STATUS AND TRENDS OF MOOSE POPULATIONS AND HUNTING OPPORTUNITY IN THE WESTERN UNITED STATES

M. Steven Nadeau[1], Nicholas J. DeCesare[2], Douglas G. Brimeyer[3], Eric J. Bergman[4], Richard B. Harris[5], Kent R. Hersey[6], Kari K. Huebner[7], Patrick E. Matthews[8], and Timothy P. Thomas[9]

[1]Idaho Department of Fish and Game, 600 S. Walnut, Boise, Idaho 83709, USA; [2]Montana Fish, Wildlife and Parks, 3201 Spurgin Road, Missoula, Montana 59804, USA; [3]Wyoming Game and Fish Department, Box 67, Jackson, Wyoming 83001, USA; [4]Colorado Parks and Wildlife, 317 W. Prospect Avenue, Fort Collins, Colorado 80526, USA; [5]Washington Department of Fish and Wildlife, 600 Capital Way North, Olympia, Washington 98504, USA; [6]Utah Division of Wildlife Resources, Box 146301, Salt Lake City, Utah 84114, USA; [7]Nevada Department of Wildlife, 60 Youth Center Road, Elko, Nevada, 89801; [8]Oregon Department of Fish and Wildlife, 65495 Alder Slope Road, Enterprise, Oregon 97828, USA; [9]Wyoming Game and Fish Department, Box 6249, Sheridan, Wyoming 82801, USA.

ABSTRACT: We review the state of knowledge of moose (*Alces alces shirasi*) in the western US with respect to the species' range, population monitoring and management, vegetative associations, licensed hunting opportunity and hunter harvest success, and hypothesized limiting factors. Most moose monitoring programs in this region rely on a mixture of aerial surveys of various formats and hunter harvest statistics. However, given the many challenges of funding and collecting rigorous aerial survey data for small and widespread moose populations, biologists in many western states are currently exploring other potential avenues for future population monitoring. In 2015, a total of 2,263 hunting permits were offered among 6 states, with 1,811 moose harvested and an average success rate per permit-holder of 80%. The spatial distribution of permits across the region shows an uneven gradient of hunting opportunity, with some local concentrations of opportunity appearing consistent across state boundaries. On average, hunting opportunity has decreased across 56% of the western US, remained stable across 17%, and increased across 27% during 2005–2015. Generally, declines in hunting opportunity for moose are evident across large portions (62–89%) of the "stronghold" states where moose have been hunted for the longest period of time (e.g., Idaho, Montana, Utah, and Wyoming). In contrast, increases in opportunity appear more common at peripheries of the range where populations have expanded, including most of Colorado, northeastern Washington, southern Idaho, and eastern Montana. There are many factors of potential importance to moose in this region, including parasites, predators, climate, forage quality, forage quantity, and humans. State wildlife agencies are currently conducting a variety of research focused on population vital rates, the development of monitoring techniques, forage quality, trace mineral levels, and evaluation of relative impacts among potential limiting factors.

ALCES VOL. 53: 99–112 (2017)

Key Words: *Alces alces shirasi*, Colorado, hunter harvest, Idaho, Montana, Nevada, Oregon, population trends, range, Shiras moose, Utah, Washington, Wyoming

The occupied range of moose (*Alces alces*) extends southward into the western United States along the Rocky Mountains and the Western Cordillera ecoregion (CEC 1997; Fig. 1). Here, we review the state of knowledge of moose in the western US with respect to range, population monitoring and management, vegetative associations, licensed hunting opportunity and hunter harvest success, and hypothesized limiting factors.

