless elk via hunter harvest—removals that were substantial in fall 2011 and 2012—calf recruitment was indexed mostly in the high teens to 100 cows range for 2012, 2013 and in the 20-30-ish calves per 100 cows in 2009. Indexed recruitment in spring 2013 was the lowest—compared to other study years—for all GMUs except GMU 556; recruitment in 556 appeared similarly low in 2013 and 2009. Depressed calf recruitment in the spring of 2013 corresponded to high mortality among radiomarked elk that same year, high observed overwinter mortality of unmarked elk, and elk counts and abundance estimates that were also low. Weather-wise, the winters of 2008-2009 and 2012-2013 had relatively deep snow at mid-elevations, whereas the winter of 2011-2012 was relatively moderate for snow accumulation. The summer-fall of 2012 was characterized by almost no precipitation from July through September, and in 2011 overall growing season precipitation was even lower, with a droughty summer and fall rain only after mid-September. In 2009, the early summer period was very dry, but rainfall did occur throughout August and September.

We found statistical associations among several performance metrics (*e.g.*, overwinter mortality, spring calf recruitment, fall body condition of adult females) and strong associations between landscape environmental metrics and some performance metrics (notably, overwinter mortality and spring calf recruitment). The environmental metrics we used (growing season precipitation and winter snow water equivalents with various temporal constraints) were selected as proxies for summer-fall forage production/quality and winter severity with intuitive implications for elk nutrition, energetics, and survival. We detected a particularly strong association of spring calf recruitment and late summer-fall precipitation across years. When droughty conditions prevailed during this timeframe, calf recruitment was depressed relative to years with a good precipitation pulse during Aug-Sept. Elk calves increasingly consume forage by late July, as they become less dependent on nursing for nutrient and energy intake (Robbins et al. 1981, Cook et al. 1994, 1996, 2004). By September they are obtaining a substantial portion of their calories from forage (Robbins et al. 1981, Cook et al. 1996, 2004). A finding that late summer-fall precipitation—a harbinger of fall forage greenup—affects spring calf recruitment, presumably by enhancing overwinter calf survival, is intuitive. Empirical evidence from tame elk feeding trials has also clearly implied that deficient summer-fall nutrition (potentially affecting both calves and their lactating dams) reduces overwinter survival probabilities for elk calves (Cook et al. 2004a).

We also found a striking association between winter snow water equivalents, particularly from mid-winter through early spring, and the recent historic overwinter mortality index derived from carcass counts on a portion of the N. Fork of the Toutle River mudflow. A link between winter severity and overwinter elk mortality is intuitive; however, elk often tolerate deep snow conditions and/or winter nutritional deprivation elsewhere (Leege and Hickey 1977, DelGuidice et al. 2001, Garrott et al. 2003, Cook et al. 2004b); winter survival probabilities can be robust if elk store adequate fat reserves prior to winter onset (Cook et al. 2004a, 2004b). However, at Mount St. Helens, and possibly in other mountainous areas of western Washington and Oregon, strong nutritional constraints on summer-fall range may predispose some individual elk—particularly lactaters—to substantial overwinter mortality risks during severe winters (Bender et al. 2008). It would be expected that high elk densities would exacerbate the risk (DelGuidice et al. 1991). Overwinter mortality data we used came from a limited area in a low elevation valley bottom. The strong correspondence we found between a winter severity metric and mortality likely reflected not only the effect of winter severity on survival, but also the effect of winter severity on elk distribution. During heavy snowfall years, more elk are typically observed on the mudflow (P. Miller, personal communication), presumably having moved in from surrounding higher elevation forested areas, such as from GMU 524. Movements of radiomarked elk somewhat corroborate this. In severe winters, more elk deaths are indexed on the mudflow both because the sampled area holds many elk and because certain nutritionally stressed individuals succumb.

We did not find strong associations relative to the estimates of cow elk body condition derived from live elk handling in February and other performance or weather metrics. This was not surprising, because we had relatively small samples (110 total samples across 4 years), because of unknown lactation histories by February, and because condition assessed in late winter is subject to variable overwinter condition loss, depending on an elk's fall body condition. Elk that are in better body condition in the fall typically lose more body fat overwinter than elk in poorer condition (Cook et al. 2013, S. McCorquodale, unpublished data). Overwinter, some equilibration of body condition tends to occur for cows entering the winter at different condition levels, but this compensation is not absolute (*i.e.*, does not typically erase all differences in fall condition) (Cook et al. 2004a).

Elk abundance (and density) has evolved considerably over the last century on the core landscape occupied by the modern Mount St. Helens herd. As late as the 1930s, the number of elk believed to occupy the Green, Toutle, and Kalama River drainages was less than 500 elk (Pautzke et al. 1939); only about 2,000 elk were approximated for that portion of southwest Washington roughly corresponding to the current Willapa elk herd area (Pautzke et al. 1939). Methods for estimating elk abundance were admittedly rudimentary 70 years ago, but presumably we can conclude that elk densities in this part of Washington were relatively low in the early part of the 20th century. Historic evidence of elk abundance on this landscape is sketchy, stemming from the lack of suitable methods to support valid estimates for many years, but it appears that the combination of fairly conservative elk management and active forestry across ownerships that created considerable early seral habitat (Starkey et al. 1982, Witmer et al. 1985) facilitated growth in elk distribution and density during the latter part of the 20th century. The eruption of the volcano in 1980 set the stage for a large area of forested habitat to revert to early seral habitat that was both highly preferred by elk and supported high fitness (Merrill et al. 1987). For a time, the post-eruption plant successional pattern across a portion of this landscape appeared to support both increasing elk habitat values and elk numbers, but eventually elk habitat potential and elk population trajectories diverged (Miller and McCorquodale 2006).

High elk density and declining habitat capability led to strong herbivory-driven modification to plant communities used by elk (see Riggs et al. 2000) and predictable declines in per capita forage availability and forage quality. Strong nutritional constraints for some elk on this landscape were eventually manifested as sub-par fat accretion patterns (Cook et al. 2013) and episodic overwinter mortality (Miller and McCorquodale 2006). This led to some of the management changes described earlier in this report designed to reduce elk density. Reducing elk density was intended to decrease intraspecific food competition, increase average elk condition, and reduce overwinter mortality.

As described in this report, elk abundance did apparently decline over our 5-GMU study area during 2009-2013, and on parts of the landscape, quite substantially. We did not have data to thoroughly evaluate whether the density reduction had any appreciable effect on individual elk condition. Much of the density reduction was apparently effected during the last 2 years of our work, and we did not collect samples from harvested elk after the fall of 2011 and only handled a few cow elk for radiocollaring in Feb 2012. Clearly, a substantive winterkill during the last winter we report on (2012-2013), indicated that reducing elk density did not eliminate overwinter mortality risks, at least in the short-term. As previously noted, the droughty summer-fall of 2012 and the relatively severe 2012-2013 winter presented a poor energetic scenario for elk in this population, even at a reduced elk density.

Density-dependence, potentially operating on fecundity (*i.e.*, productivity; Taper and Gogan 2002, Stewart et al. 2005), but usually through effects on non-hunting mortality (Guiness et al. 1978, Coughenour and Singer 1996, Lubow et al. 2002, 2004, Taper and Gogan 2002), is linked to the concept of ecological carrying capacity for large mammals such as elk (Fowler 1981). At high population density, intraspecific competition (both scramble and contest competition) occurs as per capita resource availability declines with predictable impacts to the most vulnerable individuals in a population (*e.g.*, juveniles, senescent individuals, the infirm, those with high costs associated with reproduction). Density-dependent effects on survival have been demonstrated for juveniles in elk populations many times (Sauer and Boyce 1983, Coughenour and Singer 1996, Singer et al. 1997, Lubow et al. 2002, 2004) and similarly in conspecific red deer populations (Guiness et al. 1978, Clutton-Brock et al. 1987, Coulson et al. 1997). Density-dependent survival in adult elk has also been documented (Taper and Gogan 2002, Eggeman 2012), but less commonly (see also Sauer and Boyce 1983, Coughenour and Singer 1996). Density-dependent effects on adult female red deer have been shown to influence body size (Loison and Langvatn

1998, Mysterud et al. 2001, Bonenfant et al. 2002), but not strongly survival (Clutton-Brock et al. 1985, Bonenfant et al. 2002, but see Forchhammer et al. 1998) or age of senescence (Mysterud et al. 2001).

Density-independent effects on survival, typically mediated through weather influences on energetics, have also been demonstrated for juvenile elk (Singer et al.1997, Garrott et al. 2003, Lubow et al. 2002, Lubow and Smith 2004, Eberhardt et al. 2007) and even adults (Sauer and Boyce 1983, Coughenour and Singer 1996, DelGuidice et al. 2001, Garrott et al. 2003). Irrespective of population density, the effects of poor forage years and/or severe winters can apparently often reduce survival of juveniles and, sometimes, that of adults.

Our work implied logical causal links between density-independent effects of extreme weather (both summer-fall and winter) and calf recruitment and adult survival. These effects may have been exacerbated by density-dependent influences, but we cannot unequivocally demonstrate this. Overwinter mortality during the last year of our work, although high under the combination of a droughty summer-fall and a severe winter, was substantially lower than in the spring before our work began (2008), also a year with a droughty summer and a relatively snowy winter. The much lower apparent overwinter mortality in spring 2013, relative to 2008, occurred after the documented reduction in elk population size. Whether or not the change in elk density had anything to do with the differences in the overwinter mortality index between spring 2013 and 2008 is unclear, due to the absence of relevant corroborating data prior to the initiation of our work in 2009.

