BOTTOM-UP AND TOP-DOWN FACTORS CONTRIBUTE TO REVERSING A MOOSE POPULATION INCREASE IN NORTHEASTERN WASHINGTON

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ABSTRACT: Newcomers to the state, moose increased in abundance and distribution throughout northeastern Washington from the 1970s through 2013 when we began a study of moose demography north of Spokane, Washington. The study was designed and analyzed with 2 adjacent but geographically distinct population subunits – a northern study area with wolf (*Canis lupus*) packs present and a southern study area without wolf packs. We followed the fates of 67 GPS-collared cow moose (41 and 26 in the northern and southern study areas, respectively), and monitored production and apparent survival of their (unmarked) calves using ground-based approaches during 2014–2018. We used the Cormack-Jolly-Seber estimator to account for imperfect detection of calves monitored via their mothers, and AICc to evaluate competing models of calf survival. We supplemented these analyses with indices of calf recruitment to mid-winter obtained from helicopter-based surveys over a larger survey area. The best supported calf survival model included neither study area nor temporal covariates; estimated annual calf survival in both study areas combined was 0.36 (SE = 0.05). Adult survival rates were similar in the 2 study areas (0.80 overall; 95% confidence interval 0.76–0.86) but causes of death differed. Estimated observed fecundity (calves/females in early summer) was 0.56 in the northern study area and 0.70 in the southern; pregnancy rates showed a similar trend (0.70 northern, 0.93 southern). Populations in both study areas were declining; λ was estimated as 0.87 (SE = 0.03) in the northern study area and 0.90 (SE = 0.03) in the southern. Body condition data indicated moose from both study areas entered winter with low energy reserves, increasing susceptibility to morbidity and mortality. We found multiple factors acting on the northern population including equal rates of wolf predation and winter tick mortality of adults and low marrow fat in many tick- and predation-related mortalities. We suggest the marked population decline measured during the study was related to multiple and often interacting factors including the combined and often interacting top-down effects of predation and bottom-up effects of nutrition.

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Moose (*Alces alces*) arrived in the northeastern portion of Washington from adjacent British Columbia or Idaho in the early 20th century. First documented in 1929, moose in Washington were estimated to number only 60 in 1972 and 200 in 1991 (Timmerman

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2003, Base et al. 2006). By 2001, approximate estimates by state biologists suggested abundance had exceeded 1,000 animals and the population was continuing to grow. Based on index counts from helicopter surveys in 2002–2012, Harris et al. (2015) estimated that moose increased those years at an average annual rate of ~9%; albeit, a high level of statistical uncertainty was associated with that 11-year trend despite incorporating plausible covariates affecting sightability. As of the early 2010s, Washington was 1 of only 2 western states (including Colorado) where moose were considered increasing (Nadeau et al. 2017, Timmerman and Rodgers 2017). In both, populations were newly colonizing and continuing to expand into unoccupied habitats, seemingly in an irruptive phase as described by Caughley (1970). Oyster et al. (2018) estimated 5,169 moose (95% credible interval 3,510–7,034) within a 10,513 km^2 survey area (~ 0.5 moose/km^2) encompassing most of northeastern Washington, considerably more moose than agency biologists anticipated.

Concerned that moose in northeastern Washington were unlikely to continue increasing, in 2013 the Washington Department of Fish and Wildlife (WDFW) initiated a demographic study northeast of Spokane, relying on GPS-collared adult females to estimate adult survival, and ground-observations to estimate fecundity and calf survival. Factors potentially reducing the population included "bottom-up" effects of forest succession that would reduce abundance of shrub forage, indirect effects of climate change causing increased disease and parasitism (e.g., winter ticks [*Dermacentor albipictus*]), and predation associated with a newly established wolf (*Canis lupus*) population. Wolves arriving by 2008 in northeastern Washington had established 10 packs by 2013 (WDFW et al. 2019), eliciting vocal concern from citizenry that predation ("top-down" effects) would induce declines in the local ungulate populations.

Our objective was to assess population dynamics of the moose population in northeastern Washington, specifically to: 1) quantify annual survival of adult female moose, 2) quantify annual calf survival, 3) quantify fecundity, 4) use these vital rates to project asymptotic population growth rates, and 5) interpret these data within the context of predator abundance and distribution, body condition, recruitment, prevalence of parasitic infections, local climatic patterns, and population density.

STUDY AND SURVEY AREAS

We studied vital rates of moose in northeastern Washington using GPS-collared cows during 2014–2018 in 2 study areas: 1) a northern area (~775 km^2) with at least 1 wolf pack at the outset, and 2) an adjacent southern area (~477 km^2) without wolf packs (Fig. 1). WDFW subsequently confirmed and monitored 2 packs concurrently occupying portions of the northern area. In both study areas, elevation ranged from 500 to 2,200 m and climate was characteristic of both continental and marine types with low relative humidity and moderate temperatures (June-August ave. = 16.6 °C) during summer and foggy and cool weather during winter (November–February ave. = −2.7 °C) (USGS North America Climate; www.sciencebase.gov).

Land ownership in both study areas was a matrix of private timber inholdings (21%), private landowners (45%), and public (34%) and tribal lands. The entire study area was dominated by coniferous forest (86%) and a variety of deciduous and evergreen shrubs (Franklin and Dyrness 1988, Johnson and O'Neil 2001); see Cook et al. (2021) for specific description. Potential predators of moose

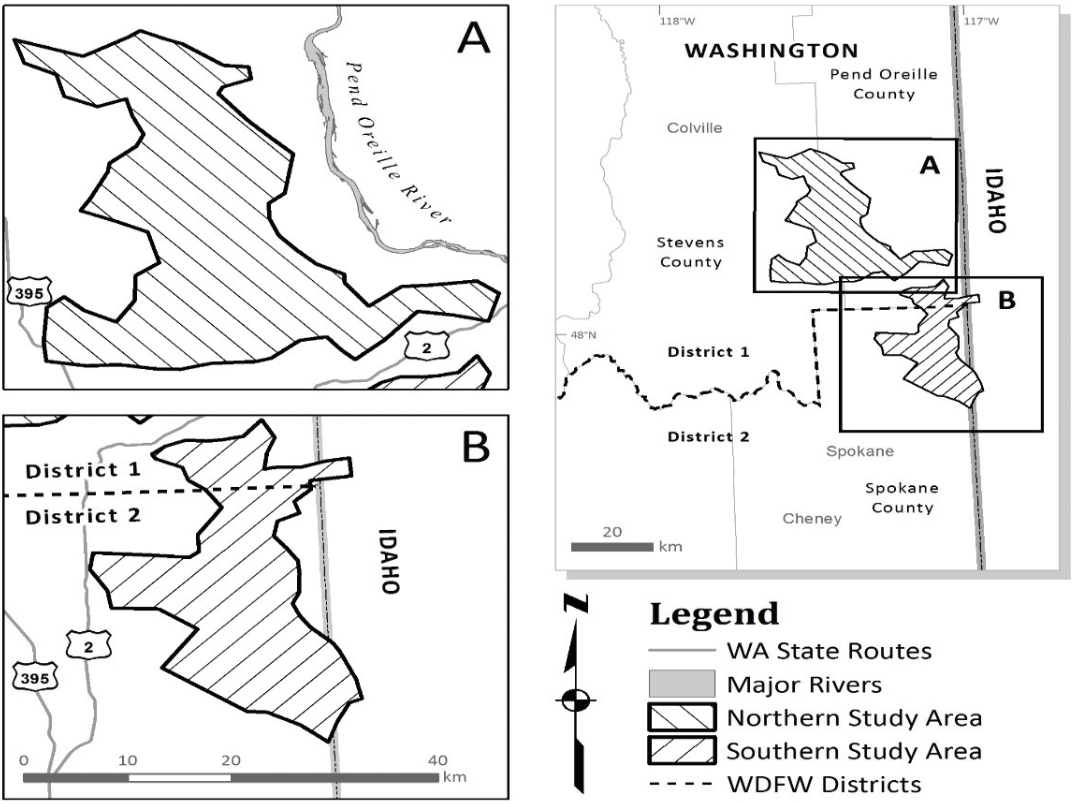

Fig. 1. Study areas (A: Northern; B: Southern) and (right-hand panel), both in context of their location in northeastern Washington. Approximate locations of population centers Spokane, Colville, and Cheney are indicated on the reference map.