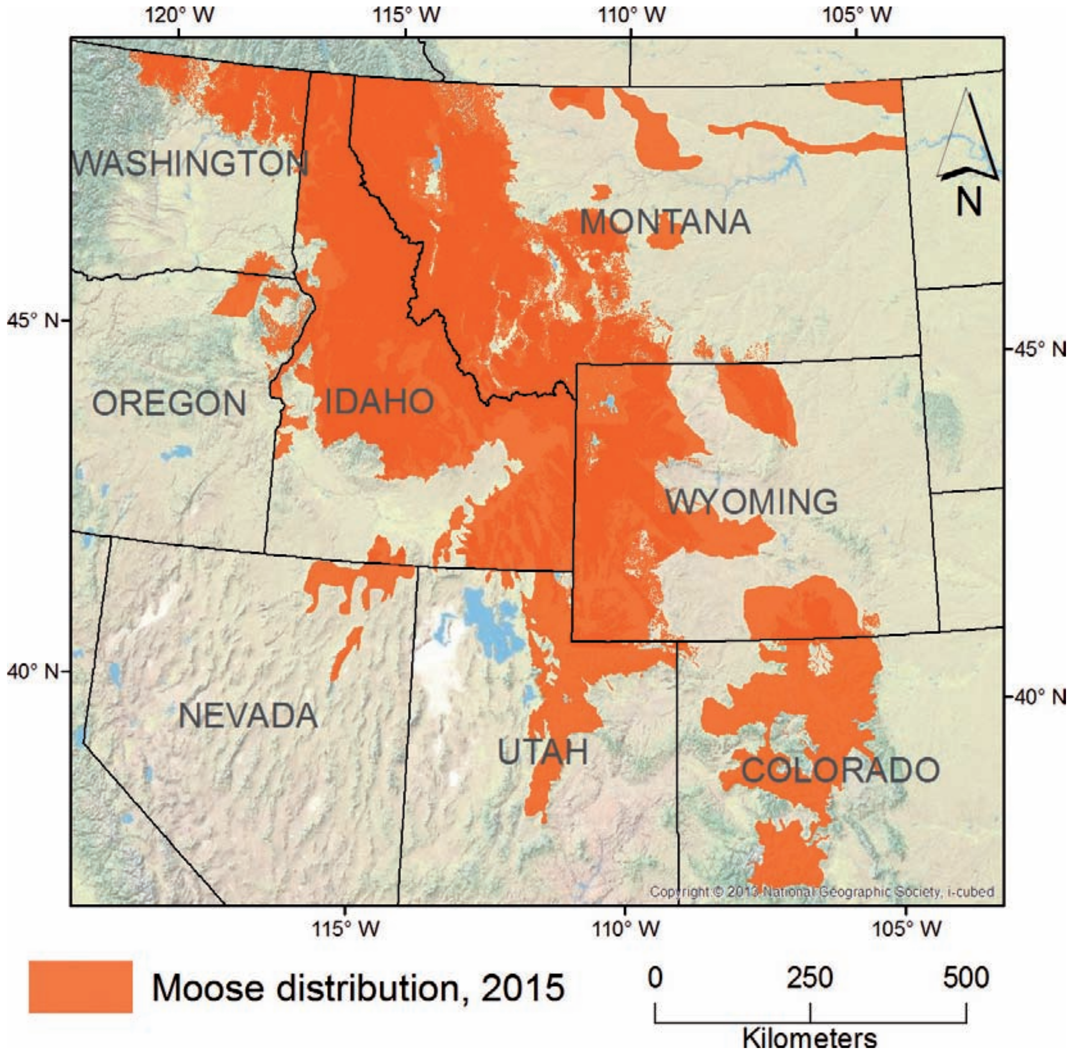

Fig. 1. Predicted range of moose in western USA *circa* 2015, based on compilation of state distribution data characterizing known occupancy by resident moose and predicted occupancy through species distribution modeling of Beauvais et al. (2013).

In particular, we use hunter opportunity and harvest data to address spatio-temporal trends in regional moose populations. We focus specifically on trends in hunting opportunity over the past decade (2005–2015) because they facilitate a simple assessment of local trends with comparable data across the 8-state region.

RANGE AND HABITAT

Moose in the Rocky Mountains of the USA and southern Canada were described as a distinct subspecies during the early part of the 20th century (*A. a. shirasi*; Nelson 1914, Peterson 1952), though historical accounts suggest they were rare throughout the US Rocky Mountains until the mid-1800s (Karns 2007). After periods of population expansion and subsequent declines due to overharvest during the late 1800s, it is largely believed that moose populations increased to new highs during the early to mid-1900s within portions of Idaho, Montana, Utah, and Wyoming (Brimeyer and Thomas 2004, Toweill and Vecellio 2004, Wolfe et al. 2010, DeCesare et al. 2014). During the latter half of the 20th century, moose also naturally colonized eastern portions of Washington and Oregon, and translocations were used to introduce moose to Colorado and unoccupied portions of Wyoming and Idaho, as well as to augment populations in Utah (Kufeld 1994, Olterman et al. 1994, Base et al. 2006, Wolfe et al. 2010, Matthews 2012). Sightings of moose occurred in Nevada as early as the late 1980s, but have increased in recent years, including multiple verified sightings of cows with calves in 2016. While numbers in outlying states such as Colorado and Washington appear to be stable or increasing, declines have been noted recently in previous stronghold portions of Idaho, Montana, Utah, and Wyoming (Harris et al. 2015, Monteith et al. 2015, DeCesare et al. 2016).

This geographic area is primarily occupied by the Shiras subspecies of moose (*A. a. shirasi*) which exists throughout the Rocky Mountains from Colorado and Utah northward to southern Alberta and British Columbia. Recent range expansion of moose into eastern Montana has come with some uncertainty regarding subspecies identity. It is unclear whether animals east of the Rocky Mountain chain in the eastern portions of Montana, with neighboring moose populations in Saskatchewan and North Dakota, would be better described as *A. a. shirasi* or as belonging to the northwestern subspecies *A. a. andersoni*.

Habitats occupied by moose vary throughout the western US with respect to gradients in abiotic conditions (e.g., elevation, temperature, and precipitation), vegetative associations, and large mammal predator-prey communities. We summarized moose management units across each state within which licensed moose hunting is offered, in terms of mean values of elevation, annual precipitation (cm), and minimum January and maximum July temperatures (°C) in a GIS using a digital elevation model and 30-year climate averages during 1981–2010 (PRISM Climate Group 2016). Though moose management units in Colorado and Utah contain the southern-most introduced and naturally occurring moose populations in the world, the relatively high elevations of occupied habitats in these regions result in climates similar to neighboring states further north (Table 1). Average elevation ranged from 911 m in Washington to 2712 m in Colorado, average annual precipitation ranged from 62–84 cm annually, and minimum January and maximum July temperatures averaged −14 to −6 °C and 24 to 27 °C, respectively, among states during 1981–2010 (Table 1).

Table 1. Descriptive statistics characterizing means per moose management unit in elevation, precipitation, minimum January temperature, maximum July temperature, summarized across units within each western state where licensed moose harvest is allowed, 1981–2010.

	Elevation (m)		Precipitation (cm)		Minimum January Temperature (°C)		Maximum July Temperature (°C)	
State	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Colorado	2712	(2075–3304)	63	(35–111)	−13	(−16 to −9)	24	(20–30)
Idaho	1656	(804–2353)	84	(24–150)	−9	(−14 to −4)	26	(23–31)
Montana	1849	(814–3071)	71	(32–119)	−11	(−15 to −6)	24	(18–29)
Utah	2226	(1896–2715)	64	(48–83)	−11	(−14 to −8)	26	(23–28)
Washington	911	(723–1169)	66	(46–101)	−6	(−8 to −5)	27	(24–28)
Wyoming	2387	(1945–2999)	62	(20–123)	−14	(−18 to −11)	24	(19–29)