Reducing the elk population within our core study area was a logical prescription, given evidence of strong food limitation effects on elk body condition, modest pregnancy rates, strong herbivory effects on plant communities, and episodically high overwinter mortality. The degree to which a lower elk density will yield the desired improvements across these parameters is likely yet to be seen. Although the elk population has been reduced, it is reasonable to expect there may be some time lag associated with subsequent changes to elk habitats, and ultimately, to the restructured elk population. Although the relatively wet southwest Washington climate produces substantial herbaceous biomass, particularly in early seral habitats preferred by elk, the proportion of this biomass that represents nutritious and palatable elk forage is actually quite small (Cook 2002, Geary 2013, J. Cook, unpublished data). Herbivory strongly influences the structure and composition of plant communities used by foraging elk (Augustine and McNaughton 1998, Riggs et al. 2000, Geary 2013), typically by reducing the density and biomass of preferred forage species and increasing the proportion of the plant community represented by species elk do not consume, or consume only as forages of last resort. These plant community changes can be dramatic under high levels of herbivory sustained for long periods, such as has likely occurred in highly preferred elk habitats at Mount St. Helens. Recovery of the herbaceous component, which has been depressed by herbivory, typically takes some time even after the plant community has been released from excessive herbivory. This has clearly been demonstrated elsewhere for red deer (Tanentzap et al. 2009). How long substantive recovery of palatable elk forage species is likely to take in these impacted habitats is difficult to predict, but it is unlikely to be immediate or very short-term.

Forsyth and Caley (2006) recently discussed what they termed "*the irruptive paradigm*" relative to large herbivores; this paradigm postulates that when released from harvest control, large herbivore populations characteristically grow past ecological carrying capacity, subsequently decline to a much reduced density, and then recover to a relatively stable density somewhat lower than the pre-crash high density. It is not clear if the Mount St. Helens elk herd actually exceeded ecological carrying capacity, despite some evidence of density-dependent effects on elk condition, and possibly, mortality. The density reduction that has recently occurred was also directed by management actions, not imposed solely by environmental constraints.

Other high-density elk populations have been associated with strong apparent herbivory-mediated habitat modification and have been surmised to be at or above ecological carrying capacity. For decades, the northern Yellowstone elk herd was managed within Yellowstone National Park under a *natural regulation* paradigm (Coughenour and Singer 1996); elk abundance rose substantially (Houston 1982, Eberhardt et al. 2007), herbivory modification to plant communities was apparent

(Houston 1982, Frank and McNaughton 1992), and population demographics were shown to be influenced by both density-dependent and density-independent processes (Houston 1982, Coughenour and Singer 1996, Singer et al. 1997, Taper and Gogan 2002). Occasional winterkills have historically occurred, mostly affecting juvenile elk (Houston 1982, Eberhardt et al. 2007); despite these observations, the evidence that these elk exceeded ecological carrying capacity prior to wolf (*Canis lupus*) reintroduction was considered equivocal, perhaps except for the short-term right after the large-scale fires of 1988 (Houston 1982, Frank and McNaughton 1992, Coughenour and Singer 1996b, DelGuidice et al. 2001, Taper and Gogan 2002).

Similarly, a high density elk population in and around Rocky Mountain National Park was previously surmised to exceed ecological carrying capacity, as evidenced by a strong herbivory signature on some plant communities, occasional winter losses of elk, and density-correlated variability in population growth rates (Lubow et al. 2002, Singer et al. 2002). However, Bender and Cook (2005) found considerable variability in individual elk condition, the population consisting of some elk at very high condition levels, some at low levels, and the average condition modest. This would seem to be similar to the recent situation at Mount St. Helens, in light of our data from hunter-harvested and live captured elk. Bender and Cook (2005) argued that the presence of elk at very high levels of condition, even if that did not typify most elk, did not support a conclusion that the population was above ecological carrying capacity at a landscape level.

A prudent near-term goal at Mount St. Helens would seem to be to continue to manage the elk population at a lower density with the objectives of promoting improved habitat condition, higher average elk condition, and reduced overwinter mortality. Again, such outcomes may operate with a time lag reflecting an evolving plant community response to reduced herbivory. Such management may well dampen the influence of density-independent effects—such as weather—on calf recruitment and overwinter mortality, but it is unlikely to completely eliminate sub-par recruitment and overwinter mortality in years with very unfavorable conditions. The degree to which the presence of hoof disease in this elk herd will complicate meeting management objectives is unclear, pending additional research to disentangle the effects of the condition on elk energetics and population processes such as age-specific mortality and fecundity.

MANAGEMENT IMPLICATIONS

Our results indicated that sightability correction modeling yielded a useful elk abundance index that should perform acceptably to support management decisions about elk in the west-central portion of the herd area. This approach will undoubtedly underestimate true elk numbers, but applied at a relatively large geographic scale, the index appears to correlate well with actual elk numbers across a range of abundance. Emerging approaches, such as integrated population models (Buckland et al. 2000, White and Lubow 2002, Newman et al. 2006), may provide potential future direction that would facilitate the use of sightability model estimates as inputs to a modeling approach supporting inference about actual elk densities. Sightability modeling, applied to aerial survey data, is both practical and cost-effective.

Our work confirmed that the Mount St. Helens elk herd, at least that portion inhabiting our 5-GMU study area, has been food limited in recent time. Although this is consistent with data for other elk herds in western Washington and Oregon, under certain environmental conditions and elk densities encountered during 2009-2013, food limitation in this herd yielded occasionally substantial overwinter mortality. Reducing elk density was a logical management response, and was achieved via liberalized antlerless elk hunting. It is unclear to what degree reducing elk density will affect elk survival in years with poor weather conditions in the immediate short-term. It is anticipated that plant community recovery in habitats exploited heavily by elk in the past will likely evolve at an unknown, but longer time scale. Periodic sampling of organ sets from hunter-harvested elk would provide a mechanism to monitor for habitat-mediated changes in elk condition levels through time.

Population dynamics in the Mount St. Helens elk herd appear to have been influenced both by density-dependent and density-independent mechanisms in recent time. There is also presumed to be an interaction between these effects (i.e., density-independent effects should be magnified at higher elk densities). Managing for a lower density elk herd is expected to modify the population level effects of elk density on intraspecific competition for food, but is unlikely to completely mitigate for density-independent effects of poor forage years (i.e., droughts) and/or severe winters.

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ASSESSING THE POTENTIAL EFFECTS OF TREPONEME ASSOCIATED HOOF DISEASE (TAHD) ON ELK POPULATION DYNAMICS IN SOUTHWEST WASHINGTON

PROJECT UPDATE
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INTRODUCTION

Various hoof diseases have been reported worldwide in numerous free-ranging ungulates, including elk (*Cervus elaphus*; Murie 1930, Gray et al. 2001, Thorne et al. 2002), mule deer (*Odocoileus hemionus*; Wobeser et al. 1975), white-tailed deer (*O. virginianus;* Sleeman et al. 2009), moose (*Alces;* Flynn et al. 1977, Clauss et al. 2009), fallow deer (*Dama*; Lavin et al. 2004), reindeer (*Rangifer tarandus*; Handeland et al. 2010), roe deer (*Capreolus*; Handeland and Vikøren 2005), and mouflon (*Ovis gmelini musimon*; Volmer et al. 2008). Reports of elk in southwestern Washington with evidence of lameness or various hoof abnormalities were historically sporadic and infrequent. In early 2008, however, the number and geographic extent of elk displaying evidence of an apparently novel hoof disease significantly increased (Mansfield et al. 2011, WDFW unpublished data).

The emergence of this disease in southwest Washington elk herds is unique in that bacteria in the genus *Treponema*, (aka "treponemes"), never previously associated with hoof diseases in any free-ranging ungulate, have been identified as causal (Clegg et al. 2015). Treponemes are strongly associated with similar diseases of domestic livestock: bovine digital dermatitis of cattle (Evans et al. 2009), contagious ovine digital dermatitis (CODD) of domestic sheep (Sayers 2009), and a CODD-like disease of domestic goats (Sullivan et al. 2015).

Elk affected by treponeme-associated hoof disease (TAHD) often have severely overgrown and deformed hooves with sole ulcers and sloughed hoof walls (Han and Mansfield 2014). TAHD can occur in multiple limbs and can affect all age and sex classes (Clegg et al. 2015). The severity of clinical signs, coupled with the seemingly rapid expansion of impacted areas, have generated a great deal of concern for the Washington Department of Fish and Wildlife (WDFW), other resource management agencies, hunters, tribes, and local citizens. In response to these concerns, WDFW continues to work with several specialists to better understand the etiology of TAHD. In addition, WDFW established a Hoof Disease Technical Advisory Group (HDTAG) and a Hoof Disease Public Working Group (HDPWG). The HDTAG has guided the diagnostic effort, identified research needs, and provided review and input to management options. The HDPWG has provided input to management and research options and serves as a venue for WDFW to share information with the public. However, it is difficult to assess what implications TAHD will have for the management of affected elk herds because the effects of TAHD on elk vital rates (e.g., survival, reproduction, etc.) are unknown.

It is reasonable to assume that elk with advanced stages of TAHD have a decreased probability of survival because their infirmities may predispose them to predation, harvest, severe weather events, or other types of disease (Bender et al. 2008). For example, mule deer with chronic wasting disease (CWD), prior to developing obvious clinical signs, have been shown to be more vulnerable to predation (Miller et al. 2008, Krumm et al. 2009), vehicle collisions (Krumm et al. 2005), and possibly harvest (Conner et al. 2000). This is an important consideration because the growth rate of large ungulate populations, such as elk, is highly sensitive to changes in adult female survival (Nelson and Peek 1982, Eberhardt 2002) and strongly correlated with the production and survival of juveniles (Gaillard et al. 2000; *see also* Smith and Anderson 1998, Raithel et al. 2007). When adult female and juvenile survival are concurrently reduced, populations would be expected to decline (Gaillard et al. 2000; *see also* Bender et al. 2007, McCorquodale et al. 2014). Consequently, if TAHD reduces the survival of adult females and calves, it has the potential to have a negative effect on the population dynamics of impacted elk herds.