included wolves, black bears (*Ursus americanus),* and mountain lions (*Puma concolor*).

The survey area on which we obtained additional information on recruitment in 2003–2019 was identical to that described by Oyster et al. (2018). Briefly, this area consisted of primarily forested lands (mix of federal, state, private industrial) bordered on the east by the Washington-Idaho border, the north by the Canadian border (latitude 49° N), the west by the Colville Indian Reservation, and the south by the predominance of rural, agricultural, and suburban lands north of Spokane. Two WDFW administrative districts were represented within the survey area: District 1 to the north which was almost entirely occupied by resident wolf packs, and District 2 to the south which had occasionally dispersing wolves. All 3 areas contained a substantial number of white-tailed deer (*Odocoileus virginianus*), much smaller numbers of elk (*Cervus elaphus*), and a few mule deer (*O. hemionus*) mostly in WDFW District 1 north of the study area (Hoenes et al. 2016, WDFW 2019a, 2019b).

Moose hunting occurred in the study area and larger survey area during all years of the study. Permits were by random-draw lottery with limits set approximately by Game Management Unit (GMU) and restricted alternatively to “antlerless only” (primarily cows) or “any moose” (primarily antlered bulls). Taking radio-collared animals was allowed, although WDFW discouraged hunters (via website and pamphlet) from taking cows accompanied by offspring. Prescribed hunting pressure was lower on the northern area than the southern (WDFW 2019a, 2019b). Historically, GMUs 113 and 117 (in the north) were managed to provide for a low opportunity/high success hunting experience, whereas GMU 124 (in the south) had been harvested more aggressively due to its proximity to rural and suburban regions where moose-human conflicts were considered more likely.

METHODS

Captures

We captured female moose by aerial darting (Pneudart Inc., Williamsport, Pennsylvania, USA) from a Bell Jet-Ranger helicopter (Northwest Helicopters, Olympia, Washington, USA) on 16–20 December 2013, 2–6 December 2014, and 1–6 December 2016; detailed description in Cook et al. (2021). Although we attempted to avoid capturing yearling females (possibly reproductively immature), we did include 1 yearling in each area in our survival estimates. Capture crews documented the association of calves with captured cows when possible. From the majority we collected blood, ear punch biopsies, fecal samples, and ectoparasites (primarily ticks for species identification) but made no attempt to quantify tick abundance. We extracted an incisiform lower canine tooth for aging from all but 7 animals (condition at capture required rapid processing time) after injecting 10 mg of bupivacaine hydrochloride into the mental foramen for pain relief (Mansfield et al. 2006). Moose ages were estimated by counting cementum annuli (Mattson's Lab, Manhattan, Montana, USA). We fitted moose with GPS collars that transmitted locations every 23 h (Survey Globalstar; Vectronic Aerospace GmbH, Berlin, Germany). From each animal, one trained observer (R. Cook) collected indices of nutritional condition, lactation status, chest girth, and pregnancy; detailed description in Cook et al. (2021).

Adult Survival

We depended on mortality signals (9 h without movement) transmitted via emails and text messages to alert us upon death of radiomarked cows. We inspected mortality sites within 24 h when possible, but logistical challenges or lack of timely mortality signals caused some delays. We surveyed mortality locations for signs of struggle, and for carnivore scat or tracks, and performed a field necropsy of intact carcasses to further assess cause of death. We also noted tick loads and hair loss, qualitatively examined arteries for presence of *E. schneideri* (see below) and removed a femur for subsequent assessment of marrow fat (see Cook et al. 2021). If available, we collected tissue samples for histopathological analysis to aid in determining cause of death. We classified winter tick mortalities based on indications of anemia (thin consistency of blood, pale color of internal organs), presence of engorged adult ticks, substantial hair loss, emaciation, and no evidence of other diseases, injuries, or predation.

Productivity and Calf Survival

We quantified presence of calves produced by collared cows through repeated ground observations (supplemented by remote camera traps in some cases) and occasional helicopter-based surveys. Ground crews attempted to obtain monthly observations of each collared moose throughout the biological year ($\text{May}_{(t)}$–$\text{April}_{(t+1)}$) to document calves, until such time as 3 successive approaches provided no evidence of a surviving calf. Fecundity (*F*, calves observed/cows monitored/summer) was likely biased low because it incorporates an unmeasurable component of undetectable neonatal mortality, especially in the case of twinning (Bergman et al. 2020); consequently, calf survival rates contain a corresponding upward bias.

Recruitment Indices and Harvest Information

To supplement calf:cow ratios developed by WDFW in the course of routine monitoring (Harris et al. 2015, Oyster et al. 2018), we conducted additional helicopter surveys during February–March 2019. With 2 observers, we focused searching in areas where we expected higher detectability of moose and acknowledge this approach was non-random. However, we have no reason to suspect a relationship between whether cows are accompanied by calves or not and their proclivity toward using open versus closed forest canopy.

We used moose harvest records routinely collected by WDFW to inform our understanding of population dynamics in both study areas. The GMU was the finest geographic scale at which harvest was documented, not geographic coordinates of the harvest site. Because there was close alignment between WDFW districts within which GMUs were nested and the 2 areas (Fig. 1), we assigned harvest by area via the closest GMU.

Potential Predators

WDFW annually estimated the numbers of wolves and packs beginning in 2009 (Wiles et al. 2011, Frame and Allen 2012, WDFW et al. 2014, 2015, 2016, 2017, 2018, 2019). We indexed wolf, black bear, and mountain lion abundance using remote cameras (Trophy Cams, Bushnell Corporation, Overland Park, Kansas, USA) placed on 24–31 game trails or areas likely to detect a predator within close proximity to randomly selected coordinates (“spsample” function within package “sp” in R 4.1.1) within each of 3 latitudinal strata in each area. Cameras remained at each location for 90–140 days during 6 periods (autumn 2015, 2016, 2017; winter 2016; summer 2016; spring 2017). We obtained data from 175 camera locations (110 in the northern area, 65 in the southern) during 18,599 camera-trap days (11,618 in the northern area, 6,981 in the southern). Multiple images of the same species within a 24-h period were considered as one individual, not as independent detections. The species-specific abundance index equaled the number of independent detections per camera-trap day X 100.

