Jennifer Sevigny[1], Stillaguamish Tribe of Indians, Natural Resources Department, P.O. Box 277, Arlington, Washington 98223

Michael Sevigny, Tulalip Tribes, Natural and Cultural Resources Department, 6406 Marine Drive, Tulalip, Washington 98271

Emily George-Wirtz, Sauk-Suiattle Indian Tribe, Natural Resource Department, 5318 Chief Brown Lane, Darrington, Washington 98241

and

Amanda Summers, Stillaguamish Tribe of Indians, Natural Resources Department, P.O. Box 277, Arlington, Washington 98223

Spatial Distribution, Site Fidelity, and Home Range Overlap in the North Cascades Elk Herd: Implications for Management

Abstract

A multi-faceted management approach on a group by group basis may be the most effective strategy for managing human-elk conflict within the North Cascades elk herd. Consideration of spatial distribution is important when developing management strategies designed to benefit or manipulate elk habitat use. We analyzed data from 23 GPS collared female elk (*Cervus elaphus*) in known conflict areas and adjacent upland forests to investigate spatial distribution, site fidelity, and home range overlap in northwest Washington. We identified 21 non-migratory sub-herds associated with our collared elk with discrete home ranges, year-round site fidelity and predictable core use areas. Home range areas ranged from 1.34–29.79 km^2 with 50% core use areas ranging from 0.02–1.67 km^2. We used seasonal median centers as indicators of site fidelity and found that all but one of the 21 groups had seasonal and total median centers < 3 km apart within their 95% home ranges. Home ranges showed minimal overlap between groups with Utilization Distribution Overlap Index values of zero or < 1 for 20 of the 21 groups. Groups that did overlap or had adjacent range boundaries showed incursion tracks suggesting that attempts were made to access occupied habitat. While the herd continues to recover, we recommend managing elk in conflict zones at the sub-herd level using a combination of techniques to manipulate behavior, block resource access, and control group size with the overall goal of influencing spatial distribution without removing elk from the landscape altogether.

Keywords: North Cascades, elk, site fidelity, spatial distribution, home range

Introduction

Elk (*Cervus elaphus*) are an important ecological, sociological, cultural, and economic resource in the Pacific Northwest (Bunnell 1997, Myers et al. 2008, Donovan and Champ 2009). The North Cascades Elk Herd (NCEH) is the smallest of ten herds residing in Washington State (WDFW 2002) with a historic range west of the Cascade Crest from the Canadian border spanning four counties to north King County (WDFW 2017). This is a native herd that was harvested to near extinction in the early 1900s (Murie 1951). Augmentations of Rocky Mountain and Roosevelt elk occurred in 1912 (Washington Department of Game 1939), 1946, and 1948 (McCall 1996, WDFW 2015) with the most recent efforts occurring between 2003 and 2005 (WDFW 2017). Preliminary genetic work (WDFW 2014) indicates that Roosevelt and Rocky Mountain elk have interbred resulting in a mixed population. The NCEH is currently co-managed by the Washington Department of Fish and Wildlife (WDFW) and Tribes signatory to the Treaty of Point Elliott (Kappler and United States 1903). The Point Elliott Treaty Tribes and the WDFW have collaborated on recovering and expanding the NCEH since the late 1990s. As the population increases, new management challenges arise between promoting herd growth and

[1]Author to whom correspondence should be addressed.
Email: jsevigny@stillaguamish.com

expansion and addressing human-elk conflicts. Elk management strategies vary depending on agency objectives, landscape configuration, elk behavior and social tolerance. The landscape across elk ranges in Washington has changed over time resulting in habitat loss and fragmentation (WDFW 2015). Human population growth, development, and encroachment into elk habitat has resulted in a greater use of Washington's road systems and increased human-elk interactions (Myers et al. 2008, McCorquodale 2013).

Growth and expansion of the NCEH has resulted in greater numbers of elk in lowland agricultural valleys. Increases in human-elk interaction present a challenge to resource managers and has led to different management strategies for elk herds and sub-herds throughout their ranges (Walter et al. 2010). Hegel et al. (2009) suggest that conflict management strategies fall into three categories: habitat modification, population size/behavior control, and altering human attitudes and behaviors. Human attitudes toward elk vary and Fricke et al. (2008) found that social acceptance was one of the primary factors influencing elk population size and growth.

Management increasingly requires consideration of social tolerance and must incorporate damage-reduction strategies into herd management plans while acknowledging the positive benefits of elk to society. The 2017 Draft North Cascades Elk Herd Management Plan (WDFW 2017) addresses human-elk conflict with strategies ranging from lethal removal to non-lethal options such as exclusion fences and forage enhancement plots. Depredation hunts target females and impact approximately 35% of the overall NCEH population (2018 Lincoln-Peterson (L-P) estimate 1,592 ± 716) and occur July 1–March 31. Modest general elk seasons (State and Tribal) also occur in upland habitats for either sex. While depredation hunts are effective at regulating group size, they are not effective at permanently moving elk away from conflict areas or at decreasing damage complaints. To effectively manage human-elk conflict in a recovering elk population, the spatial organization of elk on the landscape in conjunction with site fidelity and joint space use sharing must be considered.

Long et al. (2015) describes spatial organization as the spatial and temporal relation of animals within a population. An animal's home range is the area used for foraging, mating, and caring for young (Burt 1943, Powell and Mitchell 2012), and range size is believed to be a result of social structure (Millspaugh et al. 2004) and individual movements in relation to resource availability (Anderson et al. 2005). Many species exhibit home range fidelity (Reynolds 1984, Kricher and Davis 1998, Wittmer et al. 2006) by occupying the same area or returning to select areas over an extended period of time (White and Garrott 1990, Switzer 1993, Brough et al. 2017, Mahoney and Young 2017).

Home range fidelity often indicates stable habitat (Franklin and Lieb 1979, Bender 1992, Wolf et al. 2009) and is an important consideration for targeted management actions (Brough et al. 2017). Fidelity to a home range may increase survival and reproductive success because learned behaviors associated with resource use may enhance individual fitness (Ortega et al. 2006, Piper 2011, Mahoney and Young 2017). Many studies have documented site fidelity in both migratory and non-migratory female elk (Edge and Marcum 1985, Benkobi et al. 2005, Stubblefield et al. 2006, Van Beest et al. 2013). Millspaugh et al. (2000) suggest that the size and geographic location of elk home ranges can serve as the basis for monitoring behavior and habitat use. Philopatric behavior and social dynamics can also contribute to the stability of social groups and influence home range overlap (Lieb 1973, Franklin and Lieb 1979, Raedeke et al. 2002, Brough et al. 2017).

The probability of home range overlap is influenced by social dynamics (Lieb 1973, Franklin and Lieb 1979, Kolbe and Weckerly 2015) including group size and movement patterns. Franklin et al. (1975) describes the social organization of elk as how individuals within a group interact in relation to available habitat. Female groups are typically comprised of cows and juvenile elk of both sexes (Geist 1982). The stability and leadership of adult cows may allow the groups to respond to specific changes in the environment (Wilson 1975, Weckerly 1999). Unlike elk herds that are migratory with annual variation in social groups and no lasting associations between individuals (Geist 1982, Houston 1982), sedentary elk herds are expected to demonstrate strong site fidelity and consistency in group associations with minimal home range overlap (Jenkins and Starkey 1982, Relyea et al. 2000, Anderson et al. 2005). Adult female elk can have strong social bonds with their juvenile offspring (Weckerly 1999) and groups consisting of bonded individuals may be reluctant to associate with unfamiliar individuals (Thouless and Guinness 1985). Therefore, it is unlikely that socially bonded elk with long-term bonds between individuals would associate with adjacent groups regardless of resource availability (Kolbe and Weckerly 2015). In elk conflict areas, if socially bonded groups are removed or greatly reduced, there is a risk that other unrelated groups will move in if desirable habitat is available (Link 2004). In addition, Edge et al. (1986) suggested that landscape scale elk management practices may be ineffective and recommended sub-population level actions. Others agree that some wildlife conflict issues should be addressed at the sub-population level (Knowlton et al. 1999, Sacks et al. 1999) and group constancy can provide a useful baseline for management decisions (Franklin and Lieb 1979). Understanding the spatial and social organization of female elk groups will inform management and help address human-elk conflicts.