Although McCorquodale et al. (2014) monitored 16 adult female elk that had varying degrees of presumed TAHD (i.e., they had varying degrees of hoof deformities, but no lab samples were collected and tested) inferences from their work are limited. Twelve of 16 affected elk they monitored survived ≥ 1 year and of those that did not survive ≥ 1 year, all were harvest-related mortalities. In addition, 3 of 4 elk that were fitted with VHF collars that had a battery life of several years survived until radio contact was lost 3-4 years after they were captured. Anecdotally, this indicates that if TAHD negatively affects the natural survival of elk, it may take several years before it does so. We need to improve our understanding of how quickly TAHD progresses and if, and when, it may begin to predispose affected elk to mortality.

TAHD may also have the potential to affect the population dynamics of impacted elk herds because of its effect on the energy dynamics of female elk. The nutritional condition of female ungulates can influence age at first breeding (Cook et al. 2004), timing of estrus and subsequent birth date (Andersen and Linnell 1998, Cook et al. 2004, Bishop et al. 2009), probability of conception (Cook et al. 2004, Cook et al. 2013), fetal development and survival (Verme 1969, Ozoga and Verme 1982), birth weight (Verme and Ullrey 1984, Keech et al. 2000, Lomas and Bender 2007), milk yield or composition (Landete-Castillejos et al. 2003, Tollefson 2007), and subsequent growth and survival of juveniles (Clutton-Brock et al. 1982, Bishop et al. 2009). For example, elk from the Mount St. Helens elk herd area (MSH) and other coastal regions of Washington are characterized by pregnancy rates for prime-aged females that are consistently depressed [Kuttel 1975 (74%), Smith 1980 (61%), Cook et al. 2013 (68-100%), McCorquodale et al. 2014 (71%)] because marginal nutrition limits the level of condition female elk are able to achieve during the summer-autumn period (Cook et al. 2013). Due to the additional energetic requirements for mounting an immune response and for tissue repair (Deming 2009), TAHD may further limit the ability of affected elk to improve their condition during the summer-autumn period and therefore has the potential to reduce overall pregnancy rates even further, which could reduce demographic vigor.

Some have attributed recent declines in the MSH elk herd to TAHD because the monitored portions of the MSH herd declined by 30-35% over a 4-year period (2009–2013; McCorquodale et al. 2014) that coincided with an increase in the prevalence and distribution of the disease (WDFW, unpublished data). However, this period of population decline also occurred concurrently with a directed effort by WDFW to reduce the elk population through substantial increases in antlerless harvest because of evidence that the MSH elk herd was above ecological carrying capacity (WDFW 2006, McCorquodale et al. 2014). Moreover, density independent severe winter weather that occurred in 2012 likely contributed to the documented decline (McCorquodale et al. 2014). Because these three events overlapped temporally and elk with presumed TAHD represented <15% of the adult females that were monitored, McCorquodale et al. (2014) were not able to conclude whether or not TAHD was a contributing factor in observed declines.

The number of elk that have TAHD and the effects of TAHD on elk vital rates, collectively, will determine what the long-term implications of TAHD are for the viability, and subsequent management, of impacted elk herds (Wobeser 2007). Consequently, our primary research goals are to quantify how TAHD may affect the survival, pregnancy rates, productivity, and nutritional condition of adult female elk. Our specific study objectives include:

1. *Estimate the effects of TAHD on survival of adult (≥ 2 years old) female elk.*
2. *Determine cause-specific mortality rates for adult female elk that have TAHD.*
3. *Estimate the effects of TAHD on the pregnancy rates of adult female elk.*
4. *Estimate the effects of TAHD on elk productivity (i.e., survivorship of calves).*

5. *Estimate the effects of TAHD on the level of condition (i.e., IFBF) adult female elk are able to achieve in autumn.*

6. *Increase our understanding of how TAHD progresses in individual elk, and whether affected elk may recover from the disease.*

STUDY AREA

Our study area consists of 5 Game Management Units (GMUs) that, collectively, represent the core range of the MSH herd (Figure 1). The primary reasons we focused our work in this area are: 1) it occurs within the TAHD endemic area; 2) it decreases the probability of stochastic variation in the data independent of TAHD; and 3) it is the same study area of McCorquodale et al. (2014). Having the same study area as McCorquodale et al. (2014) afforded us the opportunity to put more emphasis on monitoring elk affected by TAHD because we could potentially use their findings for non-affected elk, 2009–2012, as baseline estimates of survival for elk independent of the disease.

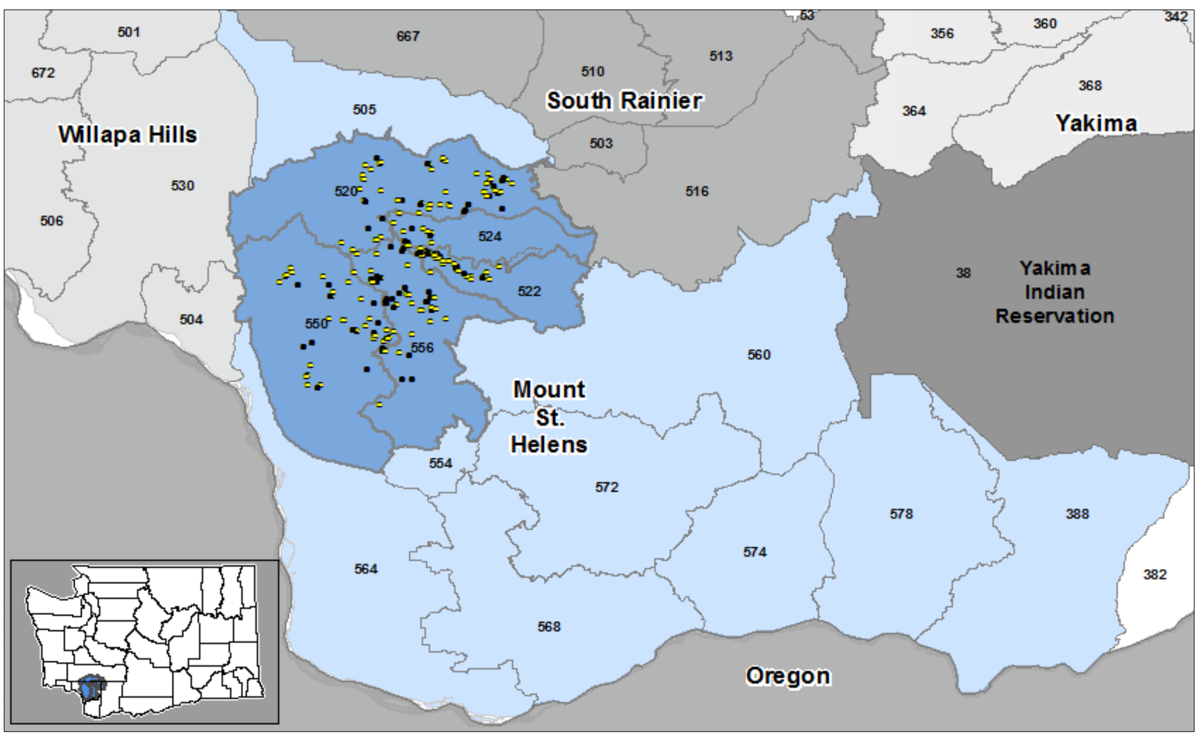

Figure 1. Map depicting the Game Management Units (GMUs) that comprise the Mount St. Helens elk herd area (light blue), the 5 GMUs that represent the core range of the herd and our study area (dark blue), and the locations where we have captured elk affected (yellow) or seemingly unaffected (black) by treponeme-associated hoof disease, February 2015–December 2017. Also included for spatial reference are GMUs associated with the Willapa Hills, South Rainier, and Yakima elk herds.

METHODS AND RESULTS

Capture and Marking

We initiated captures February 17–27, 2015 with the goal of capturing and marking 80 adult female elk at a ratio of 3 elk affected by TAHD (hereafter, diseased group) to every 1 elk that was unaffected (hereafter, control group). We conducted subsequent captures December 2015–2017, with the primary goal of maintaining our desired sample size and 3:1 ratio within each GMU. We conducted captures December 16–22 in all 3 years. When attempting to mark elk for inclusion in our diseased group, we only targeted individuals that were visibly limping, which, in most instances, was indicative of an elk having advanced stages of TAHD–of the elk we captured that were limping, only 3 were unaffected by TAHD. However, subsequent to us capturing them, we determined some elk we had captured for inclusion in our control group (i.e., not limping) had early stages of the disease. Although we were primarily interested in marking elk most severely affected by TAHD, we made the decision to include these elk in the diseased group because it afforded us the opportunity to increase our understanding of disease progression. Lastly, in order to increase the likelihood that our sample of diseased elk was an unbiased sample, we attempted to capture the first limping elk we detected within a group, regardless of their apparent condition (i.e., some elk were visibly emaciated at time of capture).

We captured female elk via aerial darting from a Bell 206B Jet Ranger helicopter using recommended immobilizing and reversal agents (Kreeger and Armeno, 2007). We blindfold elk to minimize stress during handling, administered clostridium vaccine (the first time the animal was captured), vitamin E and analgesic (flunixin meglumine) injections, and treated the dart wound. We marked each elk using a colored and numbered ear-tag and a mortality-sensitive, GPS (Global Positioning System)-equipped radio-collar. We determined disease status by having a veterinarian, knowledgeable of hoof deformities commonly associated with TAHD and other hoof diseases, examine each hoof after we had used a saline solution to remove mud and debris from the hoof. We also removed an upper canine tooth to determine age using microhistological analysis of cementum annuli (Hamlin et al. 2000; Matson's Laboratory, Milltown, MT).

We captured 80, 46, 43, and 42 female elk February 2015, December 2015, December 2016, and December 2017, respectively (Table 1). A subset of the elk we captured in December 2015 (*n* = 20 diseased, 10 control), December 2016 (*n* = 15 diseased, 8 control), and December 2017 (*n* = 6 diseased, 4 control) represented elk we had originally marked during previous capture events.

We recaptured these elk to accomplish three objectives: 1) to confirm disease status of elk in our control group; 2) to increase our understanding of disease progression; and 3) to index the proportion of elk known to be pregnant within each group that successfully raised a calf through late-autumn. Collectively, we captured 148 individuals during 211 capture events.

