Summer-fall home-range fidelity of female elk in northwestern Colorado: Implications for aspen management

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ABSTRACT

Understanding the degree of spatial fidelity exhibited by individuals within a species increases our ability to manage for desired future outcomes. Elk (Cervus elaphus) is a closely managed species in the Western US, but there is little research evaluating their summer home-range fidelity. Elk summer-fall home-ranges overlap considerably with aspen (Populus tremuloides)-dominated forest types, and elk can impact aspen regeneration because it is a preferred browse species. We evaluated the fidelity of 72 adult female elk to individual summer-fall home ranges in northwestern Colorado, USA, during two consecutive summers (1996 and 1997). To compare elk summer-fall home-range overlap and distribution based on individual kernel-estimated utilization distributions, we calculated the volume-of-intersection statistic and the inter-annual distances between centers-of-mass. We found adult female elk in the White River Study area exhibited strong fidelity to individual home ranges. Volume-of-intersection results indicated that 93% of the elk showed explicit home-range overlap between 1996 and 1997, but that all the elk returned to the same vicinity as the previous year (median = 0.42, SE = 0.02, n = 72). Between-year center-of-mass distances ranged from 183 m to 34,170 m (mean = 3819, SE = 619, n = 72), while within-year maximum distances between location points ranged from 4320 m to 31,680 m (mean = 13,958, SE = 628, n = 72). Hunting increased the distance traveled by individual elk, but did not change the center of their home-range. Understanding female elk home-range fidelity could influence forest management focused on aspen regeneration. Specifically, targeted removal of female elk from their summer-fall home ranges could create a 'window of opportunity' in which browsing pressure was reduced, and the likelihood of aspen recruitment increased.

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1. Introduction

The fidelity of an individual animal to a specific area, or philopatry, is often characterized in terms of home-range fidelity, or site fidelity. Philopatric behavior is thought to enhance individual fitness because adaptation to an area through evolution or learned behavior increases the likelihood of survival and/or reproductive success (Part, 1991). This is in direct contrast to nomadic ungulates such as the North America bison (Bison bison) whose space-use patterns are much less predictable (Knapp et al., 1999). Philopatric behavior is a common home-range procurement strategy across taxa (e.g., birds, bats, skinks, and squirrels; Brown et al., 2004; Haughland and Larsen, 2004; Stow and Sunnucks, 2004; Veilleux

and Veilleux, 2004). One example among ungulates is white-tailed deer (Odocoileus virginianus) in the eastern United States; female offspring return to the same vicinity as their mother's summer home range and establish an individual home range to which they are extremely faithful (Ozoga et al., 1982; Sage et al., 2003). This intergenerational, matriarchal mosaic of home ranges is referred to as the Rose Petal effect (Matthews, 1989), and suggests that animal density can vary locally as a function of spatially variable survival rates. Understanding philopatric behavior is important; as we improve our understanding of the spatial fidelity of individuals, we may more effectively manage critical habitats to sustain desirable species.

Elk (Cervus elaphus) are an economically important ungulate in the Intermountain West and are managed for high densities to support maximum hunting opportunity, but also aesthetics, species diversity, and associated habitat. Short-term and long-term studies have demonstrated herd fidelity to summer-fall ranges, as elk are

much less faithful to their winter range (Benkobi et al., 2005; Craighead et al., 1973; Edge et al., 1987; Hershey and Leege, 1982; Irwin and Peek, 1983; Knight, 1970), specific patterns of habitat use (Anderson et al., 2005; McCorquodale, 2003; Millspaugh et al., 2004), and have typically been conducted using locations from radio-collared elk. Although these studies described elk space use, to our knowledge only one has specifically addressed individual home-range fidelity (Webb et al., 2011).

Elk in the Interior West have large annual home-ranges, spending time in lower elevation sagebrush steppe communities during the winter, and higher elevation mid- to upper-montane forested communities during the summer and fall (Conner et al., 2001). Elk migrate to summer ranges predicated on energetic demands associated with calving (Beck et al., 2006). During the post-partum period, elk must acquire sufficient nutrients to support lactation and build fat reserves for the oncoming winter (Green and Bear, 1990). Elk exhibit a divers feeding spectrum and are considered generalists, as they readily browse as availability dictates (Hofmann, 1989). For example, shifting between grass an woody plants depending on nutrient content, including young aspen (Canon et al., 1987), and in particular when competition for other forage is strong. Consequently, female elk on summer-fall ranges are consuming large quantities of high quality forage, of which aspen is both widely available and highly palatable. Moreover, they occur in dense herds which leads to substantial local impacts on aspen regeneration.