Carotid Worm Observations

We requested successful hunters in 2014–2017 to voluntarily submit moose heads with necks attached to document presence of nematodes consistent with *E. schneideri* suspected in the region (Pessier et al. 1998). Because we presumed our visual inspection might under-estimate prevalence (LeVan et al. 2013), in 2015 we submitted 37 carotid arteries for supplementary histological examination by the Washington Animal Disease Diagnostic Laboratory at Washington State University in Pullman, Washington, USA.

Long-Term Weather Data

To better understand the climatic context of moose population dynamics, we examined long-term weather records at the Deer Park Airport, located at 47° 58.02’, −117° 25.7’ (National Centers for Environmental Information, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, www.ncdc.noaa.gov). We examined trends in two metrics that Monteith et al. (2015) found to be correlated with moose recruitment in over 3 decades in 18 Rocky Mountain study areas: mean annual temperature and spring-summer precipitation (which we defined as means during May, June, July, and August). Because tick population dynamics have been correlated to persistence of spring snow (Samuel 2007), we also examined historical spring snow depth data at the Quartz Peak SNOTEL station (47° 52.8', −117° 4.8', elevation 1,433m), the nearest station to the study area (https://www.nrcs.usda.gov/wps/portal/nrcs/main/wa/snow/). Because our analyses treat the 5 years of study as a single phenomenon, we made no attempt to relate annual variation to annual weather fluctuations but examined anomalies and trends.

Statistical Analyses

We analyzed survival of adults (including the 2 yearlings) separately from calves. We estimated annual survival (January through December) of adult females (S_a) using the staggered-entry Kaplan-Meier approach (Pollock et al. 1989). We also estimated mortality rates for predation and health-related causes in a competing risks framework using the cumulative incidence function routine "*cuminc* V. 2.2-10" in R 3.0.0 (Fine and Gray 1999, Gray 2011), treating all animals as though they began exposure on the same day. Because wolf packs were present only in the northern area and hunter harvest of moose was concentrated in the southern area, we felt it inappropriate to consider predation and harvest as competing risks. We developed approximate standard errors of annual cause-specific mortality rates derived from their respective total cumulative rates using the delta method (Powell 2007).

Because field observations of calves were prone to false negatives from non-detection (Bergman et al. 2020), we estimated calf survival (S_0) using the Cormack-Jolly-Seber (CJS) mark-recapture method in program MARK and the R package RMark (White and Burnham 1999, Laake 2013). We coded results from monthly monitoring of each cow as either 1 (calf present) or 0 (apparent absence). Calves lost to monitoring after the death of their mother were treated as censored at that point. The resulting encounter history became the basis for CJS estimates. Because twinning was rare, we treated all calf fates as independent, and because calves were not radio-marked, we lacked information on cause of mortality. Because pregnancy, fecundity, and recruitment are typically quantified for females > 1 year of age, we censored the 2 yearlings when considering these metrics. We used AICc to evaluate candidate CJS models with differing combinations of study area (northern vs. southern) and observation month, as well as null models, in both the observation and survival components. Because moose calves do not successfully emigrate, we felt justified in equating the apparent survival estimates from CJS analyses as true survival.

We estimated rates of increase (λ) for each study area using the Euler-Lotka equation:

$$1 = \sum e^{-rx}\, l_x m_x \qquad (1)$$

by iteratively finding the solutions to e^r using the Goal Seek function within program Excel (Microsoft Corporation 2018). We viewed r as the population's "demographic vigor" (r_s, sensu Caughley 1977:107, Skalski et al. 2005:332), and used field estimates of fecundity (assuming gender parity at birth [i.e., $m = F/2$]; Boer 1992, Schwartz and Hundertmark 1993) and survival (using maximum age of 15 years; l_x = proportion surviving to the beginning of age x). We used the delta method and implicit differentiation approach of Eberhardt et al. (1994) to develop approximate variances of λ from the variances of their 3 respective constituent elements (i.e., m, S_0, S; see also Skalski et al. 2005:333), and calculated SE(λ) as $\sqrt{Var(\lambda)}$.

Using animals captured in early December, we tested for differences between the northern and southern areas in age distribution, pregnancy, predicted estimates of percent body fat, and thickness of longissimus muscle (hereafter "loin") thickness (see Cook et al. 2021). We tested for differences in age distribution using a 2-sample Kolmorogov-Smirnov test, and Fisher's exact test for differences in pregnancy and fecundity rates. We used general linear models (assuming normally distributed error terms) (glm in R Version 4.0.0) with area and "calf present" as binary covariates to test for differences in predicted estimates of percent body fat and loin thickness. At capture, we considered adult females to have calves if they were lactating (i.e., milk could be extracted from the udder) or observed with calf (Cook et al. 2021). We tested for differences in mid-winter calf:cow ratios and bulls as a proportion of adults as a function of time and WDFW district using sample-size weighted analyses of covariance with the logit link and a quasibinomial error structure (to account for overdispersion) in *glm* (R Version 4.0.0), and back-transformed coefficients for display.

RESULTS

Capture and Monitoring

We captured and radio-collared 26 adult female moose in 2013, 25 in 2014, and 27 in 2016 (11 were recaptures). We monitored adult survival through December 2018; no collars failed prematurely, and no movement occurred between areas. Thus, we report on annual survival rates from 67 adult females monitored over ~2,150 cumulative months ($\bar{x}$ = 32 months per animal). Mean ages at capture in the northern and southern areas were 7.1 ± 3.2 (SD; max =14) and 5.2 ± 2.9 years (max = 10), respectively; age distribution differed marginally from each other (Kolmogorov-Smirnov 2-sample test, $D = 0.462$, $P = 0.087$).

Pregnancy and Body Condition

A lower proportion ($P = 0.035$) of adult females was pregnant in the northern (30 of 43; 0.70, 95% CI: 0.54–0.83) than southern area (26 of 28; 0.93, 95% CI: 0.76–0.99); both samples included 4 pregnancies classified as late conception (Cook et al. 2021). Probability of pregnancy was not predicted by age (−0.0388, SE = 0.112, $P = 0.730$), or by the age × area interaction (−0.168, SE = 0.221, $P = 0.447$). The proportion of females with calf at capture was similar in both study areas (0.43 in the northern, 0.45 in the southern).

We found no evidence that predicted estimates of percent body fat differed between the northern and southern areas (area effect on body fat = 0.208, SE = 0.710, $t = 0.293$, $P = 0.771$; area × with-calf interaction on body fat = 0.233, SE = 1.136, $t = -0.205$, $P = 0.838$; Table 1). Accounting for calf status, loin muscle thickness was marginally lower among female moose in the northern than southern area (0.063, SE = 0.035, $t = -1.802$, $P = 0.078$), but this relationship was confounded by other patterns in the data. Northern females with calves at capture were generally older (loin thickness as predicted by "calves at capture × age interaction" = −0.126, SE = 0.047, $t = -2.678$, $P = 0.010$), and these older females with calves at capture were responsible for the apparent area effect (loin thickness on 3-way [area × with calf × age] interaction = 0.193, SE = 0.076, $t = 2.513$, $P = 0.015$).

Fecundity, Survival, and Rates of Increase

We documented 99 calves from 96 litters (i.e., 3 sets of twins) resulting in an estimated

Table 1. Mean, standard error (SE), and sample size (n) of predicted estimates of ingesta-free body fat, body mass,[a] and longissimus dorsi thickness across 3 lactation categories of moose (Lactating = milk was expressed from the udder; Calf-At-Heel = no evidence in udder of lactation but was seen with a calf before the capture approach; Non-Lactating = no evidence in udder of lactation and was not seen with a calf before the capture approach) in the 2 study areas during December 2013, 2014, 2016 in northeastern Washington, USA.