Table 1. The number of female elk we captured in each Game Management Unit (GMU) by capture event and the number of those elk that had visible signs of being affected by treponeme-associated hoof disease (Diseased Group), or appeared to be unaffected by the disease (Control Group).

	Diseased Group					Control Group				
GMU	**Feb 2015**	**Dec 2015**	**Dec 2016**	**Dec 2017**	**Total**	**Feb 2015**	**Dec 2015**	**Dec 2016**	**Dec 2017**	**Total**
520	24	10	10	3	47	6	5	4	2	17
522	11	6	5	9	31	1	2	3	5	11
524	1	4	2	0	7	3	0	0	1	4
550	15	6	4	5	30	5	0	2	5	12
556	9	5	9	6	29	5	8	4	6	23
Total	**60**	**31**	**30**	**23**	**144**	**20**	**15**	**13**	**19**	**67**

We did not mark two of the elk we captured in February 2015 because they died during the capture process (1 yearling and 1 adult; both had TAHD). In addition, we had 1 diseased elk we captured in December 2016 and 1 control elk in December 2017 that died within 1 day of being captured. In both instances, we immediately retrieved the radio-collar and redeployed it on a different elk. We included data from these elk in all analyses, except for survival.

Ages of female elk at time of initial capture that we assigned to our diseased group (n = 101) ranged 1-16 years and averaged 6 years old (95% CI = 5-7), while ages of female elk we assigned to our control group (n = 45) ranged 1-13 years and averaged 7 years old (95% CI = 6-8) (Figure 2). We were not able to collect a tooth for age determination from 2 elk in our diseased group.

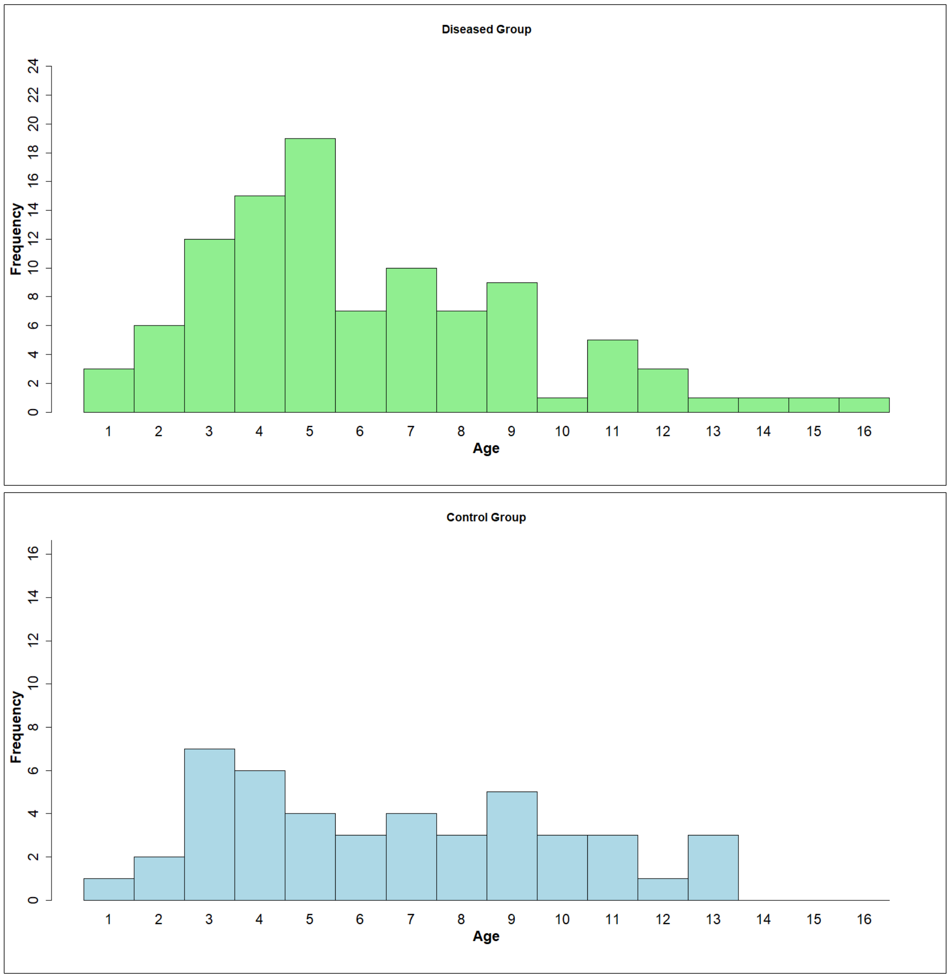

Figure 2. Distribution of ages at time of initial capture for female elk we captured, 2015–2017, that were affected by treponeme-associated hoof disease (Diseased Group) or had no visible signs of being affected by the disease (Control Group).

Disease Occurrence within Control Group

To date, we have marked and assigned 44 elk to our control group, of which, 14 are new study animals we captured for the first time in December 2017 (does not include the control elk that died during capture in December 2017). We have confirmed disease status for 25 of 30 elk we captured prior to December 2017, of which 0.48 (12/25) have contracted TAHD after we initially marked them. For elk within our control group that we captured during subsequent capture events, 0.25 (3/12), 0.22 (2/9), and 0.50 (3/6) in December 2015, 2016, and 2017, respectively, had contracted TAHD between capture events.

Disease Severity, Progression, and Recovery

We have continued to observe wide variation in hoof disease severity subsequent to our initial capture in February 2015. We initially developed grades of the disease that were related to a visual characterization of hoof deformities (Figure 3), but recognize our scoring system is subjective and may not exactly correlate with the effects of TAHD on the energy dynamics of elk. For example, we have preliminarily defined Grade IV of the disease to include any elk that is missing 1 or more hoof capsules, which would include an elk that recently sloughed its hoof capsule and is dealing with a painful, badly infected foot, and likely using a lot of energy fighting that infection. However, elk classified as having Grade IV may also include an animal that sloughed its hoof capsule several years prior and has, relatively speaking, healed and is no longer expending the same amount of energy it was when the hoof initially sloughed. Although we anticipate incorporating some measure of disease severity will strengthen the inferences we can make, our grading system is still evolving as we continue to increase our understanding of the disease during subsequent examinations of recaptured elk, from histology and microbiology examinations of hooves from study animals and hunter-harvested elk, and from evaluations of individual elk health status via clinical pathology of blood samples.

Severity.—We captured 103 elk that were affected by TAHD at the time of initial capture and we completed a full examination of all 4 hooves for 98 of them. The back hooves were involved in all 98 cases, only 1 back hoof was involved in 0.66 (65/98) of the cases, and both back hooves were involved in 0.26 (25/98) of the cases. It does not appear the rate at which TAHD involves the back right (57/98 = 0.58) or back left (66/98 = 0.67) hooves is disproportionate. The front hooves were involved in only 0.10 (10/98) of the elk we examined. The majority of elk within our diseased group either had TAHD on a single hoof with characteristics we have preliminarily associated with advanced stages of the disease (i.e., Grade 3 or Grade 4; 53/98 = 0.54) or had the disease on multiple hooves (33/98 = 0.34) (Figure 4).

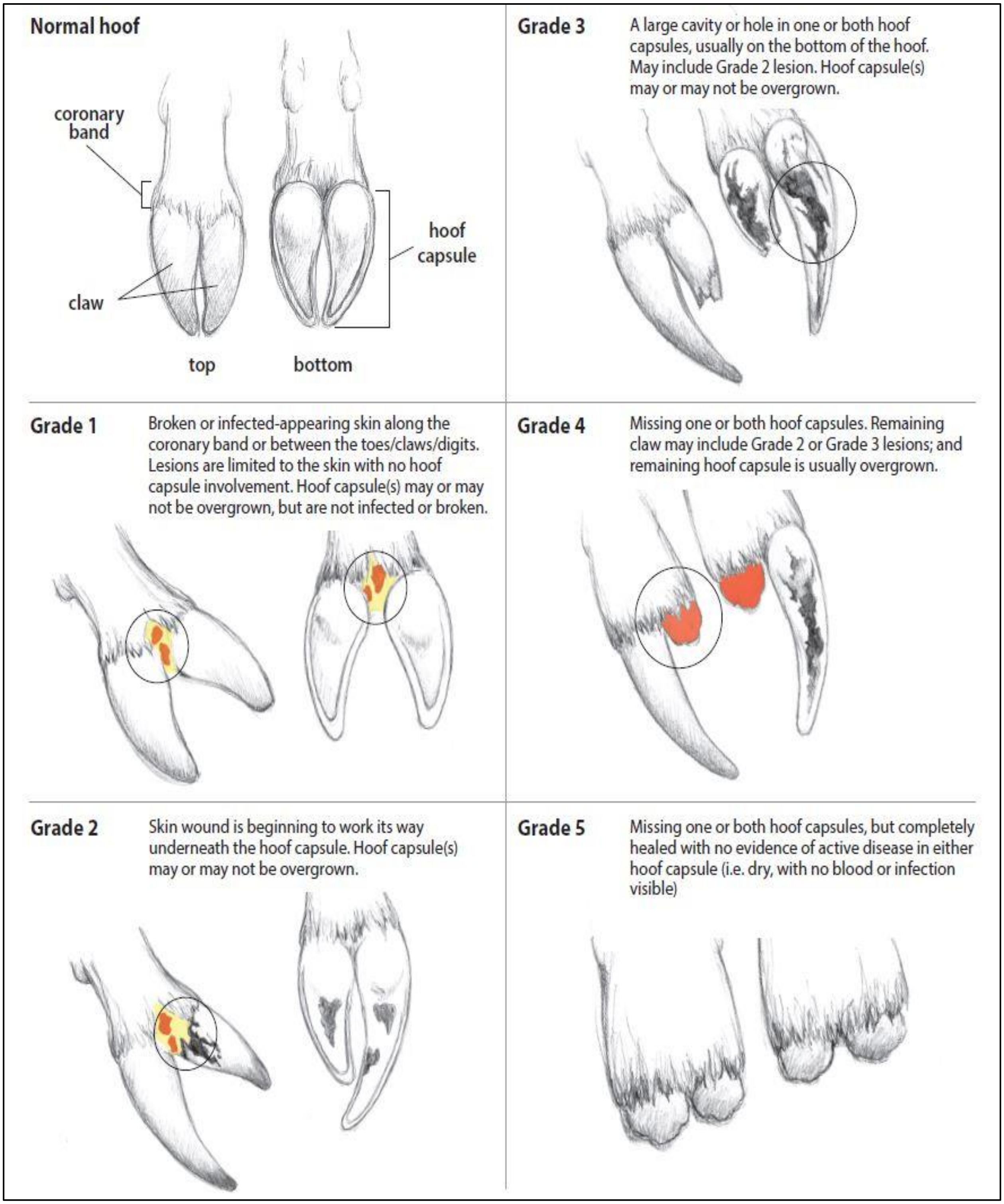

Figure 3. Diagram depicting characteristics we preliminarily associated with the 5 grades of treponeme-associated hoof disease we defined after capturing 60 female elk in February 2015, showing widely variable manifestation of the disease.