Ungulate herbivory has long been known to exert impacts in managed forests (e.g., Lyon and Jensen, 1980), but more recently has been hypothesized to have strong negative impacts on the regeneration, composition, and associated ecological services of aspen communities, whether after fire, regeneration harvests, or in unmanaged settings (Baker et al., 1997; Britton et al., 2016; Fairweather et al., 2014; Rogers and Mittanck, 2014). In the Western US, the distribution of quaking aspen occurs in vegetation communities across the range of elk distribution, e.g., from sagebrush to spruce-fir forests. Moreover, aspen is the only canopy dominant deciduous hardwood tree in much of the Interior West. Because aspen is an important, keystone species—providing a disproportionate amount of biodiversity, ecosystem functioning (e.g., water holding capacity), forage for wildlife and livestock, and aesthetics, and is the subject of concern regarding its spatial distribution and abundance (Rogers and Clair, 2016), – possible management tools focused on the maintenance and/or reproduction of aspen are highly desirable.

As has been observed for white-tailed deer (*Odocoileus virginianus*) in the eastern U.S. (Campbell et al., 2004; Oyer and Porter, 2004), the degree to which individual elk exhibit fidelity to summer-fall range could aid management decisions regarding where and when to conduct regeneration treatments, and whether and how elk should be locally controlled to ensure timely regeneration. If summer-fall home-ranges of female elk occurred in aspen-dominated communities where regeneration harvests were planned, managers could take advantage of the fidelity concept to create 'windows of opportunity' for regenerating aspen (*sensu* Sage et al., 2003) by selectively removing a limited number of elk. Because elk in the Western U.S. typically spend a substantial amount of time in aspen-dominated communities, a demonstration of home-range fidelity would open a new tool box of management potential based on sub-population-level targeted removal.

We evaluated the fidelity of individual elk to their summer-fall home-range, specifically focusing on adult female elk in the migratory White River herd of northwestern Colorado, USA. To evaluate spatial fidelity, we assessed overlap of summer-fall home ranges for 72 elk across two consecutive summers using data that were originally collected to study the impacts of hunting on elk movement to private land in the late summer. We asked the question,

to what degree do individual female elk return to the same home range in subsequent years? We hypothesized that female elk would return to the same place each year. Furthermore, because individual home-range fidelity could be influenced by changes in hunting seasons, we also addressed potential changes in home-range fidelity due to the timing of hunting. We hypothesized that hunting would act as a disturbance and alter home-range fidelity of individual elk.

2. Methods

2.1. Study area

The White River study area was located in northwestern Colorado and covered approximately 4540 km^2 (Fig. 1). Ownership was 34% private land and 66% public land managed by the Bureau of Land Management or the United States Forest Service. The study area represented a major portion of the Colorado Division of Wildlife (CDOW) elk population Data Analysis Unit E-6 but was limited to the western portion of E-6 as demarcated by Game Management Units (GMU) 12, 23, 24, and 33 (CDOW, 2005). A diversity of public land uses in this area included hiking and camping recreation, timber sales, domestic livestock grazing, hunting, and limited surface coal mining. Elevation in the study area ranged from 1600 to 3700 m. The central and eastern portions of the study area contained high elevation sub-alpine and alpine areas commonly used by elk during the summer. Generally, terrain was moderately steep north of the White River (GMU 12) while large and gorge-like canyons were more common south of the White River (GMU 33) (Fig. 1). Elevation declined from east to west, with elk winter ranges located in the western portions of the study area in the lower White River.