Nutritional condition indicator	Lactating			Calf-at-heel			Non-lactating		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
Northern study area									
Ingesta-free body fat (%)	7.0	0.9	3	7.3	0.9	9	8.2	0.5	22
Body mass (kg)	308.0	39.8	2	335.2	17.5	7	349.2	9.5	20
Longissimus dorsi thickness (cm)	4.3	0.1	3	4.6	0.1	9	4.9	0.1	21
Southern study area									
Ingesta-free body fat (%)	5.8	1.0	3	6.9	0.5	8	8.4	0.4	16
Body mass (kg)	338.1	na	1	396.2	49.3	4	355.8	12.5	10
Longissimus dorsi thickness (cm)	4.7	0.3	3	4.8	0.1	8	4.7	0.1	16

[a], Body mass estimated from measurement of chest girth circumference; see Cook et al. 2021.

study-area wide fecundity rate of 0.60. Fecundity in the northern area (0.52, 95% CI: 0.41–0.63; 46 calves in 88 moose summers) was lower (*P* = 0.026) than in the southern (0.70, 95% CI: 0.58–0.80; 53 calves in 76 moose summers).

Annual adult female survival rate was 0.80 (95% CI: 0.75–0.85) over the 5-year period and rates were similar (Fig. 2) in the northern (0.82, 95% CI: 0.75–0.88) and southern areas (0.79, 95% CI: 0.71–0.88); small sample sizes precluded meaningful comparison among year-specific rates. There was no evidence that the cumulative incidence functions for predation (annual cause-specific risk = 0.067, SE = 0.068) differed from that for health-related causes (annual risk = 0.063, SE = 0.069). That said, seasonality and cause of death appeared to differ between the northern and southern areas (Fig. 3). Proximate causes for adult mortality (n = 21) in the northern area were wolf predation (6), winter ticks (6), and unidentified health issues (4); n = 1–2 for mountain lion predation, accidental, and hunter harvest. Conversely, hunter harvest was by far the most common (73%) cause of death in the southern area (11 of 15); n = 1–2 for accidental, unidentified health, and unknown. Most adult mortality occurred in spring and early summer in the northern area, whereas in the southern study area most occurred in autumn coinciding with the hunting season. Winter tick mortalities occurred in late March-April as expected, whereas deaths due to other health issues occurred in October–January. Predation occurred exclusively during spring and summer with none documented in November–February (Fig. 3).

The top-ranked CJS calf-survival model was the base model with no area or month effect on survival (Table 2). Area and month were included as factors affecting detection, and annual calf survival was estimated as 0.36 (SE = 0.05). A model including area as a (statistically insignificant) factor affecting survival had less support (model weight 0.24); estimates of calf survival were 0.28 (SE = 0.06) in the northern area and 0.41 (SE = 0.04) in the southern area.

Moose in both areas were in decline. The area-specific estimated asymptotic rate

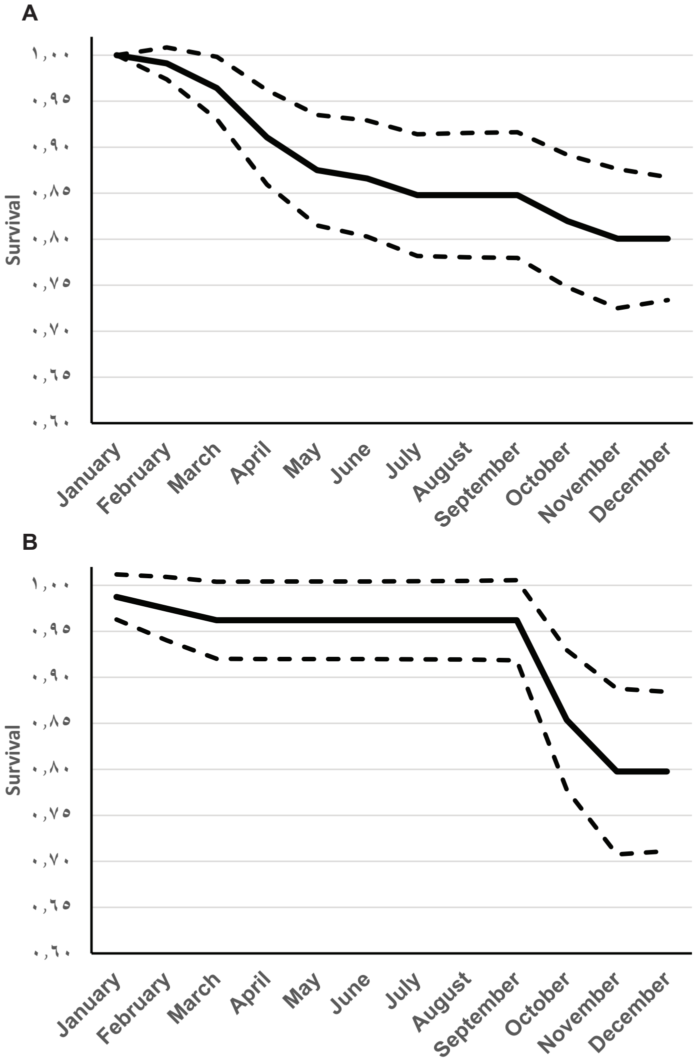

Fig. 2. Monthly Kaplan-Meier survival, adult female moose in 2 adjacent study areas in northeastern Washington, 2014–2018. Top panel (A): Northern. Bottom panel (B): Southern.

of growth (i.e., λ) was similar in both areas: 0.87 (SE = 0.03) in the northern area and 0.90 (SE = 0.03) in the southern area.

Supplementary Recruitment Information

Calf:cow ratios declined overall during the time period (logit scale $\beta = -0.073$, SE = 0.019, $t = -3.84$, $P < 0.001$), but neither the WDFW district offset (district factor = 0.102, SE = 0.265, $t = 0.385$, $P = 0.703$), nor a time x district interaction (0.030, SE = 0.030, $t = 1.009$, $P = 0.324$) were significant (Fig. 4A). A quadratic model, in which calf:cow ratios trended more downward with time, had similar AIC support. In 2003–2015, the mean proportion of adults classified as bulls in District 1 ($\bar{x} = 0.44$) was higher than that in District 2 ($\bar{x} = 0.33$, district offset = −0.362, SE = 0.154, $t = -2.361$,