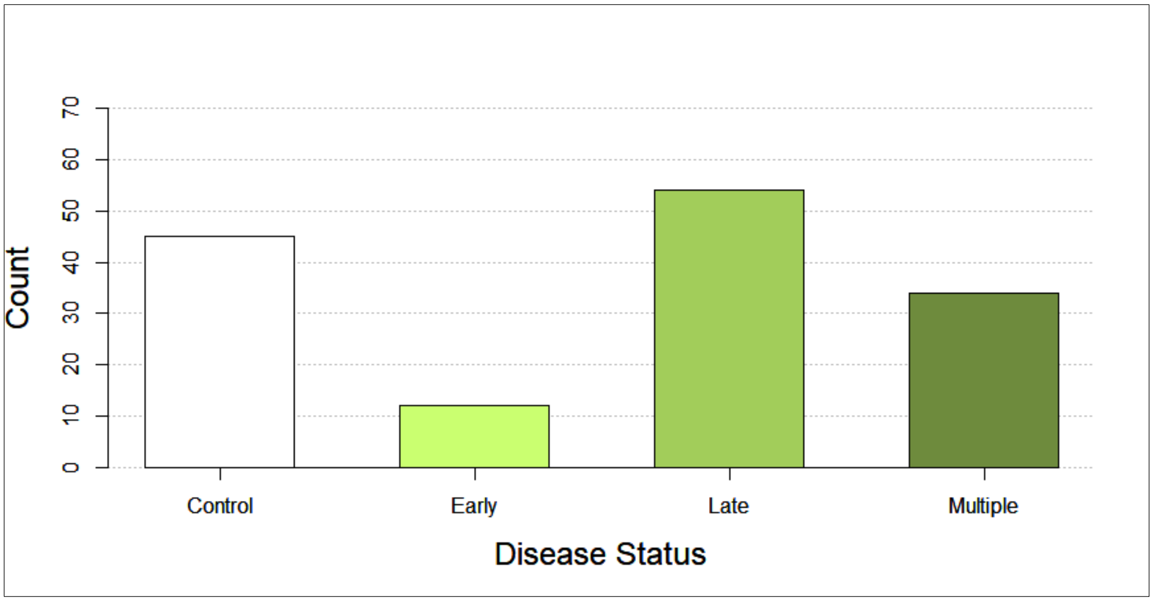

Figure 4. Distribution of hoof condition scores [Control, Early (Grade I or II), Late (Grade III or IV on a single hoof), and Multiple (present on multiple hooves)] at time of initial capture for female elk we captured February 2015–December 2017.

Progression.—We have recaptured 28 elk from our diseased group during subsequent capture events, which represented 36 hooves that were affected by TAHD during the previous capture. Of those 36 hooves, the disease progressed in 14, stayed the same in 16 (14 were Grade IV), had resolved in 6 (all were Grade I or Grade II), and 6 additional hooves had become involved. Five elk had progressed from having TAHD on a single hoof to multiple hooves, 13 had a single hoof involved during both captures, 4 transitioned from having multiple hooves involved to a single hoof, 4 had multiple hooves involved during both captures, and the disease had potentially resolved in 2 elk (Elk 161 and 162 both had Grade I on a single hoof the previous year; see below). In addition, 8 of the 27 elk from our control group had developed TAHD, with one of them having developed Grade IV on a single rear hoof between February 2015 and December 2015. Collectively, this information indicates that in many cases TAHD progresses quite rapidly and most individuals likely develop advanced stages of the disease within the first year of becoming infected.

Recovery.—We have only observed 1 case where an elk affected by TAHD had definitively recovered from the disease. We originally captured Elk 315 in December 2016, at which time we determined she had Grade II on her right hind hoof (Figure 5). She was subsequently legally harvested in November 2017 and formal examinations indicated all four hooves were grossly and histologically normal, in addition to silver stains being negative for any spiral bacteria with typical *Treponema* morphology. We are not able to definitively claim the disease resolved in Elk 161 and Elk 162 because we only made that assessment during a gross examination of the hooves in a field setting.

Figure 5. Photos of the right hind hoof from Elk 315 at time of initial capture on December 16, 2016 (left image) and photos of both rear hooves at time of histological examination at the Colorado State University Veterinary Diagnostic Laboratory, Fort Collins, Colorado, USA in 2017. The elk was legally harvested on November 5, 2017.

Body Condition

We determined body condition [i.e., percent ingesta-free body fat (IFBF)] at time of capture by having an experienced observer use a portable ultrasound to measure maximum subcutaneous rump fat thickness (MAXFAT) and determine a rump body condition score (rBCS) following the procedures of Cook et al. (2001*a*). We then used estimates of MAXFAT and rBCS to estimate IFBF at time of capture following the procedures of Cook et al. (2010). We also measured each elk's chest girth to estimate body mass following the procedures of Cook et al. (2003). Lastly, because lactation status has consistently been shown to be a primary determinant of the level of condition female elk are able to achieve in autumn (Cook et al. 2004, Cook et al. 2013), we classified elk as lactating (milk could be extracted from the udder) or non-lactating (milk was not present). The presence of milk indicated the female had been nursing a calf sometime within the previous 11 days (Flook 1970). Our non-lactating group undoubtedly included a combination of females that were not bred the previous autumn (true non-lactators), females that lost their calf at or near parturition, females that lost their calf at various times between parturition and capture, and females that successfully produced a calf, but ceased lactating prior to capture. We pooled data December 2015–2017 to increase sample sizes.

Mean estimates of IFBF were consistently lowest for elk that were affected by TAHD, albeit those differences were minimal and have a low probability of being statistically significant, except for non-lactating elk in December (Table 2 and Figure 6). However, our current estimates include all elk affected by TAHD, irrespective of disease severity, which as discussed we cannot confidently quantify at this time. For example, 12 (6 lactating, 6 non-lactating) of the elk in our diseased group that we captured in December represented elk that had early stages of the disease, and given that we have learned the disease progresses quickly, there is a reasonable likelihood these elk spent a majority of the summer-autumn period unaffected by TAHD. Although sample sizes are small, our preliminary observations indicate the condition of adult female elk with early stages of the disease may be more similar to the condition of adult female elk within our control group.

Table 2. Mean estimates and associated 95% confidence intervals (CI) of percent ingesta-free body fat (IFBF) by disease and lactation status for adult female elk we captured in February and December in the Mount St. Helens elk herd area, 2015–2017.

	Non-Lactating						**Lactating**					
	Diseased Group			**Control Group**			**Diseased Group**			**Control Group**		
Season	***n***	$\bar{x}$	**CI**	***n***	$\bar{x}$	**CI**	***n***	$\bar{x}$	**CI**	***n***	$\bar{x}$	**CI**
February	56	4.2	3.6-4.7	19	5.1	3.9-6.2	---	---	---	---	---	---
December	46	5.8	5.2-6.5	16	8.5	7.7-9.2	36	5.3	4.7-6.0	31	6.3	5.7-6.94

Pregnancy

We determined pregnancy status at time of capture via ultrasonography and analysis of Pregnancy–Specific Protein B (PSPB) in serum samples collected during capture (Noyes et al. 1997). None of the elk we classified as yearlings (n = 4) were pregnant. For adult female elk, pregnancy rates have consistently been higher for our control group (range = 0.69–0.84) than for our diseased group (range = 0.32–0.59) (Figure 7). Overall, 50% (95% CI = 41–58%) of elk within our diseased group (n = 139) and 79% (95% CI = 67–87%) of elk within our control group (n = 66) have been pregnant. For comparison, McCorquodale et al. (2014) reported an overall pregnancy rate of 67% for the 109 adult female elk they captured 2009–2012.