Studies of vegetation associations inhabited by moose in the western US include a preponderance of evidence for selection of willow (*Salix* spp.) communities and plants for space use and food habits, particularly during winter (McMillan 1953, Knowlton 1960, Dorn 1970, Wilson 1971, Pierce and Peek 1984, Van Dyke et al. 1995, Kufeld and Bowden 1996, Dungan and Wright 2005, Baigas et al. 2010, Vartanian 2011, Burkholder et al. 2017). The importance of willow has been documented primarily in relatively colder and drier portions of the range (e.g., in portions of Colorado, Utah, Wyoming, southeast Idaho, and southwest Montana), though exceptions to the importance of willow exist in local populations in these areas. For example, in certain portions of western Colorado and Utah, moose have also colonized upland shrub communities including oakbrush (*Quercus* spp.), serviceberry (*Amelanchier* spp.), and mountain mahogany (*Cercocarpus* spp). In portions of southwest Montana moose occupy forested stands of aspen (*Populus* spp.) and Douglas-fir (*Pseudotsuga menziesii*) and feed on a range of other shrubs and saplings, including but not limited to serviceberry, huckleberry (*Vaccinium* spp.), red-osier dogwood (*Cornus sericea*), and subalpine fir (*Abies lasiocarpa*) (Stevens 1970). In southeast Idaho moose forage primarily on bitterbrush (*Purshia tridentata*), willow, serviceberry, chokecherry (*Prunus virginiana*), and aspen (*Populus tremuloides*) (Ritchie 1978).

West of the continental divide where occupied portions of the range include more maritime-influenced climates, moose associate with various forest communities where willow-dominated lowlands are less prevalent. In wetter climates such as in northwest Montana, moose show strong associations with conifer forests, including but not limited to regenerating vegetation following timber harvest (Matchett 1985, Langley 1993). Forage species in these areas have included red-osier dogwood, serviceberry, and menziesia (*Menziesia ferruginea*) (Matchett 1985). In north-central Idaho moose select conifer forest including old growth and mature mixed-age stands of grand fir (*Abies grandis*) and subalpine fir (Pierce and Peek 1984) where they forage primarily on Pacific yew (*Taxus brevifolia*), Sitka alder (*Alnus viridis*), and menziesia (Pierce 1984). Moose in Washington occupy habitats typically characterized by dense conifer forest, including mixed stands of western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) and consume diets of willow, *Ceanothus* spp., and other shrubs and forbs during summer, and conifers such as cedar and hemlock during winter (J. Goerz, University of Montana, pers. comm.).

POPULATION MONITORING

Moose are widespread across broad regions of the western USA but densities are low relative to populations further north in Canada, Alaska, and the northeastern USA. Recent population estimates (2014) in our study area jurisdictions were 2,400 in Colorado, 10,000 in Idaho, 4,000 in Montana, 20 in Nevada, 70 in Oregon, 2,625 in Utah, 3,200 in Washington, and 4,650 in Wyoming (Timmermann and Rodgers 2017; Nevada estimate unpublished). These abundance estimates are not necessarily comparable as they were each derived with different methods and generally, with uncertainty. Resources to monitor moose are relatively sparse when compared with those devoted to more abundant elk (*Cervus canadensis*), deer (*Odocoileus* spp.), and pronghorn (*Antilocapra americana*) populations. Thus, population monitoring of moose in many areas is met with challenges of limited data and low statistical power (Harris et al. 2015, DeCesare et al. 2016).

To date, most monitoring programs rely primarily on a mixture of aerial surveys of various formats and hunter harvest statistics.

Colorado Parks and Wildlife biologists use spreadsheet population models that are based on estimates of survival and recruitment largely obtained opportunistically during surveys for other species (White and Lubow 2002). In Idaho biologists have similarly collected survey data incidental to elk surveys for several decades, but have not developed a statewide trend index or population estimation technique. Montana Fish, Wildlife and Parks biologists conduct minimum count aerial surveys in a subset of moose hunting units, and rely primarily on hunter harvest statistics elsewhere for assessment of trends (DeCesare et al. 2016). Moose have more recently colonized portions of Oregon and Nevada where state agency biologists primarily monitor them via public sighting reports and opportunistic ground and aerial survey detections. The Utah Division of Wildlife Resources conducts aerial surveys specifically targeting moose every 3 years within hunted units, in addition to collecting incidental observations during elk surveys. Washington Department of Fish and Wildlife biologists conduct annual helicopter surveys to construct an annual index that is useful to track general trends and recruitment rates within most of the core moose range in northeastern Washington; however, despite incorporating covariates affecting detection probabilities, these data remain imprecise (Harris et al. 2015). Wyoming Fish and Game biologists conduct annual moose-specific aerial surveys in the more abundant herd units and use these data in a modified spreadsheet simulation model (similar to that used in Colorado); incidental observations also occur in surveys of other big game populations (Monteith et al. 2015).

Given the many challenges of funding and collecting rigorous aerial survey data for small and widespread moose populations, many western state agencies are currently exploring other potential avenues for future population monitoring. These include exploration of forward-looking infrared (FLIR) technology in comparison to aerial surveys in northern Idaho (*sensu* Storm et al. 2011), patch occupancy modeling of hunter sightings data in Montana (*sensu* Rich et al. 2013), and development of a smartphone app for collecting public sightings of moose in Washington (*sensu* Teacher et al. 2013).