In consideration of this idea, we analyzed data from GPS collared female elk in known conflict areas and adjacent upland forests to determine spatial organization, site fidelity and home range overlap of groups in the NCEH. Specifically, we considered whether there was three dimensional spatial use sharing between groups and if social dynamics influenced distribution. With the goal of managing this recovering herd for long-term sustainability and promoting expansion throughout their potential range, we needed to understand social group patterns and whether we could identify targeted management actions to manipulate elk and reduce human-elk conflicts. We propose that a multi-faceted management approach on a group by group basis may be the most effective strategy for managing human-elk conflict within the NCEH range.

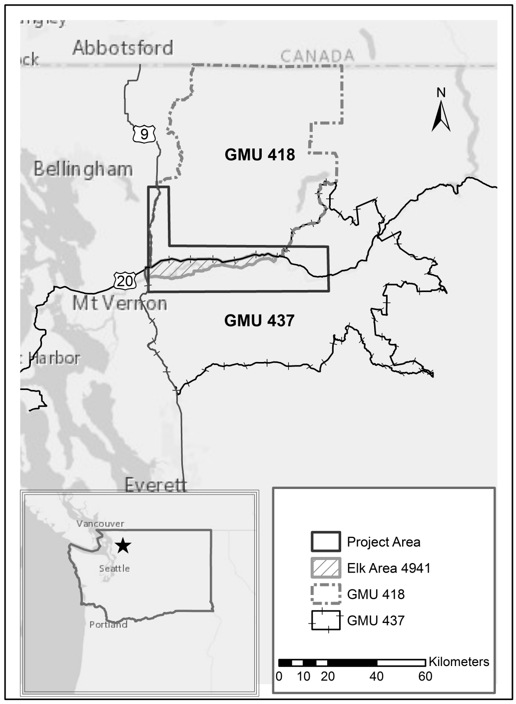

Figure 1. Location of study area with Game Management Units 418, 437, and Elk Area 4941 in northwest Washington State.

Methods

Study Area

We conducted this study in northwest Washington State on the west side of the North Cascades mountain range. Our collaring efforts targeted the eastern Skagit Valley region (48° 52' N, 121° 94' W) between the cities of Sedro Woolley and Rockport in northern Skagit County, Washington with some additional collaring in the Acme Valley region (48° 70' N, 122° 19' W) of south Whatcom County, Washington (Figure 1). We also targeted elk groups on industrial timberlands (48° 35' N, 122° 01' W) north of the State Route 20 corridor. The study area encompassed approximately 650 km^2, and was located within Game Management Units (GMUs) 418 and 437 (including Elk Area 4941). The lowland valley areas (approximately

400 km^2) included mostly private lands with some federal and state public forest lands interspersed throughout the region. Elevation ranged from 42 to 170 m. Land cover consisted primarily of agricultural crops, with riparian forest and rural residential development dispersed along the highway corridors and river valley. Agricultural uses consisted of hay, food crops, and livestock. The human population in the developed areas was approximately 6,800 (2016 census data). The upland forest area (approximately 250 km^2) was primarily private industrial timberlands with some state forest parcels dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Western redcedar (*Thuja plicata*), red alder (*Alnus rubra*) and maple (*Acer* spp.) also occurred throughout the upland regions. Forest stand rotation was typically 40 to 60 years with herbicide applications for the first three years following harvest. Upland topography was rolling foothills to mountainous with elevations ranging from 100 to 1,000 m. The climate was described as maritime (Franklin and Dyrness 1988) with annual precipitation ranging from 120 to 300 cm and annual temperature range of –4 °C to 27 °C (US Climate Data 2018).

Data Collection

Between 2013 and 2017, we collared at least one female elk (≥ 1 year old) in targeted groups throughout the study area using modified 1.2 m wide x 1.8 m high x 2.4 m long collapsible (Roper et al. 1971, McCullough 1975, Thompson et al. 1989) clover traps (Clover 1954) baited with apples and mineral licks. The NCEH was thought to be a migratory herd and we selected our trap sites at known elk use areas across the landscape using local knowledge and past elk observations. We captured elk following animal handling guidelines described in Sikes et al. (2016) between November 1 and March 31 each year. All trap sites were monitored with cameras and Vectronic trap transmitters (Vectronic Aerospace USA, Iowa, USA) were used to monitor trap activity. We placed traps on public and private lands based on elk use and landowner support. We used Vectronic GPS Plus, GPS Plus Vertex Survey-1D, and Vertex Lite-4D collars that were programmed to take multiple fixes each day (minimum time interval of 85 minutes between fixes). Collars uploaded data via the Iridium or Globalstar satellite systems. We attempted application of at least one GPS collar and numbered ear tag in each female group in order to ensure geographic representation of the study area population. Locations from one animal were assumed to be representative of a group given the aggregated structure of female elk (Craighead et al. 1973, Van Dyke 2007). Collared elk were monitored daily for capture myopathy for four weeks following capture (Beringer et al. 1996). We did not consider male elk distribution patterns, which are different than females (Peterson and Weckerly 2017), because the females are the drivers of population growth.

Data Analysis

We imported our location data into Excel 2016 (Microsoft Corp., Redmond, WA) for sorting and removal of null locations for each collared animal. Locations from individual animals monitored in multiple years were pooled across years. We estimated home range areas (HR) and core use areas using the Kernel Density Estimation (KDE) tool of the Spatial Analyst Tool Extension in ArcMap 10.5.1 (ESRI, Redlands, CA) at the 95% exceedance value (Seaman and Powell 1996, Kernohan et al. 2001). The kernel function with a variable search radius is based on the quadratic kernel function as described in Seaman and Powell (1996). We defined our HRs as utilization distributions (UDs) or the relative frequency distribution of an elk's occurrence in space and time (Keating and Cherry 2009). The shape of the KDE was dependent on the search radius or bandwidth used for the estimation. In Arc 10.5.1, we calculated the search radius (bandwidth h) based on spatial configuration and the number of input points. We selected our bandwidth parameter using the Solve-the-Equation (STE) method (Jones et al. 1996, Wand and Jones 1994). This approach corrected for spatial outliers and was most appropriate given the size of our dataset (Silverman 1986, Hemson et al. 2005).

Home range estimates provided a 95% UD for each female elk. We also estimated core use areas at a 50% isopleth to identify the most frequently used spaces within each HR. We estimated HR and core use areas for the entire period of record for each female elk group, as represented by the collared female(s) in each group. To quantify spatial fidelity, we used Median Center in the Spatial Statistics Toolbox (Kuhn and Kuenne 1962, Burt and Barber 1996) to calculate median centers (measure of central tendency) for total datasets and data pooled for summer (July–August) and winter (December–February) seasons (Franklin and Lieb 1979, Geist 1982, Van Beest et al. 2013) for each female elk. The Median Center Tool uses an algorithm with candidate median centers that are refined to minimize the Euclidean distance to all outlying points in the dataset. We used the Euclidean distance (km) between summer, winter and total median centers as a metric of year-round site fidelity (White and Garrott 1990, Gower et al. 2009, Gulsby et al. 2011).