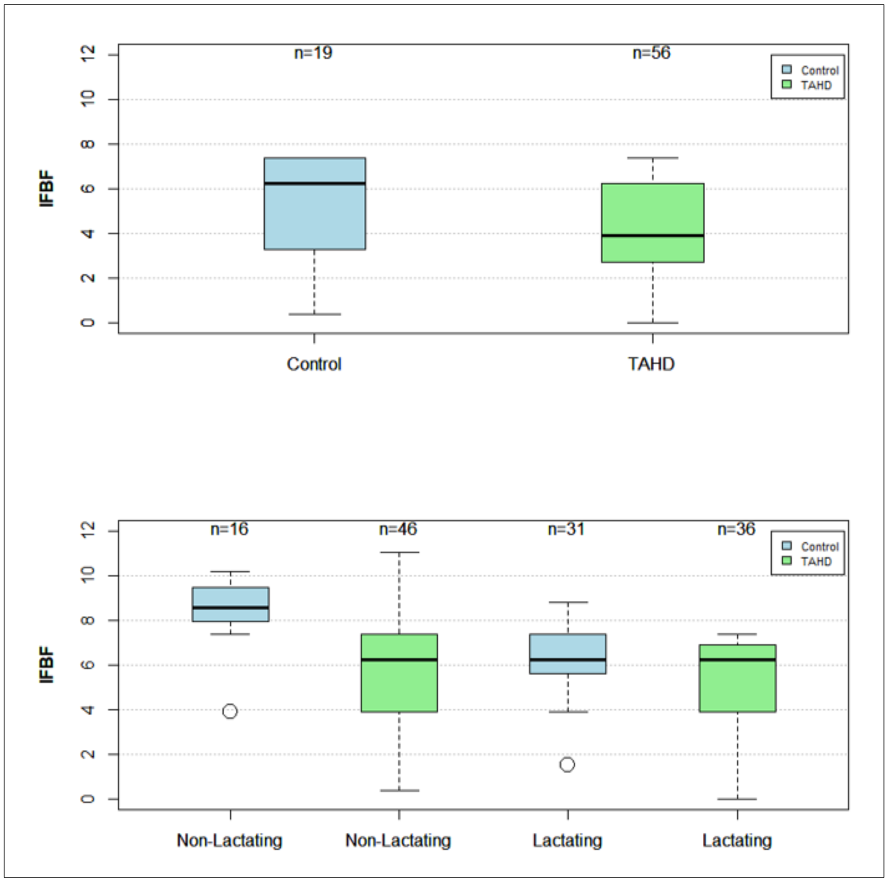

Figure 6. Boxplots of percent ingesta-free body fat (IFBF) by disease status for adult female elk we captured in the Mount St. Helens elk herd area February 2015 (top) and by disease and lactation status for adult female elk we captured December, 2015–2017 (bottom).

Productivity

In our original proposal, we defined productivity as the early survivorship of calves (e.g., to 6 months of age) and proposed we would estimate productivity using calf-at-heel ratios or lactation rates from hunter harvested elk. We have since abandoned those efforts and are only indexing calf survival using lactation rates observed in December and directly estimating calf survival from elk that we captured during subsequent capture events (i.e., we know what their pregnancy status was the previous year and assume a calf died if they were pregnant in $Year_t$, but not lactating in $Year_{t+1}$).

The proportion of adult female elk that were lactating at time of capture in December has ranged 0.63–0.69 for elk in our control group and 0.42–0.45 for elk within our diseased group (Figure 8). Overall, 0.66 (95% CI = 0.52–0.78) of elk within our control group (*n* = 47) and 0.44 (95% CI = 0.34–0.55) of elk within our diseased group (*n* = 82) have been lactating in December.

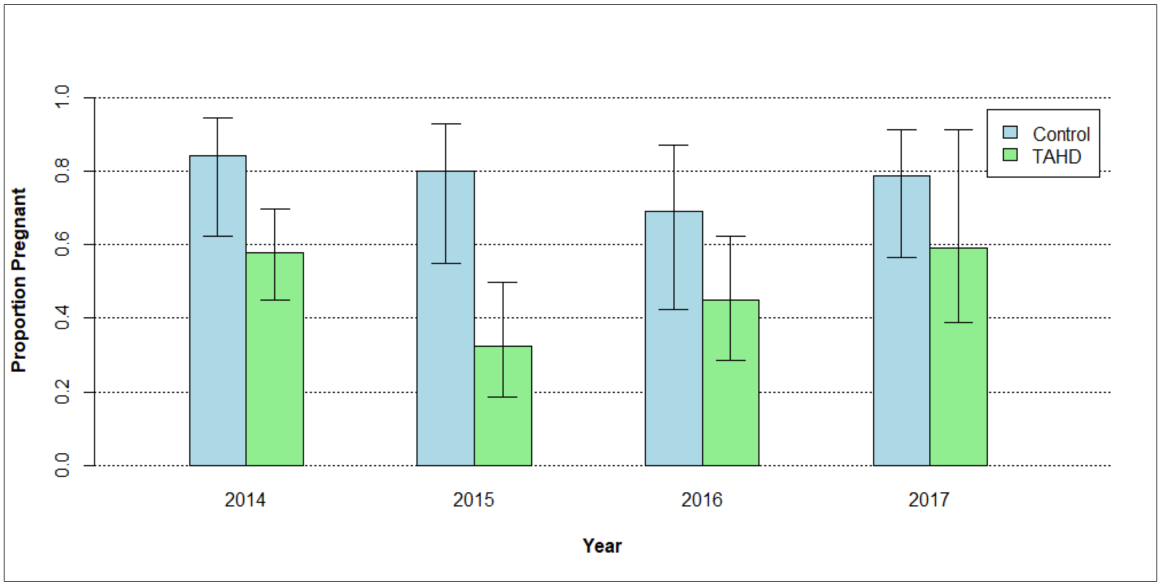

Figure 7. The proportion (and associated 95% confidence intervals) of adult female elk that were pregnant and affected by treponeme-associated hoof disease (TAHD) or had no visible signs of being affected by the disease (Control) at time of capture in the Mount St. Helens elk herd area, 2014–2017.

Although lactation rates were consistently lower for elk in our diseased group, they also had lower pregnancy rates, which indicates calf survival may not be substantially disparate between groups. Although inferences are limited by our small sample size, estimates of calf survival using pregnancy and lactation status of elk captured during subsequent capture events, also indicate calf survival to 6 months of age may be similar between groups. We estimated calf survival for our control group to be 0.60 (n = 10) in 2015, 0.75 (n = 8) in 2016, and 0.50 (n = 6) in 2017. Estimates of calf survival for our diseased group were 0.62 (n = 13) in 2015, 0.50 (n = 6) in 2016, and 0.67 (n = 3) in 2017. Overall, 0.63 of adult female elk within our control group where pregnancy status was known and 0.60 within our diseased group have successfully raised a calf through late-autumn.

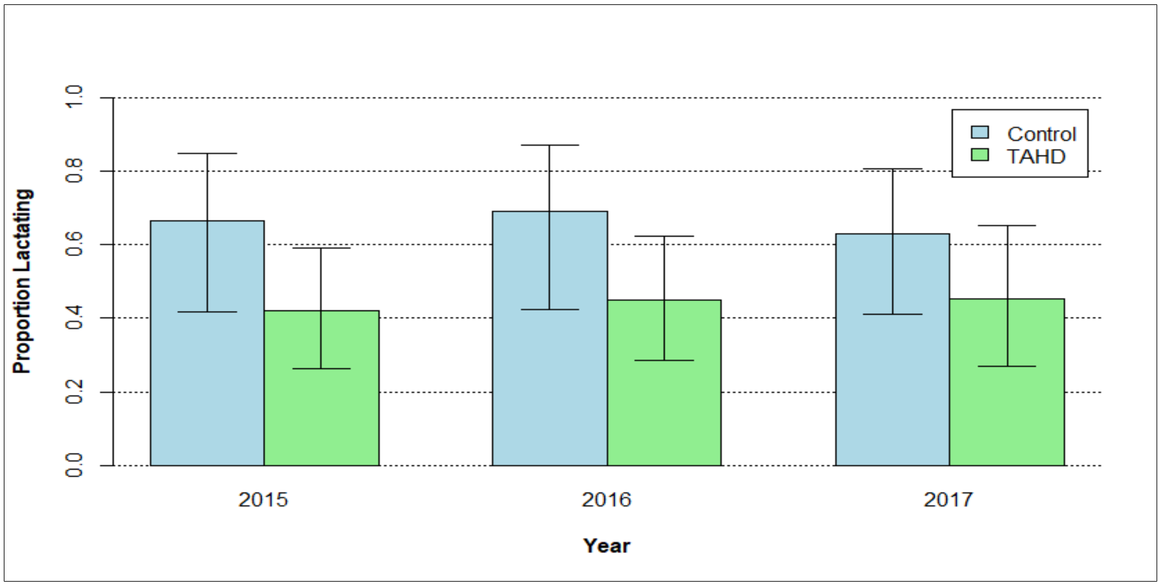

Figure 8. The proportion (and associated 95% confidence intervals) of adult female elk that were lactating in December and affected by treponeme-associated hoof disease (TAHD) or had no visible signs of being affected (Control), in the Mount St. Helens elk herd area, 2015–2017.

Survival

For our preliminary analysis, we estimated survival using the Kaplan-Meier estimator, modified for staggered-entry of individuals (Pollock et al. 1989). In addition to estimating survival since project initiation (i.e., March 2015–August 2018), we also estimated annual survival rates (i.e., May $1_{\text{Year } t}$–April $30_{\text{Year } t+1}$) and survival rates during 3 seasons that were biologically relevant to elk. These seasons included: 1) summer (May–August), the period of greatest nutritional demand for female elk supporting calves, 2) autumn (September–December), when the nutritional demands associated with lactation diminish and hunting seasons occur, and 3) winter (January–April), when elk primarily rely on fat reserves they accrued the previous summer-autumn period to meet their basic metabolic requirements.

In addition to censoring elk that died during or immediately following the capture process, we censored two mortalities from our survival analyses because, in both instances, the elk died within a couple weeks of their capture and we could not rule out capture-related stress as a contributing factor (e.g., Beringer et al. 1996). We also censored 1 elk from all analyses because she was originally captured in February 2015 as a control, missed in December 2015, and then her radio-collar quit transmitting in November 2016—thus, we have no way of knowing whether or not she had maintained her control status. In addition, we have had 5 radio-collars fail and subsequently censored these elk from our analyses at the last point in time we received a GPS location transmission or determined the elk's status via VHF monitoring. Lastly, any elk within our control group that developed TAHD and had advanced stages of the disease was censored during the time period when disease status was unknown. For example, we censored the 3 elk confirmed to have lost their control status between February 2015 and December 2015 from our analysis during the period of February 2015–November 2015 and then brought them back into the analysis as a diseased elk in December 2015. We took this approach because we have no way of knowing when exactly they developed the disease. Lastly, we have had 2 control elk die within a few months of us capturing them (February and May, both captured the previous December) that had developed early stages of the disease by the time they died. In both instances, we kept them in the control group for this preliminary analysis. We believed this decision was justified given that disease progression appears to be quite rapid (i.e., they likely contracted the disease shortly before death) and they had spent the majority of the year as an elk unaffected by TAHD, which may have influenced their probability of survival during winter months. This decision will be considered more thoroughly as the project progresses.