HUNTING OPPORTUNITY, SUCCESS RATES, AND TRENDS

Licensed hunting of moose began in the late 19th century in Idaho, Montana, and Wyoming, but these seasons were subsequently closed in 1897–1899 due to concerns of overharvest. Hunting seasons were (re)instated within 6 Rocky Mountain states in the following chronological order: 1912 (Wyoming), 1945 (Montana), 1946 (Idaho), 1958 (Utah), 1977 (Washington), and 1985 (Colorado). The number of harvested moose has declined in the past decade in 4 of 6 western states (Idaho, Montana, Utah, and Wyoming) that allow hunting (Fig. 2). Conversely, harvest numbers have continued to increase in Colorado and Washington through added opportunities in traditional and newly opened hunting units (Fig. 2). To date, moose hunting has not been initiated in Nevada or Oregon, though a bull moose was incidentally harvested in Nevada in the 1950s. In 2015, a total of 2,263 hunting permits were offered by the 6 states, resulting in 1,811 harvested moose and an average harvest success rate of 80% (Table 2). Since 1990, the highest single-year state harvest was 1,215 moose in Wyoming in 2001 (Fig. 2). In contrast, the highest harvest in 2015 was 666 moose in Idaho. Proportionate harvest of antlerless (cows and calves) moose ranged from 0 to 17% in states with generally declining opportunity, compared to 35% and 49% antlerless harvest in Washington and Colorado, respectively, where hunter opportunity continued to increase through 2015

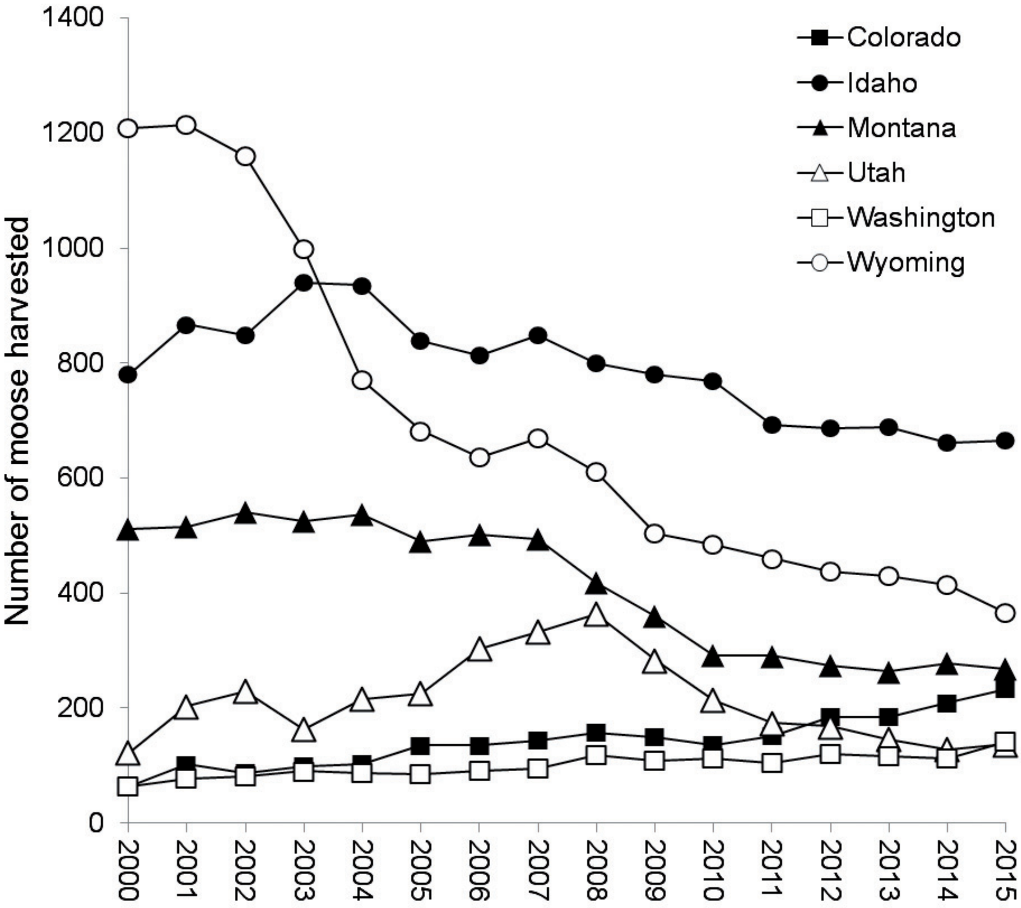

Fig. 2. Moose harvest trends in the western USA from 2000 to 2015.

(Table 2). For the states focal to this summary, moose hunting is managed through lottery permit systems that produce high harvest success rates averaging 75-95% annually (Table 2). There is a tendency for somewhat lower rates of success on antlerless permits versus antlered-only or either-sex permits (Table 2).

Spatial distribution of permits across the region shows an uneven gradient of hunting opportunity (i.e., number of moose hunting permits) across the states (Fig. 3a). Although moose occupy areas beyond hunting units alone, multi-state concentrations of moose hunting opportunity appear in approximately 4 portions of the range: 1) the Northern Rockies and Columbia Mountains region of Washington, northern Idaho, and northwest Montana; 2) the Middle Rockies region of southwest Montana, southeast Idaho, and western Wyoming; 3) the Southern Rockies region of north-central Colorado; and 4) the Wasatch and Uinta ranges in north-central Utah (Fig. 3a).

We summarized trends in hunter opportunity across the 11-year period of 2005–2015 for all hunting management units or districts (hereafter “units”) across the entire region. Given differences in population monitoring techniques across states, hunter opportunity data provide the most standardized means of assessing and

Table 2. Numbers of moose hunting permits issued and moose harvested, percentage of antlerless moose (cows and calves) in the harvest, and success rates of hunters holding antlered (including either-sex) and antlerless permitsamong states in the western USA during the 2015 hunting season.

State	Permits	Harvest	% Antlerless in harvest	% Hunter success, Antlered[1,2]	% Hunter success, Antlerless[1]
Colorado	313	233	48.9%	85.6%	65.5%
Idaho	873	666	17.4%	77.6%	73.9%
Montana	362	268	13.6%	73.8%	76.1%
Nevada	0	0	–	–	–
Oregon	0	0	–	–	–
Utah	143	137	0%	95.8%	–
Washington	168	142	35.2%	91.6%	72.1%
Wyoming	411	365	16.4%	90.8%	80.0%

[1] Hunter success measured as harvested moose per permit allocated, not accounting for number of permit-holders that actually hunted.