Climate at higher elevations of the study area was characterized by long-term mean temperatures for July and January of 14 °C and −8 °C; mean annual precipitation of 70 cm, and average total snowfall of 527 cm (Marvine Ranch Station, 2379 m elevation, WRCC, 2006). At lower elevations within the study area, mean temperatures for July and January were 19 °C and −6 °C; mean annual precipitation was 42 cm, and average total snowfall was 177 cm (Meeker COOP Station, 1903 m elevation, WRCC, 2006). Precipitation during the first study year (1996) did not vary greatly from the 100-year average. However, the precipitation in the second study year (1997) increased substantially during the July – October period with 14 cm received in September compared to the long-term average of 4 cm in that month. Temperatures during both study years were close to the 100-year averages. As result range conditions for herbivores were likely average or slightly above average during the study time period.

Vegetation composition in the higher montane/subalpine zones (>2600 m) consisted of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and aspen (*Populus tremuloides*) interspersed with meadows of grasses and sagebrush (*Artemisia* spp.), common for spruce-fir forest types of the Interior West (Peet, 2000). Vegetation at mid-elevations of 2000– 2600 m included aspen woodlands, Gambel oak (*Quercus gambelii*) shrubland, and woodlands of pinion (*Pinus edulis*) - juniper (*Juniperus scopulorum*). Sagebrush steppe, grasslands, and agriculture were prevalent at elevations lower than 2000 m. Aspen-dominated forest types covered 23% of the study area and were primarily located between 2000 m and 3400 m (CDOW, 2005; United States Geological Survey, 2004).

Elk in the White River population were considered migratory. Spring migration from winter to summer range commenced in April, calving occurred during late May and into June, usually at mid-elevations. Elk occupied summer ranges from June into
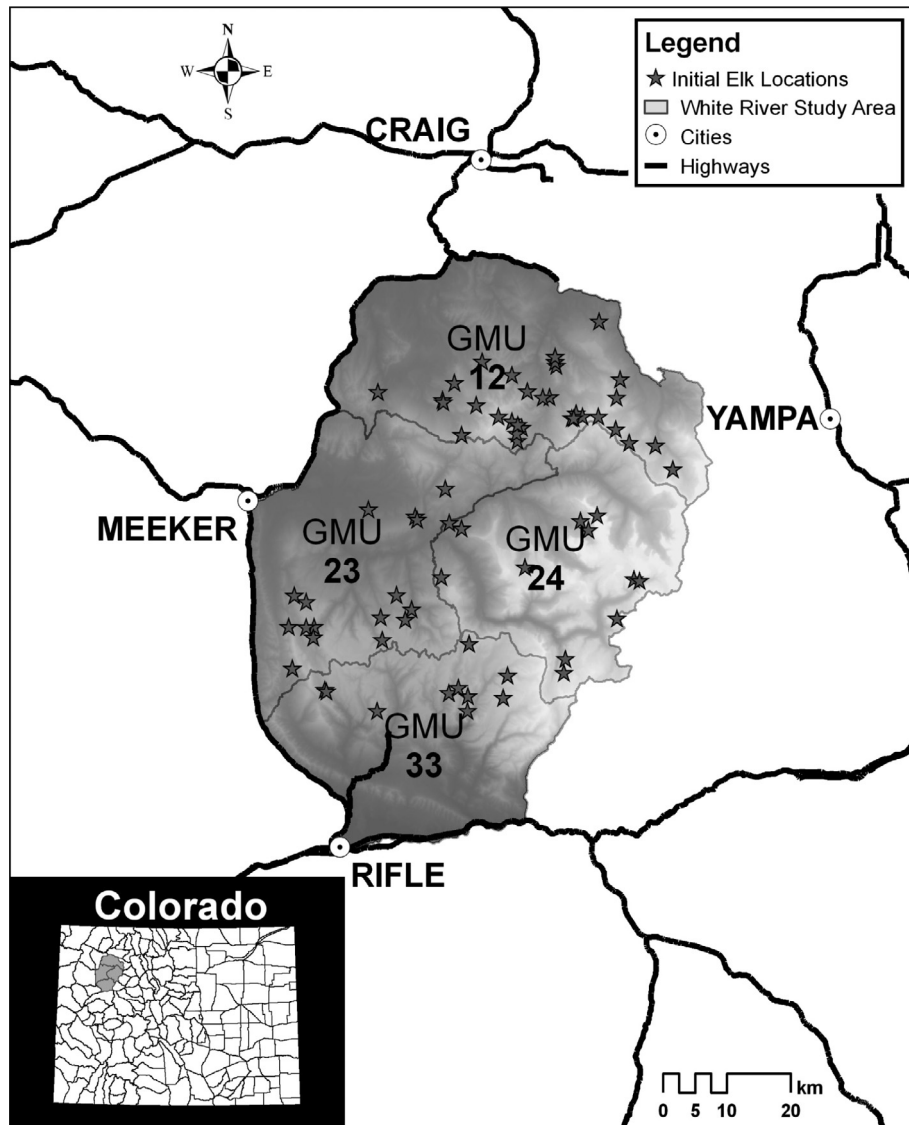
Fig. 1. The White River study area located in Western Colorado and initial elk capture locations.