We considered three dimensional HR overlap as an effective measure of joint-space use and degree of interaction among individuals (Kernohan et al. 2001, Marzluff et al. 2001, Millspaugh et al. 2004, Long et al. 2015). This method has been used to assess spatial organization in a number of ungulate species including elk (Fieberg and Kochanny 2005, Kolbe and Weckerly 2015, Brough et al. 2017). Congruence of 95% fixed kernel UDs was measured for overlapping individuals using UD_1 (*x, y*) Utilization Distribution Overlap Index (UDOI) described in Fieberg and Kochanny (2005).

$$\mathrm{UDOI} = A_{i,j} (\iint \mathrm{UD}_i (x, y)\, \mathrm{UD}_j (x, y)\, dx\, dy)$$

Where $A_{i,j}$ equals the overlapping area of two HRs and UD_i and UD_j equals the utilization distributions of animals i and j. UDOI compares the heterogeneity of use within each animal's HR where overlap occurs and quantifies the use of shared space. Values < 1 indicate less congruence in UD than would be expected from overlapping distributions, whereas values > 1 indicate greater congruence in overlapping UD than would be expected (Fieberg and Kochanny 2005). Because association or segregation between groups may occur at a finer scale than UDOI can detect, we also identified incursion lines between adjacent elk groups with low to zero UDOI values. We converted GPS fixes (full period of record) from points to lines using the Points to Line and Split Line at Vertices tools in the ArcGIS Data Management Toolbox 10.5.1 resulting in a line segment between consecutive fixes. We then selected line segments intersecting adjacent elk groups' 95% HRs to illustrate incursion tracks between neighboring groups. When the STE bandwidth (h) calculation did not render overlapping HRs but fixes overlapped, we manually selected h iteratively (ranging from 200 to 500 m) until the resulting KDEs overlapped. Given specific biological questions, it is acceptable to select bandwidths a priori (Wand and Jones 1995, Berger and Gese 2007, Jacques et al. 2009, Kie et al. 2010). This approach allowed us to select the minimum h required for overlap without overestimating potential incursions.

Results

Spatial Distribution

We collared 28 female elk in 21 groups that were determined to be non-migratory sub-herds (term used synonymously with group) with discrete year-round HRs (Figure 2). Due to collar failures and one mortality, we used 23 collars for our analyses. Group 3 had three collared females with near identical HRs so we pooled these data for analyses. The number of location fixes used to generate HRs ranged from 780 to 13,351 per group and we analyzed 73,647 locations for all GPS-collared elk during the study period providing robust KDEs (Seaman and Powell 1996). Of the 21 groups identified, 12 were located in areas with elk damage complaints; therefore, we considered 12 groups to fall within potential elk conflict areas (primarily within Elk Area 4941). We observed variation in HR size with areas ranging from 1.34–29.79 km^2 with an elevation range from 11–1,386 m (Table 1). We did not observe typical migratory elk behavior with increased social interactions and mixing of HRs during the winter months. We had one group (#11) with an isolated patch of locations approximately 46.7 km from their established HR. These fixes occurred during the first calving season following capture and did

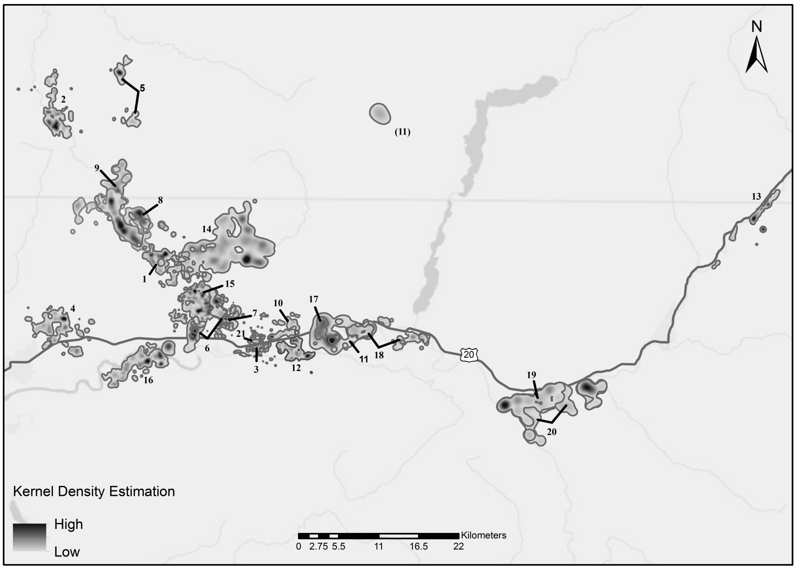

Figure 2. Home range (95% Kernel Density Estimation) distribution of North Cascades female elk groups (1–21) in northwest Washington State.

not occur again during the study period. In general, female elk in more developed agricultural areas had fewer concentrated high use areas (at 95% KDE) compared to female elk in upland industrial forest or mixed agriculture and forest habitats. Female elk in forested landscapes had high use areas dispersed throughout their 95% HRs compared to elk in lowland agricultural valleys (Figure 3). Female elk in developed agricultural areas appeared to make use of smaller ranges with minimal to solitary high use areas evident throughout the entire HR. High use areas within most HRs appeared to remain stable for the entire period of record for each collared female. Year-round 50% core use areas ranged from 0.02–1.67 km^2 (Table 1) and appeared to be consistent over the entire study period for all groups. Core areas accounted for ≤ 11% of the overall HR areas for all groups. Three groups had core areas that accounted for only 1% of their overall home range. Core use areas were similar to the 95% high use areas with multiple, dispersed cores in elk groups in upland forestlands and fewer cores, often associated with elk friendly properties in more developed agricultural regions (Figure 4).

TABLE 1. Female elk group home range (HR) areas (95%), core use areas (50%), and elevation ranges, in the North Cascades, Washington.

Group #	95% HR (km^2)	50% Core (km^2)	% HR in Core	Elevation Range (m)
1	8.68	0.31	4	152–843
2	6.47	0.50	8	72–585
3	1.72	0.02	1	27–266
4	8.46	0.14	1	17–432
5	3.13	0.18	5	176–953
6	9.92	1.13	11	19–357
7	1.34	0.10	7	29–163
8	17.06	1.67	10	117–1170
9	13.96	1.41	10	113–930
10	2.81	0.08	3	40–387
11	16.03	1.47	9	34–1386
12	3.88	0.21	6	32–152
13	2.96	0.26	9	45–1458
14	29.79	0.42	2	180–1189
15	12.80	0.89	7	20–747
16	8.40	0.37	4	11–186
17	6.92	0.33	5	34–343
18	6.25	0.44	7	35–345
19	16.32	1.14	4	59–85
20	21.79	0.60	3	58–170
21	1.65	0.02	1	27–163

Site Fidelity

We calculated median centers for the entire period of record and for winter and summer seasons for each collared female. We focused