[2] Hunter success for antlered moose includes the combined success rates of both antlered-only and either-sex permit-holders, given either-sex permit-holders harvest predominately antlered moose (e.g., 94% of hunters in Washington).

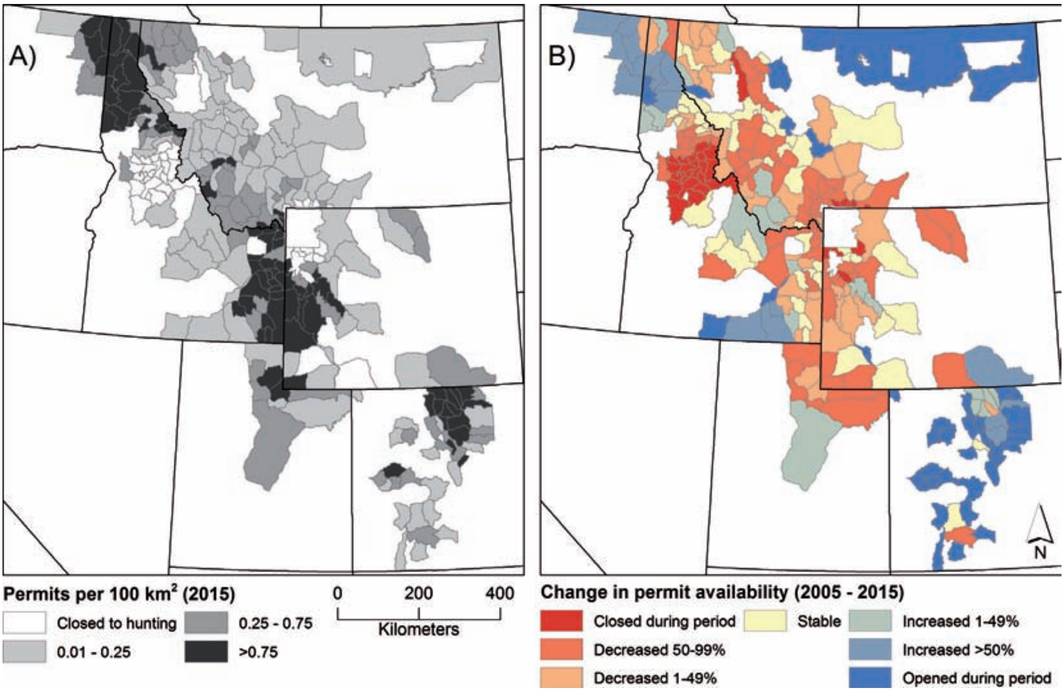

Fig. 3. Regional patterns in a) the availability of moose hunting permits in 2015 and b) changes in permit availability per hunting unit between 2005 and 2015 across the western USA. Note some hunting units were merged together for one or both years to facilitate comparisons of equal areas among years.

comparing trends among states. In the absence of consistent sampling-based surveys, we treat hunting opportunity as an index to population status, assuming that changes in opportunity within units reflect relative trends in abundance. In order to allow comparison of equal areas across years, we merged some units together for either the 2005 or 2015 seasons to accommodate changes in unit boundaries or regulations among years.

In total, we assessed changes in opportunity across 273 units within 6 states from 2005 to 2015 (Table 3). Overall, moose hunting opportunity declined by 23% across the entire region, from 2,970 permits in 2005 to 2,279 permits in 2015, but trends varied among local units. On average, hunting opportunity decreased across 56% of the units, remained stable across 17%, and increased across 27% (Table 3). Visual display of trends per hunting unit shows a diversity of dynamics, from areas that were closed to hunting to areas newly opened to hunting (Fig. 3b). Generally, declines in hunting opportunity for moose are evident across much of their occupied area in the western US, including large portions (62–89%) of "stronghold" states where moose have been abundant enough to support hunting for the longest period of time (i.e., Idaho, Montana, Utah, and Wyoming). We note that this trend was evident prior to 2005 in Wyoming where loss of 527 permits occurred between 2000 and 2005.

In contrast, increases in hunting opportunity were more common at peripheries of the range where populations expanded, including most of Colorado, central Utah, southern Idaho, northeastern Washington, and eastern Montana. The increases in eastern Montana mirror those in similar prairie habitats of neighboring jurisdictions in southeast Alberta, western North Dakota, and southwest Saskatchewan where moose populations have generally increased in recent years (Laforge et al. 2016). Increases in hunting opportunity in Colorado were partially in response to continued introductions of moose into new areas including the Grand Mesa National Forest (2005–2007) and the White River National Forest (2009–2010). Not coincidentally, the few units in Colorado where hunting opportunity declined were also those serving as source populations for translocations. The Wasatch Unit has the most recently established population and offers the most hunting opportunity in Utah.

Table 3. Trends in moose hunting opportunity (i.e., number of moose hunting permits) from 2005–2015, summarized per hunting unit across 6 western states.

			Trends in moose permits per unit during 2005–2015		
State	N_{units}	Median unit area (km^2)	Decreased	Stable	Increased
Colorado	42	1127	5%	5%	90%
Idaho	92	834	62%	21%	17%
Montana	85	1490	67%	20%	13%
Utah	9	2431	89%	0%	11%
Washington	7	2468	14%	0%	86%
Wyoming	38	1810	66%	24%	11%
Area-weighted average[1]			56%	17%	27%

[1] Area-weighted averages were estimated by weighting states according to the product of the number of hunting units and median area per unit for each state.