Estimated survival since project initiation (i.e., March 2015–August 2018) has been 0.23 (95% CI = 0.16–0.29) for our diseased group and 0.37 (95% CI = 0.24–0.51) for our control group. Annual survival rates were similar between groups in 2017, but greater for elk in our control group in 2015 and 2016 (Table 3). Survival during summer has been similar between groups and among years within groups (Table 3). Substantial differences in estimates of survival between groups have primarily occurred during the winter season and survival of elk in both groups was lowest in winter 2016 when abnormally severe winter conditions persisted (Table 3). Although survival during autumn has not been markedly dissimilar between groups, and lower for elk in our control group 2 of 3 years, all 6 mortalities we have documented for elk in our control group during autumn have been human-caused (i.e., natural survival has been 1.00), compared to only 5 of 15 mortalities in our diseased group.

Table 3. Estimated survival rates (Ŝ) and associated 95% confidence intervals (CI) for elk affected by treponeme-associated hoof disease (Diseased Group) and for elk that were seemingly unaffected by the disease (Control Group) during 3 seasons of biological relevance to elk in the Mount St. Helens elk herd area, 2015–2017.

Diseased Group										
	Summer		**Autumn**		**Winter**		**Annual**	
Year	**Ŝ**	**CI**	**Ŝ**	**CI**	**Ŝ**	**CI**	**Ŝ**	**CI**
2015	0.93	0.86-0.99	0.92	0.85-0.99	0.80	0.70-0.90	0.68	0.57–0.79
2016	0.94	0.87-0.99	0.91	0.84-0.99	0.68	0.56-0.79	0.58	0.47–0.69
2017	1.00	–	0.86	0.76-0.96	0.75	0.65-0.86	0.65	0.54–0.76
Control Group								
	Summer		**Autumn**		**Winter**		**Annual**	
Year	**Ŝ**	**CI**	**Ŝ**	**CI**	**Ŝ**	**CI**	**Ŝ**	**CI**
2015	0.93	0.81-0.99	0.85	0.65-0.99	1.00	–	0.79	0.61–0.97
2016	0.94	0.81-0.99	1.00	–	0.83	0.66-0.99	0.78	0.60–0.97
2017	1.00	–	0.67	0.43-0.91	1.00	–	0.67	0.51–0.84

[1]Summer = May–August; Autumn = September–December; and Winter = January–April

Cause-specific Mortality

We have documented 86 mortalities (73 diseased group, 13 control group) since project initiation and attempted to investigate all deaths within 24 hours of receiving a message that a mortality event had occurred. In instances where the carcass was fully, or mostly, intact, we performed a field necropsy to determine proximate cause of death and to collect tissue samples that we submitted to the Colorado State University Veterinary Diagnostic Laboratory (CSU) for histological examination. Samples we collected and submitted to CSU included tissue samples from the heart, lungs, liver, kidney, spleen, pancreas, mammary gland, brain, popliteal and pre-scapular lymph nodes, any other tissues that seemed abnormal in appearance, and all 4 hooves. We also collected a femur and measured bone marrow fat content to estimate percent body fat at time of death (Neiland 1970). We were not able to collect all samples from every mortality event. We have received final histology reports from CSU for all but 3 mortalities to date, but have not completed bone marrow analysis for 8 elk that died April 2018–present.

To date, we have classified proximate causes of mortality as malnutrition (only applies to our control group), general debilitation (only applies to our diseased group), disease (non-TAHD), human-caused (legal and illegal harvest), unknown, accident, and predation. Mortalities we classified as general debilitation were typically characterized by severe emaciation, the presence of advanced hoof disease, and no evidence of another primary disease based on histology of all major organs sampled. The emaciation observed in these animals indicates that they are in an extreme negative energy balance. However, we have no way of determining the relative contribution of the catabolic effects of a chronic severe disease such as TAHD (Demling 2009), compared to the catabolic effects resulting from nutritional limitations, such as those already known to occur in this herd (Cook et al. 2013, McCorquodale 2014), and how they may interact to affect the survival of elk. Mortalities we classified as disease (non-TAHD) have included cases where histological findings indicated the elk was afflicted by a severe case of pneumonia, severe renal disease, or septicemia. Lastly, mortalities we have classified as accidents have included 4 elk that have gotten stuck in bogs/mud, 1 elk that apparently drowned, and 1 elk that fell down an extremely steep and rocky slope—in all 6 cases the elk were in extremely poor condition, which we believe contributed to their plight.

Of the 13 mortalities we have documented for our control group, we have preliminarily classified 1 as unknown. Of the remaining 12, we have classified 6 (0.50) as human-caused (3 legal, 2 wounding loss, 1 illegal), which has been the leading cause of mortality (Figures 9 and 10). Of the 73 mortalities we have documented for our diseased group, we censored 3, 2 are pending histological findings, and have preliminarily classified 14 as unknown. Of the remaining 54, the leading causes of mortality have been general debilitation (0.44, n = 24) and predation (0.28, n =15). Most mortality events for our diseased group have occurred January–April (Figure 10). In instances where we have classified mortalities in our diseased group as general debilitation, predation, and unknown, 1.00, 0.83, and 0.89, respectively, have had bone marrow content levels indicative of severe negative energy balance.

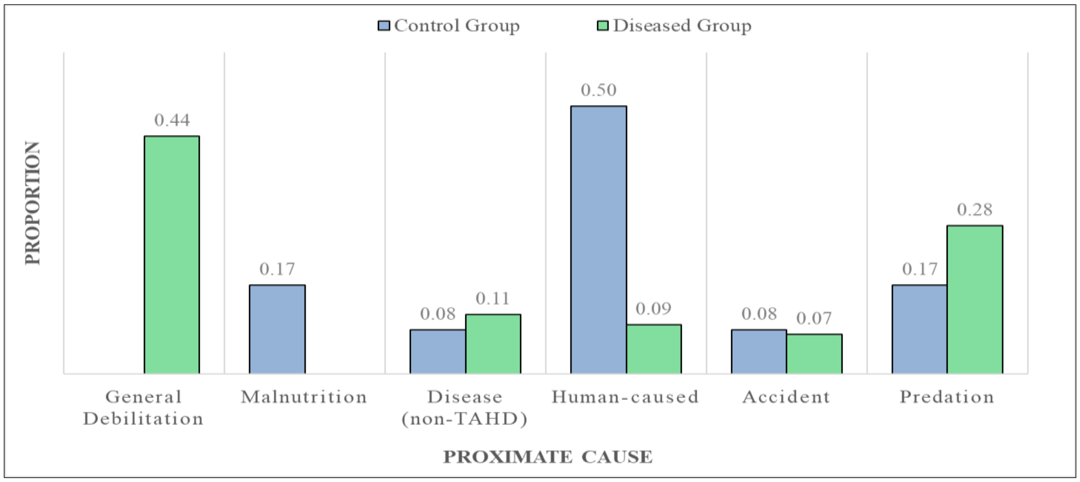

Figure 9. Proportion of deaths by proximate cause for adult female elk that were affected by treponeme-associated hoof disease (Diseased Group) or had no visible signs of being affected by TAHD (Control Group) in the Mount St. Helens elk herd area, February 2015–August 2018.

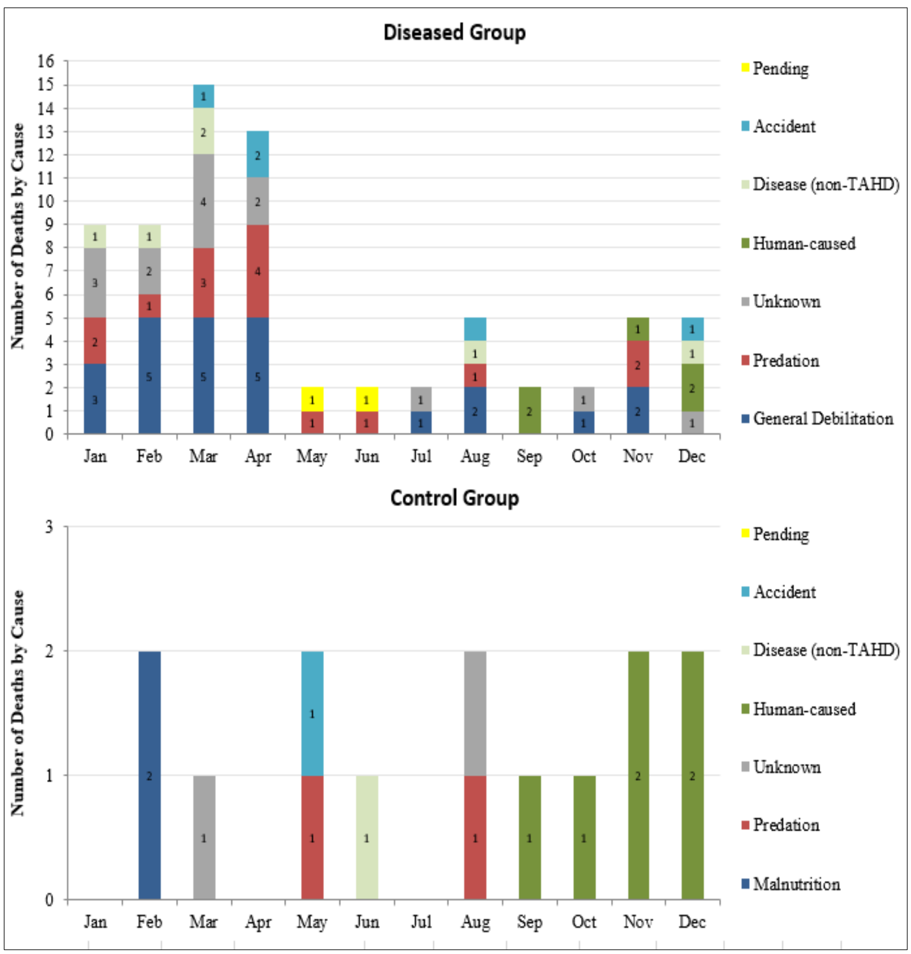

Figure 10. Number of deaths by cause and month for elk that were affected by treponeme-associated hoof disease (Diseased Group) or had no visible signs of being affected by the disease (Control Group) in the Mount St. Helens elk herd area, February 2015–August 2018.