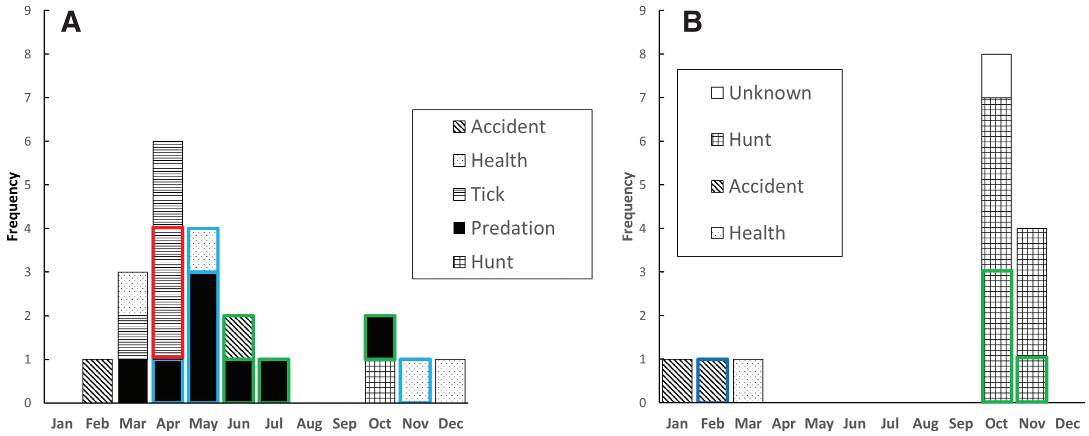

Fig. 3. Proximate causes of death among radio-marked adult (age ≥ 1) female moose in northeastern Washington, 2014–2018, by month. Colored boxes surrounding histogram bars indicate moose for which percent femur marrow fat was estimated (Cook et al. 2021): red < 12% (starvation), blue ≥ 12% and ≤ 80% (nutritional stress), green > 80% (> 5% body fat). Six predation moralities were attributed to wolves, the remaining 2 to mountain lions. Left panel: Northern study area. Right panel: Southern study area.

Table 2. Top five ranked models for Cormack-Jolly-Seber estimates of apparent survival of moose calves in 2 study areas in northeastern Washington, 2014–2018. Shown are predictors in both the apparent survival and detection portions of the model, ΛAIC_c, model weight, and number of parameters (k). Area refers to study areas (north or south).

Apparent survival	Detection	ΛAIC_c	Model weight	k
Null (.)	Month[a]+Area[b]	0.000	0.415	13
Area	Month+Area	1.123	0.237	14
Area	Month	2.155	0.141	13
Month+Area	Month	2.627	0.112	23
Month+Area	Month+Area	2.952	0.095	24

[a], Probability of detection generally increased from June through January before declining in February and staying low through spring.

[b], Probability of detection was about 37% higher in the southern study area than the northern study area.

$P = 0.028$), but did not change significantly during the time period (year = −0.015, SE = 0.022, $t = 0.669$, $P = 0.510$; Fig. 4B).

Presence of Potential Predators

WDFW confirmed and radio-tracked 2 wolf packs within the northern area (Table 3); no packs were detected in the southern area. The wolf index calculated from remote cameras was 0.24/100 trap nights in the northern area; no images were collected in the southern area. Wolves increased in the survey area during monitoring (northeastern Washington; Table 3). The remote camera index for mountain lions was 0.70 in the northern area and 0.41 in the southern, and for black bears was 1.22 and 0.31, respectively.

Harvest History

WDFW records indicate that 86 female moose were legally harvested in GMU 117 (in which the northern study area was

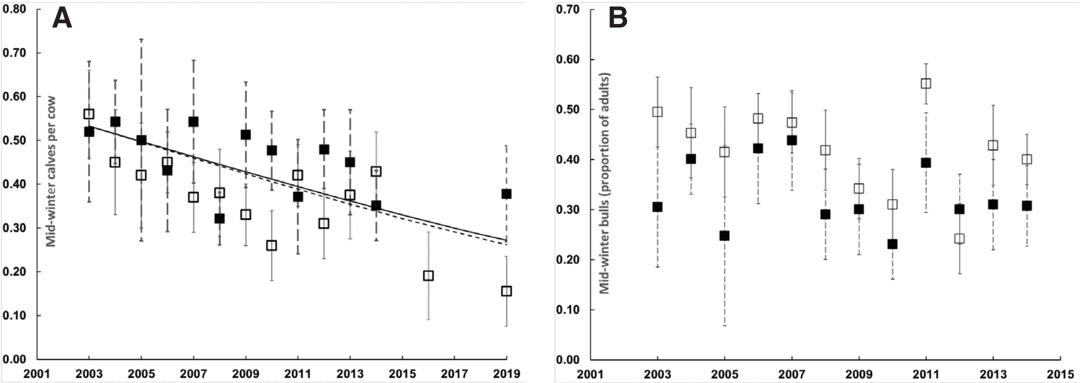

Fig. 4. Left panel (A): Calves per cow (calf:cow ratios) obtained from helicopter-based aerial surveys in January and February, in WDFW District 1 (open symbols, solid 90% confidence intervals) and District 2 (solid symbols, heavy dashed 90% confidence intervals), 2003–2019 for surveys observing n ≥ 25 cows. For both Districts, counts of cows and calves during 2003–2012 were from trend counts (see Harris et al. 2015), during 2015–2017 were from transects conducted for hierarchical distance sampling-based density estimates (see Oyster et al. 2018), and for 2019 from recruitment index surveys. Also shown are back-transformed binomial regression lines (see text) for District 1 (dashed line) and District 2 (solid line) for reference, although separate trend lines were not statistically supported. Right panel (B): Bulls as proportion of all adults. Data and symbols same as above, except that the 2019 survey was not considered useful for counting bulls, and no regression line is shown because slope was non-significant.

Table 3. Estimated number of wolves in the 2 packs with territories overlapping the northern study area as of December of each year. Right-hand column displays minimum number of wolves estimated each year in the (larger) survey area. Adapted from Wiles et al. (2011), Frame and Allen (2012), and WDFW et al. (2013, 2014, 2015, 2016, 2017, 2018, 2019).

Year	Northern study area			Northeastern WA survey area
	Carpenter Ridge pack	Dirty Shirt pack	Sub-total	
2009	-	-	-	8
2010	-	-	-	12
2011	-	-	-	18
2012	-	-	-	43
2013	2	2	4	38
2014	2	3	5	55
2015	2	8	10	76
2016	6	13	19	93
2017	13	7	20	99
2018	11	5	16	90

primarily nested) during 2005–2017, and an additional 21 in GMU 113 (east of the Pend Oreille River) where 2 of the 41 northern area moose were captured and maintained home ranges (Fig. 5). In contrast, 270 female moose were legally harvested during the same time frame in what WDFW termed "moose areas 1 and 2" which closely aligned with the southern area, and which together, were slightly smaller in area than GMU 117. The higher harvest in the southern GMU reflected our marked animal data; 11 of 12 harvested animals were in the southern area.