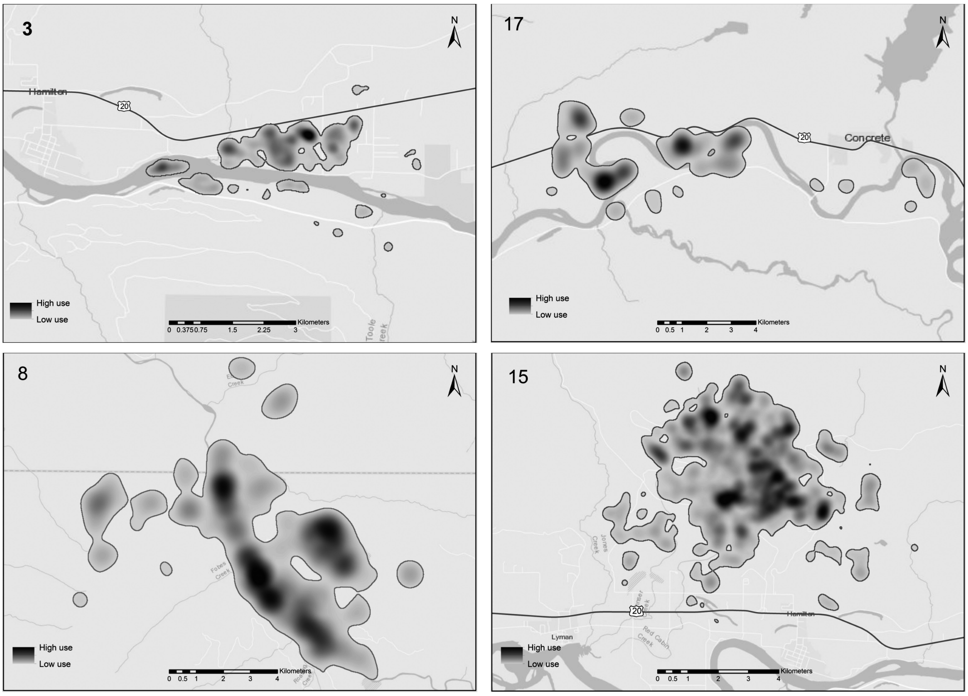

Figure 3. Home ranges (95%) with high density use areas for four female elk groups in the North Cascades, Washington. Groups 3 and 17 were located in developed agricultural areas and Groups 8 and 15 were located in upland industrial forestlands.

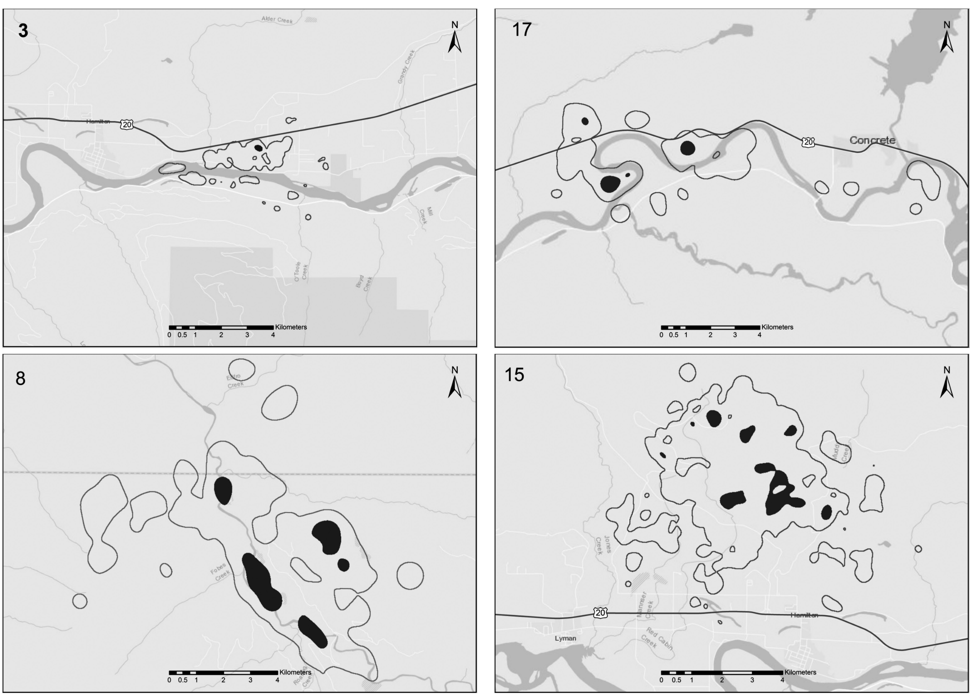

Figure 4. Home ranges (95%) with 50% core use areas for four female elk groups in the North Cascades, Washington. Groups 3 and 17 were located in developed agricultural areas and Groups 8 and 15 were located in upland industrial forestlands.

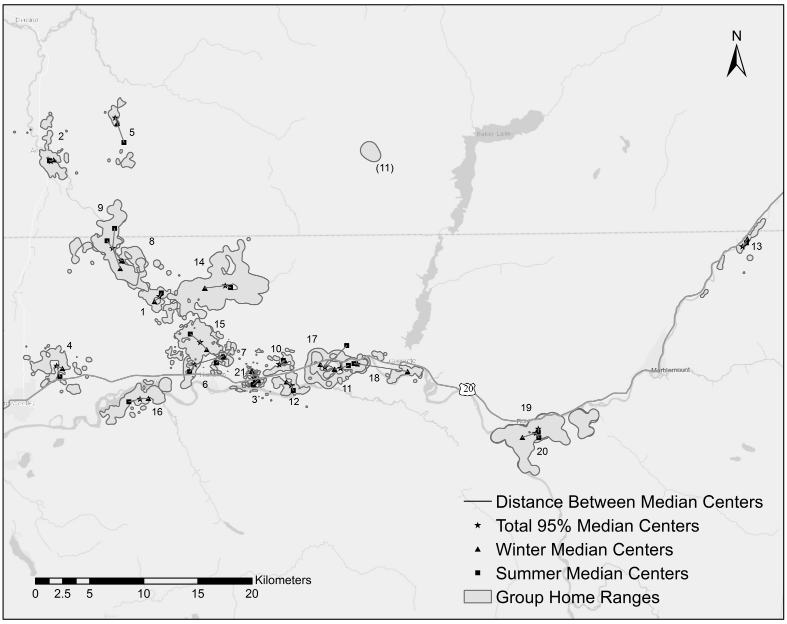

Figure 5. Site fidelity in 95% home ranges represented as summer, winter, and total median centers for 21 female elk groups in the North Cascades, Washington.

on the summer and winter medians for confirmation of year-round fidelity within the 95% home range. Small Euclidean distances between medians reflected high year-round home range fidelity and little shift in distribution centers from year to year (Figure 5). Distances between seasonal medians and total median centers were < 3 km with one exception (Table 2). Seasonal median distances from median centers were < 1 km for 10 of the 21 groups. Four groups (2, 10, 13, and 19) had distances between summer and winter medians of < 0.4 km (Table 2), indicating they spent the majority of their time in the same general area year-round (Figure 6). In general, summer to winter median distances were greater in the female elk groups associated with industrial forestlands (≥ 1.5 km). However, the greatest summer to winter median distance was 4.99 km and occurred in a lowland female group that eventually split into multiple adjacent groups.

TABLE 2. Home range site fidelity of female elk groups represented as distances from median centers (summer to total, winter to total, and summer to winter) in the North Cascades, Washington.

Group #	Summer to Total (km)	Winter to Total (km)	Summer to Winter (km)
1	0.36	0.69	1.03
2	0.13	0.29	0.39
3	0.09	0.51	0.61
4	1.10	0.58	0.80
5	2.40	0.55	1.87
6	0.83	2.80	3.49
7	0.78	0.05	0.80
8	2.23	0.13	2.32
9	1.83	2.01	3.77
10	0.51	0.61	0.15
11	2.83	0.52	2.99
12	0.52	0.55	1.03
13	0.49	0.84	0.39
14	0.52	1.91	2.38
15	1.19	0.91	2.09
16	1.06	0.78	1.83
17	0.78	0.55	1.32
18	0.33	4.67	4.99
19	0.30	0.07	0.24
20	0.51	1.32	1.52
21	0.29	0.63	0.90

Home Range Overlap

The geographical distribution of the HR and core areas showed minimal interchange between female elk groups. For all 21 groups, we had nine UDOI values greater than zero and only three groups had UDOI values of ≥ 0.6 indicating that these groups spatially overlapped and may have interacted during the study period (Table 3). The remaining six UDOI values were ≤ 0.5 indicating little spatial overlap in HR during the study period. We identified four groups that appeared to have ranges adjacent to each other but had low (0.001) or zero UDOI values. For these groups, we identified track lines of incursion into adjacent groups' HRs using manually selected bandwidths and STE bandwidths (Figure 7). In the example of groups