DISCUSSION

It is far too soon for us to make any definitive statements that relate to our research objectives or to discuss our results in any detail. Preliminarily, elk affected by TAHD have had lower levels of condition in December, lower pregnancy rates, lower lactation rates, and lower annual survival rates. Our estimates of IFBF in December indicate elk in the Mount St. Helens elk herd area continue to experience strong nutritional limitations during late-summer and autumn, regardless of disease status. Irrespective of proximate cause, 0.88 of the mortalities we have documented for elk affected by TAHD, have included animals that had bone marrow content levels indicative of a severe negative energy balance. However, at this time we are not able to quantify the degree to which the catabolic effects of TAHD are contributing to those observations.

Our preliminary observations indicate that it will be important for us to consider disease severity when we complete our final analysis and we will continue to evaluate how we define disease status and severity as the study progresses. Similarly, we will continue to examine when we censor elk in our survival analysis that transition from our control group to our diseased group. At this point in time, we do not anticipate any changes to our study design and plan to conduct captures in December 2018.

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From: afa@mcn.org <afa@mcn.org>
Sent: Sunday, April 19, 2020 10:40 PM
To: Office of the Secretary CNRA <secretary@resources.ca.gov>; FGC <FGC@fgc.ca.gov>; Wildlife DIRECTOR <DIRECTOR@wildlife.ca.gov>; Cornman, Ari@FGC <Ari.Cornman@FGC.ca.gov>
Cc: senator.stern@senate.ca.gov
Subject: [Fwd: JAPAN TIMES - China and Wildlife Trade - comments?]

Warning: This email originated from outside of CDFW and should be treated with extra caution.

---------------------------- Original Message ----------------------------
Subject: JAPAN TIMES - China and Wildlife Trade - comments?
From: afa@mcn.org
Date: Sun, April 19, 2020 10:37 pm
To: afa@mcn.org
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https://gcc01.safelinks.protection.outlook.com/?url=https%3A%2F%2Fwww.japantimes.co.jp%2Fopinion%2F2020%2F04%2F18%2Fcommentary%2Fworld-commentary%2Fcan-china-end-wildlife-trade%2F%23.Xp0zgJllCM8&data=02%7C01%7Cfgc%40fgc.ca.gov%7C46e101ecc9704dfa556e08d7e4ed4e18%7C4b633c25efbf40069f1507442ba7aa0b%7C0%7C0%7C637229580177766460&sdata=RRIWtpducwqOQaqusOfL5kIN7Q%2Be%2FddpRJkRUv7v7tQ%3D&reserved=0

From: kathy Lynch <lynch@lynchlobby.com>
Sent: Tuesday, May 26, 2020 4:03 PM
To: Wildlife PIO ALL <PIOALL@wildlife.ca.gov>; FGC <FGC@fgc.ca.gov>
Cc: kathy Lynch <lynch@lynchlobby.com>
Subject: Press Release: PERC Research Fellow Testifies before Senate Natural Resources & Water Committee at Hearing on Wildlife Trade and the COVID-29 Pandemic

Warning: This email originated from outside of CDFW and should be treated with extra caution.

Please see the attached press release:

PERC Research Fellow Testifies before California Senate Committee at Hearing on Wildlife Trade and the COVID-19 Pandemic.

Lynch & Associates

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https://www.perc.org/2020/05/26/perc-research-fellow-testifies-before-california-senate-committee-at-hearing-on-wildlife-trade-and-the-covid-19-pandemic/

May 26, 2020

News for Immediate Release
May 26, 2020
Contact: Hannah Downey, 406-587-9591, hannah@perc.org

PERC RESEARCH FELLOW TESTIFIES BEFORE CALIFORNIA SENATE COMMITTEE AT HEARING ON WILDLIFE TRADE AND THE COVID-19 PANDEMIC

Catherine Semcer testifies before the California Senate on the role of hunting in conserving wildlife habitat in Africa

(Sacramento, California)—PERC research fellow Catherine Semcer testified today before the California Senate Committee on Natural Resources and Water on SB-1175 and the need to ensure that efforts to reduce future pandemics by addressing the international trade in wildlife are focused and equitable. The hearing was held by telephone, and Semcer's testimony centered on a proposal to ban the import and possession of certain African hunting trophies in California as part of the state's pandemic response policy. Semcer specifically addressed the positive contributions of hunting in Africa to conservation, discussed the role of conservation in securing public health, and highlighted the fact that the importation of hunting trophies into the United States has never been linked to an outbreak of disease.

"Africa's hunting industry creates economic incentives that conserve wildlands on a grand scale. The total area conserved by hunting in Africa is more than six times the size of the U.S. national park system," said Semcer. "Trophy import bans like those being considered by the California Senate will make it even harder for Africa's hunting industry to recover from the effects of the Covid-19 pandemic. This will undoubtedly result in African

wildlands being cleared for logging and agriculture, something scientists say we must avoid in order to prevent the next deadly pathogen from emerging. Since the importation of hunting trophies has never been linked to an outbreak of deadly disease, the California Senate would be ill advised to make it harder for African countries to use this market-based tool for keeping wildlands intact."

Researchers with the Georgetown Center for Global Health and Science Security estimate that 60 percent of emerging human pathogens are zoonotic, and that of these, 70 percent have wildlife origins. Primates, birds, bats, and pangolins, none of which are commonly hunted for trophies, are thought to present an especially high risk of disease transmission to people. The game species covered by the hunting trophy provisions of the legislation being considered by the California Senate have not been identified as presenting a risk to human health and are nonetheless already subject to strict import controls to mitigate any risk that might arise.

Stemming the loss of wildlands in Africa and elsewhere is recognized as a critical step toward reducing the likelihood of future pandemics. Previous outbreaks of Ebola, Lassa fever, and other deadly diseases have been closely linked to the clearing of wildlife habitat for logging and agriculture, which bring groups of people into closer contact with disease-carrying wildlife. **"Africa's hunting industry helps to keep the continent's remote areas remote. Importantly it does so in a way that is not dependent on philanthropy or foreign aid because it turns wild areas into an economic asset. Rather than undermine the industry with trade restrictions that will do nothing to benefit conservation or public health, policymakers should appreciate the benefits the industry provides and work to amplify them," said Semcer.**

Semcer's testimony highlighted several key points:

- Hunting provides economic incentives and revenue critical to conserving African wildlife in a manner that is self-sustaining and resilient. This includes the conservation of large expanses of habitat and discouraging poaching and illegal wildlife trafficking.
- Hunting and photo-tourism are not interchangeable, and restrictions on hunting have a track record of undermining the conservation of ecosystems and wildlife.

Catherine Semcer's full written testimony is available here.

From: PETER FLOURNOY 2
Sent: Tuesday, June 9, 2020 4:30 PM
To: FGC <FGC@fgc.ca.gov>
Subject: LETTER TO FISH AND GAME COMMISSIONERS ON BEHALF OF ADAM ALIOTTI

Warning: This email originated from outside of CDFW and should be treated with extra caution.

Good Afternoon Melissa:

Thank you for your letter yesterday accompanying my public records request documents.

This is an entirely different matter. I have attached as a word document an unsigned letter to the Commissioners as well as a pdf of the signed letter. Unfortunately, my scanner at home apparently put an unsightly line down the center of the signed letter.

I think either one would suffice to bring my request to the Commissioners, if you could distribute it.

I hope you and your loved ones are all safe and healthy and staying away from the COVID 19 outbreak!

Thank you, Pete

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PETER H. FLOURNOY

June 9, 2020

California Fish and Game Commission
President Eric Sklar
1416 Ninth Street, Suite 1320
Sacramento, CA 9581

Sent by Email Only to: https://fgc.ca.gov/

Re: **Adam Robert Salvatore Aliotti, (No. 17 ALJ04-FGC, July12, 2018) and Alecia Dawn, Inc. (N0.17 ALJ-FGC, July 12, 2018), Aliotti, *et al*. v Fish and Game Commission (Sup. Ct. Case No. 19(CV001590)**

Dear Commissioners:

This is an unusual request made because of the uncertain times we are living in and because of the devastating impact that COVID 19 has had on all of California's commercial fishermen, and in particular Adam Aliotti. As you know his commercial fishing license is under suspension until October of 2021 pursuant to a settlement agreement. We request that in accordance with following the fundamental principles of fairness in the Commissioners' Code of Conduct that Adam's license suspension be lifted now.

There is no intention to challenge the administrative law judge's decision, nor the Commission's decision. There is no request to overturn the settlement agreement signed on September 11, 2019 in the Superior Court. Rather, this request is made based on the unusual circumstances Adam faces in this time of a pandemic which has caused the shuttering for months of California restaurants leading to a 65 to 80 percent drop in the businesses to which commercial fishermen sell their catch. Adam's spot prawn permit was restored two months before the 2019-2020 season closed, but that was of no benefit or solace given the COVID 19 closures.

The Department of Fish and Wildlife, recognizing this coastal tragedy is starting to develop a program for dispersing the millions of dollars California has received for its commercial fishermen. While from what I have learned this will be a very generous program, however, it will be keyed to those fishers who have suffered 30% losses in 2020 over their 2019 incomes and who have spent money on licenses and permits. This also does not help Adam since his fishing license and permits were suspended in 2019.

We are asking you to exercise your discretion and in fairness during this unprecedented time to restore Adam's fishing license now. He will still be on probation through March 1, 2024 and under the terms of probation under the settlement agreement if he is found to have committed any fisheries violation he has waived his right to appeal such a finding. The Commission will still have a hammer over Adam's head when you reduce the time of his fisheries license suspension.

Sincerely,

Peter H. Flournoy