Carotid Worm Observations

A total of 125 heads were submitted (22 in 2014, 44 in 2015, 33 in 2016, and 26 in 2017) for detecting *E. schneideri*. After excluding specimens that provided < 7.5 cm of the carotid artery (to ensure we examined the terminal portion), we examined 80

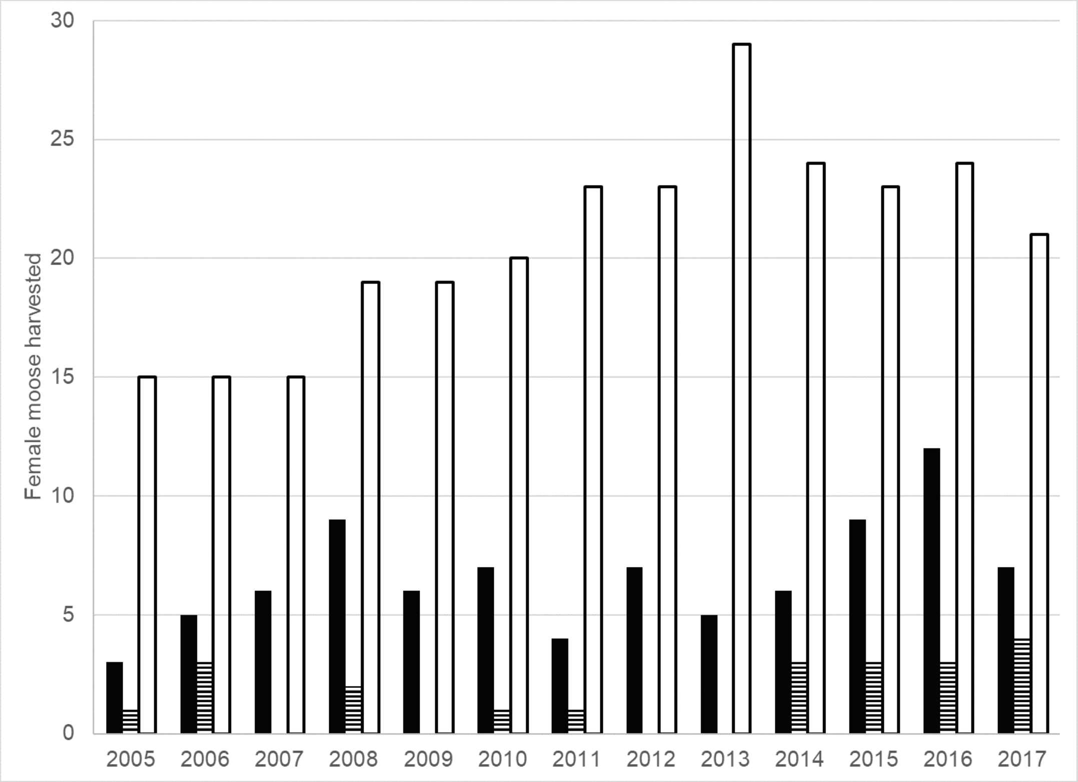

Fig. 5. Number of female moose legally harvested in the game management units (GMU) in and surrounding the study area, 2005–2017. Solid bars: GMU 117 where the majority of the northern study area resides; hatched bars, GMU 113 where 2 moose in the northern study area lived; open bars: GMU 124 which encompasses the entire southern study area.

samples combined (49 female, 31 male) from District 1 (n = 37) and District 2 (n = 43). We documented presumed *E. schneideri* nematodes in 3 samples (4% prevalence, 95% CI: 1–11%); 2 from District 1 and 1 in District 2, range = 3–8 worms per sample). Two of these 3 samples were among 37 examined at WADDL, both of which were consistent with subclinical infections (LeVan et al. 2013). We also observed 1 collared moose with cropped ears that can be characteristic of Elaeophorosis (Henningsen et al. 2012).

Weather

Mean annual temperature during 2014–2018 was slightly warmer than during 2000–2013 (the period during which Harris et al. 2015 concluded that moose were increasing): 8.21°C (SE = 0.37) during the study period compared with 7.30°C (SE = 0.18) during the earlier period. Mean annual temperature during 4 of the 5 study years exceeded the previous mean. However, the increasing temperatures were not so much anomalous as consistent with the long-term trend of warming (Fig. A1). Spring-summer precipitation during the study period (0.37 cm/month, SE = 0.03) appeared to be lower than the previous long-term mean (0.49 cm/month, SE = 0.05); all 5 years were lower than the long-term mean (although individual seasons during the earlier period had been as dry or drier). Unlike the long-term warming trend, there was no evidence of a long-term trend in spring-summer precipitation near the study area (Fig. A2). Mean cumulative snowfall (sum of all monthly cumulative totals) at the Quartz Pk. SNOTEL station was 500 cm (SE = 87.0) during 2014–2018, compared with 647 cm (SE = 80.0) during 2004–2013. Although quite variable, spring snow depth evidently declined throughout the 2004–2019 period, particularly in late May (Fig. A3).

DISCUSSION

We initiated our telemetry study in 2013 when we suspected that the long-term increase we'd observed among northeastern Washington moose was likely to cease, particularly with recent colonization by wolves. Our study area and design used 2 adjacent areas for comparison; a northern area with established wolf packs and a southern area which we presumed would remain wolf-free during the study, thus allowing inference about the potential effects of wolf predation. Our design worked as intended because no marked moose moved between the areas, and wolves continued to increase in the northern area and remained essentially absent in the southern. We recognized from the outset that inference from such a simple design would not be straight-forward because we lacked area replicates and were unable to measure (much less control for) other potentially important differences between the areas.

With those limitations in mind, we interpret the lower growth rates in the northern area as suggestive of a top-down effect, albeit an effect that was likely mediated by bottom-up effects (Cook et al. 2021). We identified predation as the proximate cause of 8 of 21 (38%) adult mortalities in the northern area and zero in the southern area. However, predation effects may have been stronger on calves. Although our best-fitting model of calf survival did not include an area effect, a model estimating higher calf survival in the south where predators were rarer than in the predator-rich northern area had modest support (Table 2).

Although we lack information on proximate cause of death for calves, we suspect that wolf predation accounted for some portion of what may have been lower calf-survival in the northern area. The relatively constant temporal pattern of calf mortality appears inconsistent with the hypothesis that black bears were important calf predators because their effects are typically restricted to ~2 months post-parturition (Patterson et al. 2013), if not less (Jones et al. 2017). Although mountain lions may have contributed to calf mortality, a major role seems unlikely as we documented only 2 associated adult mortalities despite lions in both areas. Where mountain lions overlap in geographic distribution with moose and predation has been noted, it has typically been idiosyncratic, opportunistic, and relatively rare (Kunkel et al. 1999, Bartnick et al. 2013); but see Ross and Jalkotzy (1996) for an example of male lions evidently specializing on moose calves. We also know from studies focused on cattle depredation in the general area that wolves killed adult and calf moose (Spence 2017; T. Roussin, WDFW, pers. comm. 2017). Although not statistically significant, the difference in calf survival between the 2 areas in the 2nd ranking model (ΛAIC$_{c =}$ 1.123) was similar to that documented in Norway (Sivertsen et al. 2012).

We also interpret our data as supporting the presence of considerable bottom-up effects (Cook et al. 2021). Notably, and contrary to our expectation had predators reduced moose density substantially, both pregnancy at capture and fecundity documented from subsequent field observations were lower in the northern area than in the south with fewer predators. Fecundity in the northern study area was estimated at only 0.52, and although early calf loss from predation or other factors may have contributed to this low number, the low pregnancy rate (0.70) is associated with populations above carrying capacity (Gasaway et al. 1992, Schwartz 1998) suggesting that contributing factors were manifested prior to parturition.

Although there were no statistical differences in our measures of body condition between the 2 areas, Cook et al. (2021) found that ~80% of sampled moose entered winter with body fat levels indicative of moderate to severe nutritional limitations. Depressed pregnancy rate, evidence of delayed conception, low fecundity, that body condition in December was related to survival and marrow fat indicative of severe nutritional stress in 56% of 18 femurs collected suggest that bottom-up (Cook et al. 2021) and top-down factors were not mutually independent. Our estimated adult survival rate – even where predators were rare and/or ineffective – lies toward the lower end of the range consistent with a stable moose population (Van Ballenberghe and Ballard 1998).