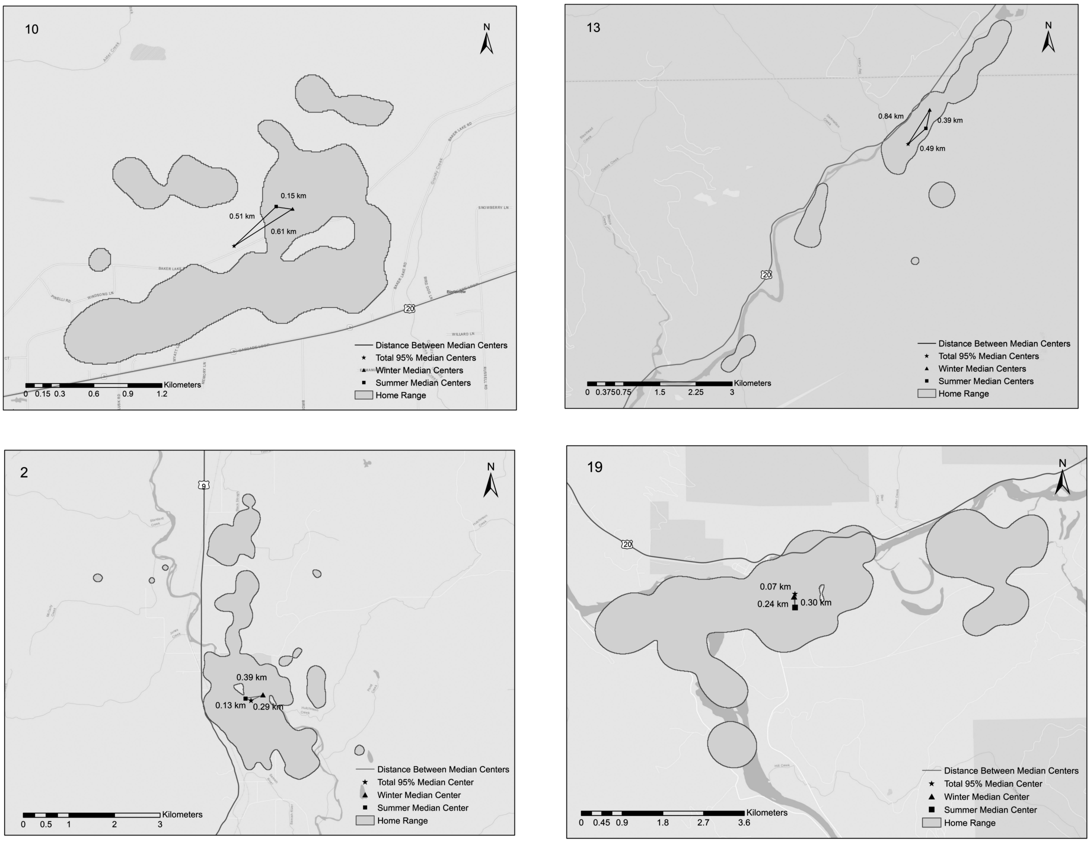

Figure 6. Site fidelity in 95% home ranges represented as summer, winter, and total median center distances (km) for four female elk groups in the North Cascades, Washington.

TABLE 3. Three-dimensional home range overlap of female elk groups calculated using the Utilization Distribution Overlap Index (values > 0 displayed) in the North Cascades, Washington.

Group # A	Group # B	UDOI Value
19	20	1.211
8	9	0.766
11	17	0.669
17	18	0.482
3	21	0.293
11	18	0.119
6	7	0.038
1	14	0.009
1	8	0.001

10 and 12 and 10 and 3 (UDOIs = 0), the incursions into each HR appeared to be clustered near the edges of the ranges with the lowland groups (3 and 12) showing a greater number of incursion tracks into the upland forest group (10). Lowland valley groups 3 and 12 (UDOI = 0) show incursions with a greater number of attempts made by group 3. Forest groups 1 and 8 (UDOI = 0.001) showed almost equal numbers of incursions and track lines were visible using the standard STE bandwidth selection.

Discussion

Our data suggest that female elk groups in the NCEH are sedentary and do not display typical migratory behavior (Shoesmith 1979, Rudd et al. 1983, Brough et al. 2017). This is true for NCEH groups in upland industrial forests and in lowland agricultural areas. Tabor (1976) stated that Rocky Mountain elk translocated to western Washington were non-migratory and remained in lowland areas

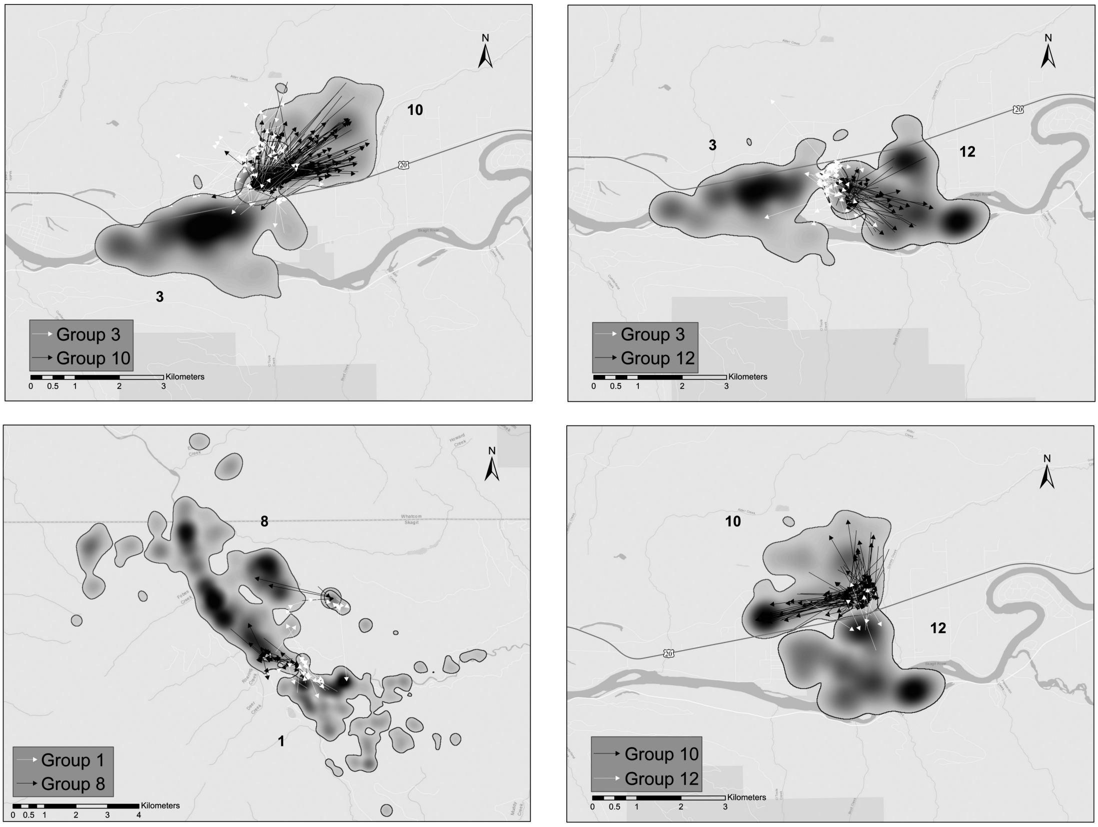

Figure 7. Incursion track lines between 95% home ranges of female elk groups in the North Cascades, Washington. Groups 3 and 12 were located in developed agricultural areas and Groups 1, 10, and 8 were located in industrial forestlands. Utilization Distribution Overlap Index values between all groups except 1 and 8 (UDOI = 0.001) were zero. High density use is represented as dark areas within each home range.

year-round. Our collared elk maintained discrete year-round HRs with well-defined boundaries during the study period regardless of human disturbance. These ranges were relatively small in size and in some cases in close proximity to each other. Consequently, managers can address elk conflict issues by strategizing damage control actions on a group by group basis. Conover (2001) suggests that managing local groups (or sub-herds) in stable habitats as opposed to entire populations is an effective method of reducing wildlife damage complaints.