POTENTIAL LIMITING FACTORS

There are many factors of potential importance to moose population dynamics across the western USA, and data concerning their presence, prevalence, or effects on moose vary across populations. Multiple parasites and diseases including the arterial worm (*Elaeophora schneideri*), winter tick (*Dermacentor albipictus*), giant liver fluke (*Fascioloides magna*), chronic wasting disease, hydatid worm (*Echinococcus granulosus*), and other tapeworms (*Taenia* spp.) have been documented in the region from examination of hunter-killed, live-captured, or opportunistically collected specimens of moose or other ungulate species (e.g., Worley et al. 1972, Samuel et al. 1991, Dunkel et al. 1996, Pessier et al. 1998, Henningsen et al. 2012, LeVan et al. 2013). Large predator communities may have up to 4 species - black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*), cougars (*Puma concolor*), and wolves (*Canis lupus*) - that vary in density and potential to affect moose population dynamics within individual states (*sensu* Griffin et al. 2011, Brodie et al. 2013). Presence of wolves, grizzly bears, and chronic wasting disease vary most across states (Table 4).

The potential importance of nutritional limitations has been documented in certain western moose populations. For example, Ruprecht et al. (2016) reported low fat levels in moose in Utah relative to northern populations, as well as lower pregnancy and twinning rates than in other North American populations at lower latitudes. Both are suggestive of nutritional limitation, although nutritional condition is affected by factors other than forage including disease, parasites, and combined influences related to climate change.

Climate change may have particularly pronounced effects on populations at the periphery of a species' range (Hampe and Petit 2005). Although climate change has been linked to expansion of moose in Alaska through habitat change (Tape et al. 2016), and some southern populations remain stable or increasing (Murray et al. 2012), we share the speculative concern of Lenarz et al. (2010) over the long-term viability of moose populations along their southern range edge. Current climate projections suggest that temperature will increase during all seasons in the Rocky Mountain region, and precipitation may increase in northern portions (Rocca et al. 2014). Warmer temperatures may possibly induce heat stress-related impacts in free-ranging moose as measured in captive moose (Renecker and Hudson 1986, McCann et al. 2013). Indirect effects of warmer climate may also impact moose, as mediated by changes in parasite-host communities or plant communities and/or phenology (Rempel 2011, Monteith et al. 2015).

Interestingly, we find that the southernmost global populations of moose found in Colorado appear to be the most stable in the western USA as evidenced by population growth and increased hunting opportunity (Fig. 3b). However, latitude alone may not sufficiently characterize variation in climate across this region, as portions of Colorado are similar in temperature regime to more northern areas (Table 1), and increasing populations such as those in Colorado or Washington are also relatively young and expanding into unoccupied habitats. It is possible that the dynamics of these populations are still in accordance with the earlier stages of the eruptive cycle of introduced ungulate populations identified by Caughley (1970). The complexities of time since establishment and density dependence may confound comparisons among populations with respect to climate- or habitat-related conditions; however, direct physiological impacts of heat stress should manifest regardless. In short, multiple factors other than latitude alone are influential on the short- and long-term

Table 4. Documented presence, absence or uncertainty regarding parasites and predators of potential importance to moose dynamics across states of the western USA, *circa* 2015.

	Parasites and disease						Predators			
State	*Elaeophora schneideri*	*Dermacentor albipictus*	*Echinococcus granulosus*	Chronic wasting disease	*Fascioloides magna*	*Parelaphostrongylus tenuis*	Black bear	Grizzly bear	Cougar	Wolf
Colorado	++	++	+	+	–	–	++	–	++	–
Idaho	++	++	++	–	++	–	++	+	++	++
Montana	++	++	++	–	++	–	++	++	++	++
Nevada	+	+	–	–	–	–	+	–	++	–
Oregon	++	++		–		–	++		++	
Utah	++	++	+	+		–	++		++	
Washington	+	++		–		–	++	+	++	++
Wyoming	++	++		+	+	–	++	++	++	++

++ = Documented as commonly present in moose or areas occupied by moose.
\+ = Documented as present among ungulate populations, but rare in moose or areas occupied by moose.
– = Not documented and presence seen as unlikely in moose or areas occupied by moose.
[blank] = Not documented and presence unknown in moose or areas occupied by moose.

dynamics of moose populations in North America.

State-regulated hunter harvest, tribal harvest, and illegal harvest of moose are expected to play some role in regulating moose populations across the western USA. Hunting permits are allocated considering local objectives throughout this region, and range from conservative permit numbers to minimize impacts of hunting, to liberal numbers of permits to reduce populations and their impacts on humans and the environment (Table 2; DeCesare et al. 2014). Tribal harvest of moose is permitted in most western states through treaty rights, but the availability of specific data varies by jurisdiction. In Montana, tribal harvest was estimated to increase the total annual harvest by 7–16% during 1986–2012. Illegal harvest may also have measurable impact on moose; for example, the result of multiple studies in Idaho suggested that 31–50% of known mortality was associated with illegal harvest (Ritchie 1978, Pierce et al. 1985, Toweill and Vecellio 2004).

FUTURE RESEARCH

State wildlife agencies are conducting research in conjunction with universities and coordinating research among states to leverage resources across jurisdictions. Research objectives include work focused on population vital rates (e.g., adult female survival, fecundity, and calf survival), movements and spatial ecology, resource selection, nutritional ecology and forage monitoring, baseline disease and mineral monitoring, the development of monitoring techniques, and identification of limiting factors. Research objectives regarding limiting factors include the assessment of relative impacts of predation, parasites, climate change (direct effects of heat stress and indirect effects on moose foraging behavior and parasite loads), and habitat changes (e.g., decline of early seral forests) on moose vital rates.