We can confidently dismiss a paucity of bulls as an explanation for lower pregnancy rate in the northern area because the ratio of bulls as a proportion of adults was higher than in the southern area (Fig. 4B), and much higher than thresholds suggested for incomplete fertilization of otherwise reproductively capable females (Bishop and Rausch 1974, Laurian et al. 2000). In the southern area where we believe predation of neonates was rare, fecundity (0.70) was measurably lower than pregnancy (0.93), suggesting that calf loss was early and undetected. On a broader geographic scale, we found no difference between the northern and southern districts in a long-term series of mid-winter calf:cow ratios, an index that integrates fecundity with early calf loss. We documented a significant decline over time in this recruitment index (Fig. 4A), but the decline occurred in both districts and began a few years before wolves recolonized (Table 3).

Adding to the complexity, we attributed 6 of 21 (29%) adult moose mortalities to winter tick parasitism in the northern area, a frequency equal to wolf predation and suggesting that ticks were also influential. Persistent tick infestations in New England resulted in substantial annual mortality of calves in March-April, lower growth and delayed maturation of yearlings, lower productivity in adults, and negative population growth (Musante et al. 2010, Jones et al. 2019, Ellingwood et al. 2020, Pekins 2020). Despite our lack of data on proximate causes of calf mortality, we suspect that ticks also took a toll on calves in northeastern Washington. Our data did not clearly indicate the dramatic surge in calf deaths during March and April that was found in heavily-infested New England moose, although we had little power to detect seasonal patterns. Previous studies have suggested that locally high moose density may facilitate increases in tick abundance, inducing a density-dependent host-parasite relationship (Samuel 2007, Severud and DelGuidice 2016) and modelling with empirical data indicates that it can be perpetuated by a self-sustaining, habitat use-infestation relationship (Healy et al. 2018, 2020). We concur with DelGiudice et al. (1997) that interactions between nutritional state and tick infestations are complex; evidence suggests that tick infestation can cause poor body condition (Glines and Samuel 1989, Musante et al. 2007, Ellingwood et al. 2019) or, alternatively, result from it (DelGiudice 1997:900). Unfortunately, we lacked data to tease apart cause and effect. We also confirmed Elaeophorosis in a small number of moose but have no evidence of impact on either an individual or population level.

At a broad scale, Monteith et al. (2015) found that moose recruitment was negatively affected by warm temperatures during the previous year, and by dry spring-summers, both of which they hypothesized as being mediated through effects on maternal condition. With only a single study over only 5 years, our study can at best be seen as anecdotal support for their conclusions. We note, however, that the patterns we observed were consistent with those observed by Monteith et al. (2015) and suggest that climate may have acted indirectly on several proximate causes of the reversal in moose population trend we observed, although the mechanistic pathway remains unclear.

Because we censored orphaned calves when their mother died (having no way to monitor their fates), all calf survival rates were likely biased high because orphans probably faced greater risks than calves with maternal care. Estimating this bias is problematic because the proportion of orphaned calves that died prematurely is unknown, and because of uncertainty of whether calves were alive when the mother died (due to imperfect detection of calves); in some cases, 3–4 months separated the last documentation of a calf and its mother's death. The probability of a calf dying undetected before its mother died was accounted for in the mark-recapture approach to calf survival. In total, 13 cows (with 14 calves, 7 in each study area) died when calves may have been present, and in half these cases of possible orphaning, calves were ≤ 4 months old with low probability of surviving their first year.

Improved understanding of the differences between the areas, as well as the perceived bottom-up effects occurring generally within the study area (Cook et al. 2021), would benefit from estimates of moose density at these geographic scales. Unfortunately, the density estimate produced by Oyster et al. (2018) was not designed for down-scaling to a smaller area. We considered estimating density using the marked animals and applying either the zero-truncated Poisson log-normal or immigration-emigration log-normal mark re-sight estimators (McClintock and White 2009, McClintock et al. 2009a, 2009b), but concluded that low precision would render the effort a poor expenditure of resources. Observations made from vehicles (but without the aid of telemetry) while documenting calf survival during 2014–2016 yielded 88 incidental observations of moose, but only 2 were of collared animals. To investigate if additional aerial surveys could improve expected precision, we used the simulation function in program MARK to generate likely scenarios, using the number of marks available in early 2017 ($n = 48$) and an estimated re-sight probability of 25% as calculated from observations of marked animals during mark-recapture distance sampling transect surveys (Oyster et al. 2018). These simulations indicated that developing estimates with acceptable precision (defined as 95% CI width/$\widehat{N} < 1.0$) would require more replicate aerial surveys than funding allowed.

Our data and related analyses by Cook et al. (2021) indicate that during the study (2014–2018) most moose in northeastern Washington entered winter with low energy reserves indicating moderate to severe nutritional limitations operating during summer-autumn, which heightened susceptibility to predation (see also Joly et al. 2017), parasitism, and other morbidity and mortality factors. Unfortunately, we had limited ability to tease apart the relative influence of each. Our data on pregnancy and fecundity rates, body condition (Cook et al. 2021), and population density (Oyster et al. 2018) during the reversal of the earlier population increase suggests that a very abundant population had reached or exceeded the long-term capacity of the forage base; however, we lack specific and accurate information on moose density and forage assessment.

Although we speculate that the ecological carrying capacity of moose populations in northeastern Washington has been reduced by the permanent return of wolves, we lack data to quantify this reduction. The loss of adult female moose to wolf predation was equal to that associated with winter tick parasitism, neither were alarmingly high, and declines occurred in the southern area despite fewer predators and no wolves; albeit harvest was much higher. Clearly the high abundance of moose observed in the early 2010s was temporary and the subsequent population decline, in part, is presumed a function of density dependent mechanisms. Reducing predator density in this system might generate local, short-term increases in moose numbers, but previous peak abundance levels would be unsustainable if density dependent factors have been the principal population influences. We encourage managers to view the top-down and bottom-up forces in this system as linked and encourage further study of density dependent influences including forage nutrition and parasitism.

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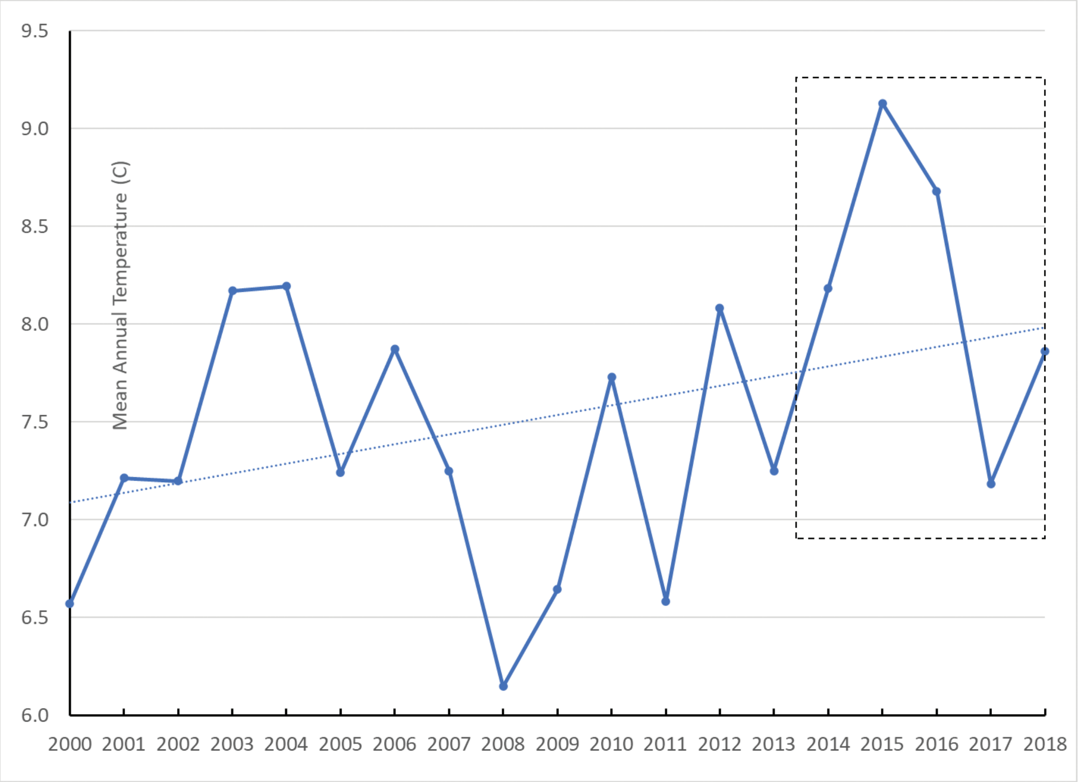