Given the stable year-round HR distributions, targeted damage hunts or general hunting activities did not appear to influence the spatial organization of female groups across the landscape during our study period (i.e. elk did not leave established HRs during hunting seasons). With an elk herd that is currently between 1400 and 1600 animals, depredation hunts that target approximately 35% of the herd (with a cow preference) should be implemented with caution while the NCEH recovers throughout its range. In addition to controlling group size, understanding high use areas within HRs in elk conflict zones may allow managers to manipulate elk movement and behavior. Core areas are used more frequently than other areas and may contain refuge sites and the most dependable resources (Vander Wal and Rodgers 2009, Van Beest et al. 2001). Given that core areas accounted for ≤ 11% of the overall ranges for all groups, we can target spatially appropriate habitat manipulation strategies. All HRs in agricultural or developed areas contained some conflict properties with elk damage complaints. However, with the exception of group 2, we found that the 50% cores of female groups in more developed agricultural areas were located on known elk friendly or elk tolerant properties. Given these results, managers could use a combination of lethal and non-lethal strategies (e.g. elk exclusion fences and forage enhancement) to regulate group size, block resources, and improve forage quality to minimize elk movement into elk intolerant zones. Our data show that female elk groups recognize elk tolerant zones and will use these areas year-round if stable resources are available. Therefore, managers can work with private and public landowners willing to support elk to create refuge areas along with using harvest as a means of regulating population size. Depredation hunts alone may not be the most effective short-term or long-term strategy in the NCEH range given the year-round home range site fidelity.

In response to methods such as damage hunts or hunter presence, female groups in the NCEH appear to demonstrate a behavioral shift (avoidance effects such as going nocturnal, seeking cover) as opposed to a shift in spatial distribution (Visscher et al. 2017). This means that hunting and hazing activities (regardless of season length) may not be successful at pushing elk groups out of conflict zones. A more effective strategy to reduce conflict and possibly group size is removing access to preferred resources through fencing or landscape changes such as crop selection and habitat enhancement in elk tolerant zones. Nixon et al. (1989) reported that crops closer to cover may be more vulnerable to damage. Given the salmon recovery focus in Washington State, many agricultural lands are adjacent to protected riparian forest. Therefore, altering the landscape in terms of cover habitat removal is not realistic in the NCEH range. In some instances, it may be possible for farmers to plant crops further away from cover to reduce ease of access.

Contrary to other studies that show larger HRs and dispersion patterns in response to human presence (Wertz et al. 1996, Millspaugh et al. 2000, Conner et al. 2001, Vieira et al. 2003), our collared elk maintained small ranges regardless of disturbance (e.g. hunting, hazing, land use). Distances between summer and winter median centers for collared elk groups were ≤ 2 km for 17 of the 21 groups. Bender and Haufler (1999) suggested that a stable resource base influences spatial fidelity on the landscape. Retention of HRs may be due to cognitive approaches such as spatial memory and preference for familiar areas (Greenberg 1984, Linnell and Anderson 1995, Stamps and Karishnan 1999, Wolf et al. 2009) or memory of resource quality (Thorndike 1911). Group organization and stability may be based on group size (mostly by reproduction within the group) and composition through time as social bonds and hierarchies develop (Franklin and Lieb 1979, Geist 2002). The stability and leadership of adult cows may allow the groups to respond to specific changes in the environment (Wilson 1975, Weckerly 1999) and the resulting spatial clustering may reduce competition (Thouless and Guinness 1985, Crampe et al. 2007).

We observed spatial distributions of female elk groups with little overlap. Four groups showed occasional mixing and two groups overlapped enough (UDOI = 1.21) that they were considered a single group. Groups with some social familiarity may combine over time because recent or distant bonds allow for some association (Lieb 1968, Franklin and Lieb 1979). Wiseman et al. (2006) suggested that HR overlap occurred when female offspring established ranges in or near their mother's social group. Spatial attachment and social affinity that develop in the first years of a female's life could explain some of the group overlap and interaction (Crampe et al. 2007). Our incursion maps indicate that several groups were closely organized on the landscape, but not necessarily interacting. This means that groups in conflict zones could be preventing more elk from moving into the area. Managers need to incorporate this concept into management strategies because removal or near removal of an entire female group could allow an adjacent group to move into what may be more desirable habitat. We are recommending a knowledge-based management approach followed by monitoring outcomes and adapting the approach as necessary. The carrying capacity of elk habitat in northwest Washington is not currently limiting the growth and expansion of the NCEH (WDFW 2014). Managers may be most effective at controlling elk in conflict zones on a group by group basis using a combination of techniques to manipulate behavior, block resource access and regulate group size with the overall goal of influencing spatial organization without removing elk from the landscape altogether.

In order to maintain stable female elk groups on the landscape and minimize human-elk conflict, we need to determine if there is a group size threshold and how much harvest a group can sustain before becoming vulnerable to displacement. We also need to investigate habitat composition in core areas and identify associations (e.g. wetlands, forest cover) that are critical for group stability and site fidelity, with consideration of climate change vulnerability. Seasonal fidelity and socially informed movement models (Jonsen et al. 2003, Morales et al. 2004, Haydon et al. 2008) could also help us refine management strategies along with understanding the impacts of dissected habitat by State Route 20.

Acknowledgments

We would like to thank the Skagit Land Trust, Sierra Pacific Industries, Seattle City Light, Puget Sound Energy, Washington Department of Natural Resources, Skagit County, Whatcom County, Coldstream Dairy, Upper Skagit Indian Tribe, Robert and Terry Brown, Mack Judd, John Bates, Barb Trask, and Ger van den Engh for land access for collaring activities. In addition, we thank Sarah Blake of Blake Environmental LLC and Rick Rogers for assistance with GIS analyses and Tribal and State technical staff for assistance with collar applications. Funding for this project was provided by the Stillaguamish Tribe of Indians, Tulalip Tribes, Sauk-Suiattle Indian Tribe, Bureau of Indian Affairs, Puget Sound Energy, and Seattle City Light.

Literature Cited

Anderson, D. P., J. D. Forester, M. G. Turner, J. L. Frair, E. H. Merrill, D. Fortin, J. S. Mao, and M. S. Boyce. 2005. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American Landscapes. Landscape Ecology 20:257-271.

Bender, L. C. 1992. The Michigan elk herd: ecology of a heavily exploited population. Ph.D. Dissertation, Michigan State University, East Lansing.

Bender, L., and J. B. Haufler. 1999. Social group patterns and associations of nonmigratory elk (*Cervus elaphus*) in Michigan. The American Midland Naturalist 142:87-95.

Benkobi, L., M. A. Rumble, C. H. Stubblefield, R. S. Gamo, and J. J. Millspaugh. 2005. Seasonal migration and home ranges of female elk in the Black Hills of South Dakota and Wyoming. The Prairie Naturalist 37:151-166.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76:1075-1085.

Beringer, J., L. P. Hansen, W. Wilding, J. Fischer, and S. L. Sheriff. 1996. Factors affecting capture myopathy in white-tailed deer. Journal of Wildlife Management 60:373-380.

Brough, A. M., R. J. DeRose, M. M. Conner, and J. N. Long. 2017. Summer-fall home-range fidelity of female elk in northwestern Colorado: Implications for aspen management. Forest Ecology and Management 389:220-227.

Bunnell, S. D. 1997. Status of elk in North America: 1975–1995. Rocky Mountain Elk Foundation, Missoula, MT.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Burt, J. E., and G. Barber. 1996. Elementary Statistics for Geographers. Guilford, New York, NY.