September, and began migrating back to winter ranges in October (USDA, 2002). During 1996 and 1997 detailed population estimates for the 4 GMUs in the study area were ~25,000–30,000 elk (CDOW, unpublished data). Based on total elk population estimates for the E-6 Data Analysis Unit (from 2005 through 2015) (http://cpw.state.co.us/thingstodo/Pages/Statistics-Elk.aspx), elk in our White River study area represented 64–76% of the unit total. Previous work that has detailed the study area and elk population estimates (Boyd, 1970; Freddy, 1987) indicated that due to the generally remoteness of the area random effects on the spatial distribution of elk (e.g., climate, depredation, human activity) were negligible (Conner et al., 2001).

2.2. Data collection

Eighty adult, female elk (⩾2 years old) residing in the White River study area (Fig. 1) during July 1996 were captured and radio-collared to evaluate the effects of the timing of fall hunting seasons on elk movements. Elk were captured near randomly chosen locations distributed throughout the study area using a helicopter and net-gunning. Although some capture constraints existed due to private land access and time, a reasonably representative spatial sample was obtained (Fig. 1).

For the current study, we only used data for the 72 females located during both summers. Between 20 July and 10 October, each female was relocated twice a week (every 2–4 days) between 0700 and 1500 h using fixed-winged aircraft (Conner et al., 2001). Mean telemetry plus aircraft Global Positioning System (GPS) error was 333 m (95% CI = 265–401) based upon 24 blind tests conducted on randomly located radio collars (Conner et al., 2001).

The original study included purposeful manipulations of hunting seasons to test the effects on elk movement. The study area was divided in half to create two treatment areas: north and south. In 1996, archery hunting opened 1 week early in the south area (24 August) and 2 weeks late in the north (14 September). Treatments were reversed in 1997, with archery hunting opening early in the north area (23 August) and late in the south (13 September). A detailed description of the original study design can be found in Conner et al. (2001).

2.3. Data analysis

We obtained 20–23 relocations per female during each summer-fall monitoring period. We used the 95% fixed-kernel home range estimator with least squares cross-validation to estimate home ranges based on factors of required sample size, utilization calculation, nonparametric estimation, and sensitivity to outliers (Kernohan et al., 2001; Seaman et al., 1999; Seaman and Powell, 1996). Although we had a relatively low number of observations per animal, the fixed-kernel estimator provided the least biased estimates of home ranges (Seaman et al., 1999). Home ranges were represented by calculating 95% utilization distributions (UDs) using the Animal Movement ArcView Extension (Hooge and Eichenlaub, 2000) in ArcView (version 3.3). To evaluate inter-annual fidelity of individual females to a home range, we calculated the overlap between the 1996 and 1997 UDs for each female using the Volume of Intersection (VI) index statistic (Millspaugh et al., 2004; Seidel, 1992). This index represents the overlap between UDs according to:

$$VI = \iint \min(\hat{f}_1(x,y), \hat{f}_2(x,y)) dx dy$$

where $\hat{f}_1$ is the 1996 UD for an individual elk and $\hat{f}_2$ is the 1997 UD for the same individual. The VI value was bounded between 0 and 1, where 1 represented maximum overlap. A VI value equal to 0 indicated that none of the area used by the female in 1996 (as represented by the 1996 UD) overlapped with the area used in 1997. A VI value equal to 1 indicated that the female used exactly the same area during the summers of 1996 and 1997. To obtain VI values, we first converted the UDs to grids in ArcView 3.3. We then used the VI_V4.aml script (Fieberg et al., 2005; Millspaugh et al., 2004) in ArcInfo Workstation (version 9.1). We considered any non-zero VI value as indicative of summer-fall home-range fidelity (*sensu* McCorquodale, 2003).