Fig. A1. Mean annual temperature (mean of each monthly mean) at Deer Park airport weather station, 2000–2018. Box shows years of this study. Dotted line shows least squares linear trend during the entire period.

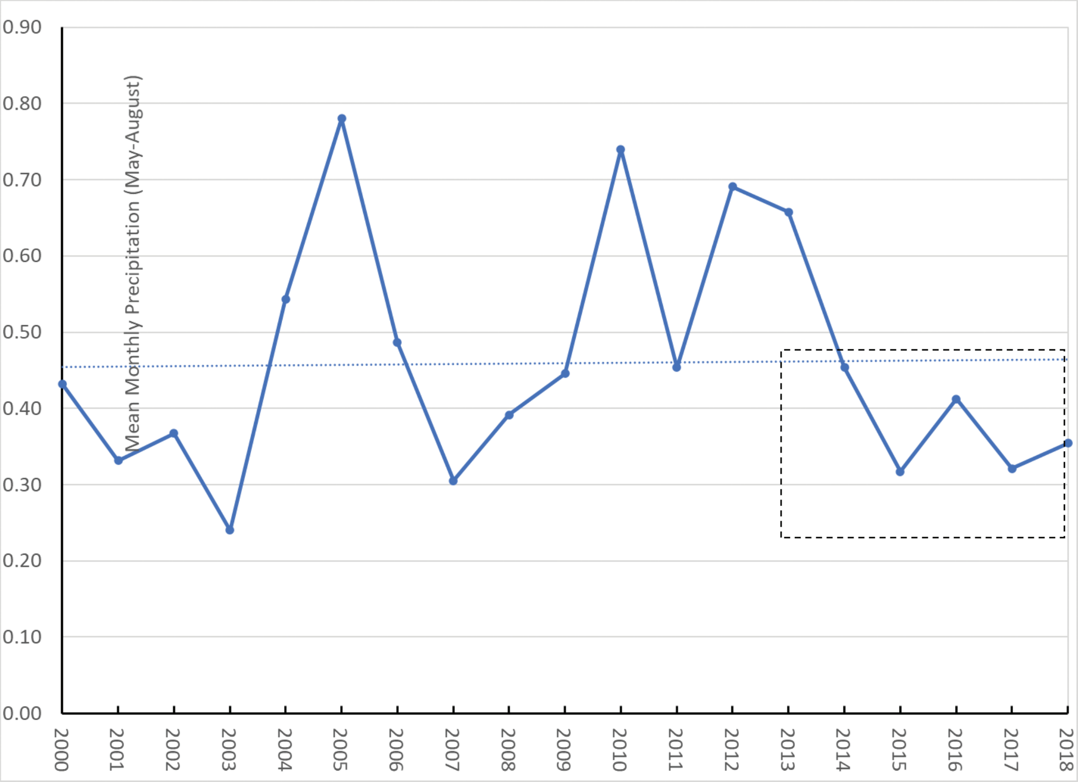

Fig. A2. Mean monthly precipitation (cm) during May-August 2000–2018 at the Deer Park airport weather station. Box indicates years of this study. Dotted line shows least squares linear trend during the entire period.

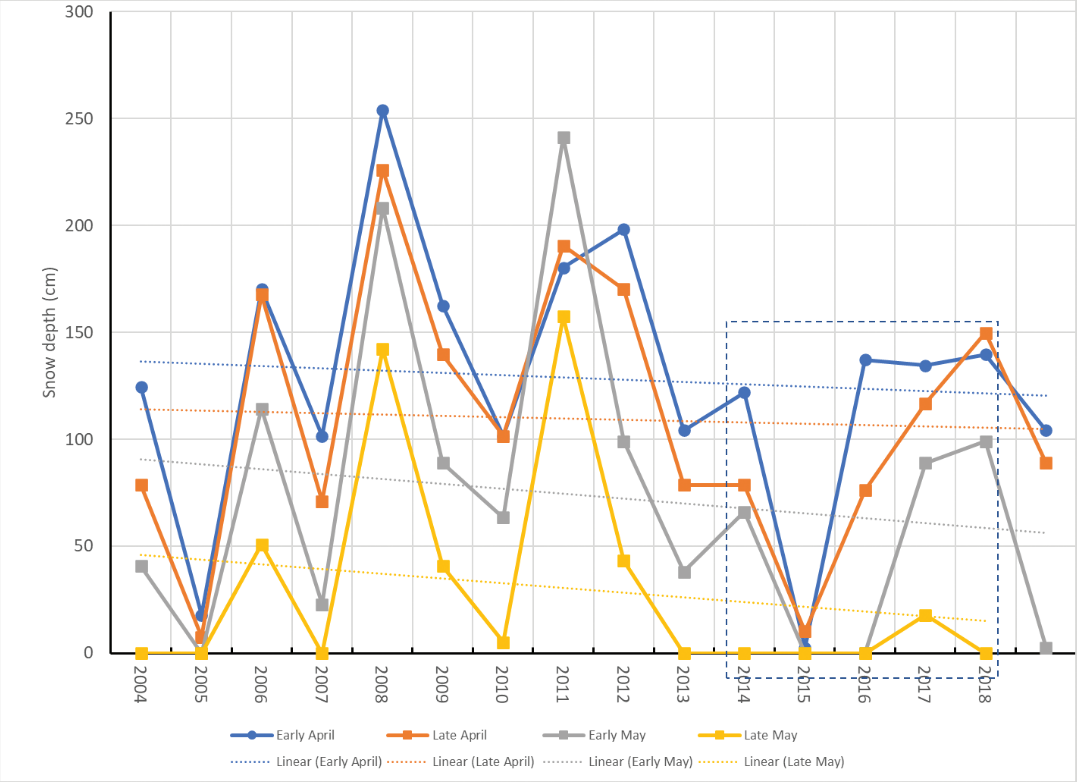

Fig. A3. Spring snow depths at the Quartz Peak SNOTEL station, 2004–2018. Dotted lines illustrate linear trends for early April (blue), late April (orange), early May (gray), and late May (yellow). Box shows period of this study.