Clover, M. R. 1954. A portable deer trap and catch-net. California Fish and Game 40:367-373.

Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. Journal of Wildlife Management 65:926-940.

Conover, M. R. 2001. Effect of hunting and trapping on wildlife damage. Wildlife Society Bulletin 29:521-532.

Craighead, J. J., F. C. Craighead, R. L. Ruff, and B. W. O'Gara. 1973. Home ranges and activity patterns of non-migratory elk of the Madison drainage herd as determined by biotelemetry. Wildlife Monographs No. 33. The Wildlife Society, Washington DC.

Crampe, J. P., R. Bon, J. F. Gerard, E. Serrano, P. Caens, E. Florence, and G. Gonzalez. 2007. Site fidelity, migratory behavior, and spatial organization of female isards (*Rupicapra pyrenaica*) in the Pyrenees National Park, France. Canadian Journal of Zoology 85:16-25.

Donovan, G., and P. Champ. 2009. The economic benefits of elk viewing at the Jewell Meadows Wildlife Area in Oregon. Human Dimensions of Wildlife 14:51-60.

Edge, W. D., and C. L. Marcum. 1985. Effects of logging activities on home range fidelity of elk. Journal of Wildlife Management 49:741-744.

Edge, W. D., C. L. Marcum, S. L. Olson, and J. F. Lehmkuhl. 1986. Nonmigratory cow elk herd ranges as management units. Journal of Wildlife Management 50:660-663.

Fieberg, J., and C. Kochanny. 2005. Research and management viewpoint—quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69:1346-1359.

Franklin, J. F., and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis.

Franklin, W. L., and J. W. Lieb. 1979. The social organization of a sedentary population of North American elk: a model for understanding other populations. *In* M. S. Boyce and L. D. Hayden-Wing (editors), North American Elk: Ecology, Behavior and Management, University of Wyoming, Laramie. Pp. 185-198.

Franklin, W. L., A. S. Mossman, and M. Dole. 1975. Social organization and home range of Roosevelt elk. Journal of Mammalogy 56:102-118.

Fricke, K. A., M. A. Cover, S. E. Hygnstrom, S. R. Groepper, H. H. Genoways, K. M. Hams, and K. C. VerCauteren. 2008. Historic and recent distributions of elk in Nebraska. Great Plains Research 18:189-204.

Geist, V. 1982. Adaptive behavioral strategies. *In* J. W. Thomas and D. E. Toweill (editors), Elk of North America: Ecology and Management, Stackpole Books, Harrisburg, PA. Pp. 698.

Geist, V. 2002. Adaptive behavioral strategies. *In* D. E. Toweill and J. W. Thomas (editors). North American Elk: Ecology and Management, Smithsonian Institution Press, Washington, DC. Pp. 389.

Gower, C. N., R. A. Garrott, P. J. White, F. G. R. Watson, S. S. Cornish, and M. S. Becker. 2009. Spatial responses of elk to wolf predation risk: using the landscape to balance multiple demands. *In*: R. A. Garrott, P. J. White, and F. G. R. Watson (editors), The Ecology of Large Mammals in Central Yellowstone; Sixteen Years of Integrated Field Studies, Academic Press, San Diego, CA. Pp. 373-399.

Greenberg, R. 1984. Neophobia in the foraging-site selection of a Neotropical migrant bird: an experimental study. Proceedings of the National Academy of Sciences 81:3778-3780.

Gulsby, W. D., D. W. Stull, G. R. Gallagher, D. A. Osborn, R. J. Warren, K. V. Miller, and L. V. Tannenbaum. 2011. Movements and home ranges of white-tailed deer in response to roadside fences. Wildlife Society Bulletin 35:282-290.

Haydon, D. T., J. M. Morales, A. Yott, D. A. Jenkins, R. Rosatte, and J. M. Fryxell. 2008. Socially informed random walks: incorporating group dynamics into models of population spread and growth. Proceedings of the Royal Society B 275:1101-1109.

Hegel, T. M., C. C. Gates, and D. Eslinger. 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. Journal of Environmental Management 90:222-235.

Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. MacDonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. Journal of Animal Ecology 74:455-463.

Houston, D. B. 1982. The Northern Yellowstone Elk: Ecology and Management. Macmillan Publishing Company, Inc., New York, NY.

Jacques, C. N., J. A. Jenks, and R. W. Klaver. 2009. Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. Journal of Mammalogy 90:433-441.

Jenkins, K. J., and E. E. Starkey. 1982. Social organization of Roosevelt elk in an old-growth forest. Journal of Mammalogy 63:331-334.

Jones, M. C., J. S. Marron, and S. J. Sheather. 1996. A brief survey of bandwidth selection for density estimation. Journal of the American Statistical Association 91:401-407.

Jonsen, I. D., R. A. Myers, and J. Mills Flemming. 2003. Meta-analysis of animal movement using state-space models. Ecology 84:3055-3063.

Kappler, C., and United States. 1903. Indian affairs. Laws and treaties. 57th Congress (1st session, No. 319, 91st Congress, 2nd session). Washington, DC.

Keating, K. A., and S. Cherry. 2009. Modeling utilization distributions in space and time. Ecology 90:1971-1980.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. *In* J. J. Millspaugh and J. M. Marzluff (editors). Radio Tracking and Animal Populations, Academic Press, San Diego, CA. Pp. 125-166.

Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J. Gaillard, and P. R. Moorcroft. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of the Royal Society B 365:2221-2231.

Knowlton, F. F., E. M. Gese, and M. M. Jaegere. 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52:398-412.

Kolbe, N. R., and F. W. Weckerly. 2015. Home-range overlap of Roosevelt elk herds in the Bald Hills of Redwood National Park. California Fish and Game 101:208-217.

Kricher, J. C., and W. E. Davis. 1998. Species richness and site fidelity among resident Neotropical birds. The Southwestern Naturalist 43:228-233.

Kuhn, H. W., and R. E. Kuenne. 1962. An efficient algorithm for the numerical solution of the Generalized Weber Problem in spatial economics. Journal of Regional Science 4:21-33.

Lieb, J. 1968. Aggression in the social behavior of Roosevelt elk. California-Nevada Section TWS Transactions, Humboldt State College, Arcata, CA.

Lieb, J. 1973. Social behavior in Roosevelt elk cow groups. M.S. Thesis, Humboldt State College, Arcata, CA.

Link, R. 2004. Living With Wildlife in the Pacific Northwest. University of Washington Press, Seattle.

Linnell, J. D. C., and R. Andersen. 1995. Site tenacity in roe deer: short-term effects of logging. Wildlife Society Bulletin 23:31-36.

Long, J. A., S. L. Webb, T. A. Nelson, and K. L. Gee. 2015. Mapping areas of spatial-temporal overlap from wildlife tracking data. Movement Ecology 3:38-61.

Mahoney, P. J., and J. K. Young. 2017. Uncovering behavioral states from animal activity and site fidelity patterns. Methods in Ecology and Evolution 8:174-183.

Marzluff, J. M., S. T. Knick, and J. J. Millspaugh. 2001. High-tech behavioral ecology: modeling the distribution of animal activities to better understand wildlife space use and resource selection. *In* J. J. Millspaugh and J. M. Marzluff (editors). Radio Tracking Animal Populations, Academic Press, San Diego, CA. Pp. 309-326.

McCall, T. 1996. Final environmental impact statement for the Washington State management plan for elk. Washington Department of Fish and Wildlife, Wildlife Management Program, Olympia.

McCorquodale, S. M. 2013. A brief review of the scientific literature on elk, roads, and traffic. Washington Department of Fish and Wildlife, Olympia.