ACKNOWLEDGEMENTS

We thank M. Atamian, D. Base, J. Goerz, H. Ferguson, S. Hansen, A. Holland, M. Lloyd, J. Newby, J. Oyster, K. Podruzny, A. Prince, T. Smucker, and P. Wolff for their contributions to the collection and compilation of moose monitoring data that went into this manuscript. J. Gude, J. Maskey, M. Mitchell, and J. Smith contributed to meetings and discussions that led to the development of this manuscript. We thank A. Apa, K. Logan, the associate editor and 1 anonymous reviewer for helpful edits and feedback.

REFERENCES

Baigas, P., R. A. Olson, R. M. Nielson, S. N. Miller, and F. G. Lindzey. 2010. Modeling seasonal distribution and spatial range capacity approximations of moose in southeastern Wyoming. Alces 46: 89–112.

Base, D. L., S. Zender, and D. Martorello. 2006. History, status, and hunter harvest of moose in Washington state. Alces 42: 111–114.

Beauvais, G., M. Andersen, D. Keinath, J. Aycrigg, and J. Lonneker. 2013. Predicted vertebrate species habitat distributions and species richness. Pages 58–110 *in* J. Aycrigg, M. Andersen, G. Beauvais, M. Croft, A. Davidson, L. Duarte, J. Kagan, D. Keinath, S. Lennartz, J. Lonneker, T. Miewald, and J. Ohmann, editors. Ecoregional Gap Analysis of the Northwestern United States: Northwest Gap Analysis Project. Draft report. University of Idaho, Moscow, Idaho, USA.

Brimeyer, D. G., and T. P. Thomas. 2004. History of moose management in Wyoming and recent trends in Jackson Hole. Alces 40: 133–144.

Brodie, J., H. Johnson, M. Mitchell, P. Zager, K. Proffitt, M. Hebblewhite, M. Kauffman, B. Johnson, J. Bissonette, C. Bishop, J. Gude, J. Herbert, K. Hersey, M. Hurley, P. M. Lukacs,

S. McCorquodale, E. McIntire, J. Nowak, H. Sawyer, D. Smith, and P. J. White. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. Journal of Applied Ecology 50: 295–305.

Burkholder, B. O., N. J. DeCesare, R. A. Garrott, and S. J. Boccadori. 2017. Heterogeneity and power to detect trends in moose browsing of willow communities. Alces 53: 23–39.

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

Commission for Environmental Co-operation (CEC). 1997. Ecological regions of North America – toward a common perspective. CEC, Montreal, Quebec, Canada.

DeCesare, N. J., J. R. Newby, V. J. Boccadori, T. Chilton-Radandt, T. Thier, D. Waltee, K. Podruzny, and J. A. Gude. 2016. Calibrating minimum counts and catch per unit effort as indices of moose population trend. Wildlife Society Bulletin 40: 537–547.

———, T. D. Smucker, R. A. Garrott, and J. A. Gude. 2014. Moose status and management in Montana. Alces 50: 35–51.

Dorn, R. D. 1970. Moose and cattle food habits in southwest Montana. Journal of Wildlife Management 34: 559–564.

Dungan, J. D., and R. G. Wright. 2005. Summer diet composition of moose in Rocky Mountain National Park, Colorado. Alces 41: 139–146.

Dunkel, A. M., M. C. Rognlie, G. Rob Johnson, and S. E. Knapp. 1996. Distribution of potential intermediate hosts for *Fasciola hepatica* and *Fascioloides magna* in Montana, USA. Veterinary Parasitology 62: 63–70.

Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, D. H. Jackson, B. K. Johnson, W. L. Myers, J. D. Raithel, M. Schlegel, B. L. Smith, C. White, and P. J. White. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. Journal of Animal Ecology 80: 1246–1257.

Harris, R., M. Atamian, H. Ferguson, and I. Keren. 2015. Estimating moose abundance and trends in northeastern Washington State: index counts, sightability models, and reducing uncertainty. Alces 51: 57–69.

Hampe, A., and R. J. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8: 461–467.

Henningsen, J. C., A. L. Williams, C. M. Tate, S. A. Kilpatrick, and W. D. Walter. 2012. Distribution and prevalence of *Elaeophora schneideri* in moose in Wyoming. Alces 48: 35–44.

Karns, P. D. 2007. Population distribution, density, and trends. Pages 125–140 *in* A. W. Franzmann and C.C. Schwartz, editors. Ecology and Management of the North American Moose. Second edition. University Press of Colorado, Boulder, Colorado, USA.

Knowlton, F. F. 1960. Food habits, movements and populations of moose in the Gravelly Mountains, Montana. Journal of Wildlife Management 24: 162–170.

Kufeld, R. C. 1994. Status and management of moose in Colorado. Alces 30: 41–44.

———, and D. C. Bowden. 1996. Movements and habitat selection of Shiras moose (*Alces alces shirasi*) in Colorado. Alces 32: 85–99.

Laforge, M. P., N. L. Michel, A. L. Wheeler, and R. K. Brook. 2016. Habitat selection by female moose in the Canadian prairie ecozone. Journal of Wildlife Management 80: 1059–1068.

Langley, M. A. 1993. Habitat selection, mortality and population monitoring of Shiras moose in the North Fork of the Flathead River valley, Montana. M.S.

Thesis, University of Montana, Missoula, Montana, USA.

Lenarz, M. S., J. Fieberg, M. W. Schrage, and A. J. Edwards. 2010. Living on the edge: viability of moose in northeastern Minnesota. Journal of Wildlife Management 74: 1013–1023.

LeVan, I. K., K. A. Fox, and M. W. Miller. 2013. High elaeophorsis prevalence among harvested Colorado moose. Journal of Wildlife Diseases 49: 666–669.

Matchett, M. R. 1985. Habitat selection by moose in the Yaak River drainage, northwestern Montana. Alces 21: 161–190.

Matthews, P. E. 2012. History and status of moose in Oregon. Alces 48: 63–66.

McCann, N. P., R. A. Moen, and T. R. Harris. 2013. Warm-season heat stress in moose (*Alces alces*). Canadian Journal of Zoology 91: 893–898.