McCullough, D. R. 1975. Modification of the clover deer trap. California Fish and Game 61:242-244.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing. Journal of Wildlife Management 64:994-1003.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2004. Herd organization of cow elk in Custer State Park, South Dakota. Wildlife Society Bulletin 32:506-514.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. EEB Articles. Available online at http://digitalcommons.uconn.edu/eeb_articles/4 (accessed 18 April 2018).

Murie, A. 1951. The Elk of North America. Stackpole Company, Harrisburg, PA.

Myers, W. L., W. Y. Chang, S. S. Germaine, W. M. Vander Haegen, and T. E. Owens. 2008. An analysis of deer and elk-vehicle collision sites along state highways in Washington State. Washington Department of Fish and Wildlife, Olympia.

Nixon, C. M., L. P. Hansen, P. A. Brewer, and J. E. Chelsvig. 1989. Ecology of white-tailed deer in an intensively farmed region of Illinois. Wildlife Monographs 118:1-77.

Ortega, Y. K., K. S. McKelvey, and D. L. Six. 2006. Invasion of an exotic forb impacts reproductive success and site fidelity of a migratory songbird. Oecologia 149:340-351.

Peterson, L. M., and F. W. Weckerly. 2017. Male group size, female distribution and changes in sexual segregation by Roosevelt elk. PLoS ONE 12:e0187829.

Piper, W. 2011. Making habitat selection more "familiar": a review. Behavioral Ecology and Sociobiology 65:1329-1351.

Powell, R. A., and M. S. Mitchell. 2012. What is home range? Journal of Mammalogy 93:948-958.

Raedeke, K., J. Millspaugh, and P. Clark. 2002. Population characteristics. *In* D. E. Toweill and J. W. Thomas (editors). North American Elk: Ecology and Management, Smithsonian Institute Press, Washington, DC. Pp. 449-491.

Relyea, R. A., R. K. Lawrence, and S. Demarais. 2000. Home range of desert mule deer: testing the body size and habitat productivity hypothesis. Journal of Wildlife Management 64:146-153.

Reynolds, T. D. 1984. Daily summer movements, activity patterns, and home range of pronghorn. Northwest Science 58:300-310.

Roper, L. A., R. L. Schmidt, and R. B. Gill. 1971. Techniques of trapping and handling mule deer in northern Colorado with notes on using automatic data processing for data analysis. Proceedings of the Western Association of Game and Fish Commissioners 51:471-477.

Rudd, W. J., A. L. Ward, and L. L. Irwin. 1983. Do split hunting seasons influence elk migrations from Yellowstone National Park? Wildlife Society Bulletin 11:328-331.

Sacks, B. N., M. M. Jaeger, J. C. C. Neale, and D. R. McCullough. 1999. Territoriality and breeding status of coyotes relative to sheep predation. Journal of Wildlife Management 63:593-605.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analyses. Ecology 77:2075-2085.

Shoesmith, M. W. 1979. Seasonal movements and social behavior of elk on Mirror Plateau, Yellowstone National Park. *In* M. S. Boyce and L. D. Hayden-Wing (editors). North American Elk: Ecology, Behavior and Management, University of Wyoming, Laramie, WY. Pp. 166-176.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663-688.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Monographs on Statistics and Applied Probability, Kluwer Academic Publishers, London, UK.

Stamps, J. A., and V. V. Karishnan. 1999. A learning-based model of territory establishment. Quarterly Review of Biology 74:291-318.

Stubblefield, C. H., K. T. Vierling, and M. A. Rumble. 2006. Landscape-scale attributes of elk centers of activity in the Central Black Hills of South Dakota. Journal of Wildlife Management 70:1060-1069.

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533-555.

Tabor, R. D. 1976. Seasonal landscape use by elk in the managed forests of the Cedar River drainage, western Washington. Washington Department of Fish and Game, Olympia.

Thompson, M. J., R. E. Henderson, T. O. Lemke, and B. A. Sterling. 1989. Evaluation of a collapsible clover trap for elk. Wildlife Society Bulletin 17:287-290.

Thorndike, E. L. 1911. Animal Intelligence. The Macmillan Company, Toronto.

Thouless, C. R., and F. E. Guinness. 1985. Conflict between red deer hinds: the winner always wins. Animal Behavior 34:1166-1171.

US Climate Data. 2018. Temperature—Precipitation—Sunshine—Snowfall. Available online at https://www.usclimatedata.com (accessed 03 December 2018).

Van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2001. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? Journal of Animal Ecology 80:771-785.

Van Beest, F. M., E. Vander Wal, A. V. Stronen, P. Co. Paquet, and R. K. Brook. 2013. Temporal variation in site fidelity: scale dependent effects of forage abundance and predation risk in a non-migratory large herbivore. Oecologia 173:409-420.

Vander Wal, E., and A. R. Rodgers. 2009. Designating seasonality using rate of movement. Journal of Wildlife Management 73:1189-1196.

Van Dyke, F. 2007. Colonization of non-traditional range in dispersing elk, *Cervus elaphus nelsoni*, populations. Canadian Field Naturalist 121:133-141.

Vieira, M. E. P., M. M. Conner, G. C. White, and D. J. Freddy. 2003. Effects of archery hunter numbers and opening dates on elk movement. Journal of Wildlife Management 67:717-728.

Visscher, D. R., I. MacLeod, K. Vujnovic, D. Vujnovic, and P. D. DeWitt. 2017. Human risk induced behavioral shifts in refuge use by elk in an agricultural matrix. Wildlife Society Bulletin 41:162-169.

Walter, W. D., M. J. Lavelle, J. W. Fischer, T. L. Johnson, and S. E. Hygstrom. 2010. Management of damage by elk (*Cervus elaphus*) in North America: a review. Wildlife Research 37:630-646.

Wand, M. P., and M. C. Jones. 1994. Kernel Smoothing. Chapman and Hall, London.

Wand, M. P., and M. C. Jones. 1995. Kernel Smoothing. Monographs on Statistics and Applied Probability, Chapman and Hall, New York, NY.

Washington Department of Fish and Wildlife. 2002. North Cascade (Nooksack) elk herd. Washington Department of Fish and Wildlife, Olympia.

Washington Department of Fish and Wildlife. 2014. Final supplemental environmental impact statement for the 2015-2021 game management plan. Washington Department of Fish and Wildlife, Olympia.

Washington Department of Fish and Wildlife. 2015. Washington's state wildlife action plan: 2015 update. Washington Department of Fish and Wildlife, Olympia.

Washington Department of Fish and Wildlife. 2017. Draft North Cascades elk management plan. Washington Department of Fish and Wildlife, Olympia.

Washington Department of Game. 1939. Washington elk report. Washington Department of Game, Seattle.

Weckerly, F. W. 1999. Social bonding and aggression in female Roosevelt elk. Canadian Journal of Zoology 77:1379-1384.

Wertz, T. L., A. Blumton, L. E. Erikson, L. M. Kemp, and T. Thomas. 1996. Strategies to keep wildlife where you want them—do they work? *In* K. E. Evans (editor), Sharing Common Ground on Western Rangelands: Proceedings of a Livestock/Big Game Symposium. United States Forest Service, Intermountain Research Station, Ogden, Utah. Pp. 70-72.

White, G. C., and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego, CA.

Wilson, E. O. 1975. Sociobiology: The New Synthesis. Belknap Press, Cambridge.

Wiseman, P. A., M. D. Carling, and J. A. Byers. 2006. Frequency and correlates of birth-site fidelity in pronghorns (*Antilocapra americana*). Journal of Mammalogy 87:312-317.

Wittmer, H. U., B. N. McLellan, and F. W. Hovey. 2006. Factors influencing variation in site fidelity of woodland caribou (*Rangifer tarandus caribou*) in southeastern British Columbia. Canadian Journal of Zoology 84:537-545.

Wolf, M., J. Frair, E. Merrill, and P. Turchin. 2009. The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. Ecography 32:401-410.

Received 30 April 2018
Accepted 11 October 2018