McMillan, J. F. 1953. Some feeding habits of moose in Yellowstone Park. Ecology 34: 102–110.

Monteith, K. L., R. W. Klaver, K. R. Hersey, A. A. Holland, T. P. Thomas, and M. J. Kauffman. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. Oecologia 178: 1137–1148.

Murray, D. L., K. F. Hussey, L. A. Finnegan, S. J. Lowe, G. N. Price, J. Benson, K. M. Loveless, K. R. Middel, K. Mills, D. Potter, A. Silver, M.-J. Fortin, B. R. Patterson, and P. J. Wilson. 2012. Assessment of the status and viability of a population of moose (*Alces alces*) at its southern range limit in Ontario. Canadian Journal of Zoology 90: 422–434.

Nelson, E. W. 1914. Description of a new subspecies of moose from Wyoming. Proceedings of the Biological Society of Washington 27: 71–74.

Olterman, J. H., D. W. Kenvin, and R. C. Kufeld. 1994. Moose transplant to southwestern Colorado. Alces 30: 1–8.

Pessier, A. P., V. T. Hamilton, W. J. Foreyt, S. Parish, and T. L. McElwain. 1998. Probable elaeophorosis in a moose (*Alces alces*) from eastern Washington state. Journal of Veterinary Diagnostic Investigation 10: 82–84.

Peterson, R. L. 1952. A review of the living representatives of the genus *Alces*. Contributions of the Royal Ontario Museum of Zoology and Palaentology 34. Royal Ontario Museum, Toronto, Ontario, Canada.

Pierce, J. D. 1984. Shiras moose forage selection in relation to browse availability in north-central Idaho. Canadian Journal of Zoology 62: 2404–2409.

———, and J. M. Peek. 1984. Moose habitat use and selection patterns in north-central Idaho. Journal of Wildlife Management 48: 1335–1343.

———, B. W. Ritchie, and L. Kuck. 1985. An examination of unregulated harvest of Shiras moose in Idaho. Alces 21: 231–252.

PRISM Climate Group. 2016. PRISM gridded climate data. Oregon State University, Corvallis, Oregon, USA. <http://prism.oregonstate.edu> (accessed October 2016).

Rempel, R. S. 2011. Effects of climate change on moose populations: exploring the response horizon through biometric and systems models. Ecological Modelling 222: 3355–3365.

Renecker, L. A., and R. J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Canadian Journal of Zoology 64: 322–327.

Rich, L. N., E. M. Glenn, M. S. Mitchell, J. A. Gude, K. Podruzny, C. A. Sime, K. Laudon, D. E. Ausband, and J. D. Nichols. 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. Journal of Wildlife Management 77: 1280–1289.

Ritchie, B. W. 1978. Ecology of Moose in Fremont County, Idaho. Wildlife Bulletin No. 7. Idaho Department of Fish and Game, Boise, Idaho, USA.

Rocca, M. E., P. M. Brown, L. H. MacDonald, and C. M. Carrico. 2014.

Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. Forest Ecology and Management 327: 290–305.

Ruprecht, J. S., K. R. Hersey, K. Hafen, K. L. Monteith, N. J. DeCesare, M. J. Kauffman, and D. R. MacNulty. 2016. Reproduction in moose at their southern range limit. Journal of Mammalogy 97: 1355–1365.

Samuel, W. M., D. A. Welch, and B. L. Smith. 1991. Ectoparasites from elk (*Cervus elaphus nelsoni*) from Wyoming. Journal of Wildlife Diseases 27: 446–451.

Stevens, D. R. 1970. Winter ecology of moose in the Gallatin Mountains, Montana. Journal of Wildlife Management 34: 37–46.

Storm, D. J., M. D. Samuel, T. R. Van Deelen, K. D. Malcolm, R. E. Rolley, N. A. Frost, D. P. Bates, and B. J. Richards. 2011. Comparison of visual-based helicopter and fixed-wing forward-looking infrared surveys for counting white-tailed deer *Odocoileus virginianus*. Wildlife Biology 17: 431–440.

Tape, K. D., D. D. Gustine, R. W. Ruess, L. G. Adams, and J. A. Clark. 2016. Range expansion of moose in arctic Alaska linked to warming and increased shrub habitat. PloS One 11:e0152636.

Teacher, A. G. F., D. J. Griffiths, D. J. Hodgson, and R. Inger. 2013. Smartphones in ecology and evolution: a guide for the app-rehensive. Ecology and Evolution 3: 5268–5278.

Timmermann, H. R., and A. R. Rodgers. 2017. The status and management of moose in North America – circa 2015. Alces 53: 1–22.

Toweill, D. E., and G. Vecellio. 2004. Shiras moose in Idaho: status and management. Alces 40: 33–43.

Van Dyke, F., B. L. Probert, and G. M. Van Beek. 1995. Seasonal habitat use characteristics of moose in south-central Montana. Alces 31: 15–26.

Vartanian, J. M. 2011. Habitat condition and the nutritional quality of seasonal forage and diets: demographic implications for a declining moose population in northwest Wyoming, USA. M.S. Thesis, University of Wyoming, Laramie, Wyoming, USA.

White, G. C., and B. C. Lubow. 2002. Fitting population models to multiple sources of observed data. Journal of Wildlife Management 66: 300–309.

Wilson, D. E. 1971. Carrying capacity of the key browse species for moose on the north slopes of the Uinta Mountains, Utah. M.S. Thesis, Utah State University, Logan, Utah, USA.

Wolfe, M. L., K. R. Hersey, and D. C. Stoner. 2010. A history of moose management in Utah. Alces 46: 37–52.

Worley, D. E., C. K. Anderson, and K. R. Greer. 1972. Elaeophorosis in moose from Montana. Journal of Wildlife Diseases 8: 242–244.