As an additional metric of home-range fidelity, we calculated the distance between centers-of-mass (COM) for the 1996 and the 1997 UD for each elk, as well as the maximum distance between locations within the home range of each elk for each year. We first calculated the COM for each UD using the Center of Mass extension V.1.b in ArcView 3.3 (Jenness, 2006). We then calculated the Euclidean distance between the 1996 and 1997 COM for an individual elk using ArcMap (version 9.1). A distance equal to 0 signified that the COM of the 1997 UD was in exactly the same location as the COM of the 1996 UD, indicating that the elk was returning to the same location inter-annually. A large distance between COM signified a change in home range location between 1996 and 1997. We used the maximum within-year distance across the calculated home-range as a reference to quantify distances between COM as being small or large. That is, if the maximum within-year distance was less than the between-year COM distance, then there was little support for elk fidelity. Conversely, if the between-year distance was much less than the maximum within-year distance, then elk fidelity was supported. The maximum within-in year distance could occur in either 1996 or 1997 and varied for each elk. To evaluate support for elk fidelity based on within- and between-year distances, we used a paired *t*-test (within elk) for the following null and alternative hypotheses:

H1$_O$. Mean within-year maximum distance $\leqslant$ mean between-year COM distance.

H1$_A$. Mean within-year maximum distance > mean between-year COM distance.

After performing the analysis above, we repeated the procedure with a subset of the elk locations, excluding any elk locations collected after the start of the area-specific hunting season. We compared hunting and non-hunting data using 2×2 contingency tables, which we analyzed using a chi-square test (χ) for difference between two medians, because the sample sizes were small and non-normally distributed (Zar, 1999). This analysis allowed us to evaluate possible effects on our assessment of elk home-range fidelity due to elk movement as influenced by hunting season. We specifically evaluated the hypotheses:

H2$_O$. Non-hunting median within-year maximum distance $\leqslant$ hunting median within-year maximum distance.

H2$_A$. Non-hunting median within-year maximum distance > hunting median within-year maximum distance.

And

H3$_O$. Non-hunting median between-year COM distance $\leqslant$ hunting median between-year COM distance.

H3$_A$. Non-hunting median between-year COM distance > median hunting between-year COM distance.

3. Results

The distribution of VI values (Fig. 2) indicated that 93% of the females (67 of 72) exhibited some degree of home-range overlap between the summers of 1996 and 1997. Actual UD overlap varied widely, as VI values ranged from zero (no overlap, e.g., Fig. 3i) to 0.81 (nearly complete overlap, Fig. 3a), with a median value of 0.42 (SE = 0.02, n = 72). Although 5 females had zero overlap between 1996 and 1997, they were located within the same general area during both years (Fig. 3i). Many UDs were fairly typical in shape, size and relative location (Fig. 3b–h), while others illustrated more diversity (Fig. 3a and i). The distribution of location points varied greatly among females, ranging from highly clustered to more uniformly dispersed, and from single to multiple activity centers. Because the relative distance between points heavily influences UD shape, some UDs consisted of a single polygon (e.g., Fig. 3a) while other UDs consisted of multiple polygons (e.g., Fig. 3f).

The area of UD varied widely among females (e.g. Fig. 3c and d). For example, areas of the 1996 UDs ranged from 821 to 28,092 ha (mean = 7185, SE = 619, n = 72), while areas of the 1997 UDs ranged from 726 to 46,254 ha (mean = 6356, SE = 809, n = 72). Areas for 1996 and 1997 UDs were significantly different (t_{71} = 2.83, P = 0.006). While some females had similar UD sizes between years (e.g., Fig. 3a), other females exhibited large variation in range size with a larger UD occurring in either 1996 or 1997 (e.g., Fig. 3b and h, respectively).

Distances between the 1996 and 1997 COM distances ranged from 183 m to 34,170 (mean = 3819, SE = 619, n = 72), with a median of 2108 m. Distances between COM were negatively associated with VI overlap (Fig. 4; P $\leqslant$ 0.001). Within-year maximum distances between location points (occurring in either 1996 or 1997) ranged from 4320 m to 31,680 m (mean = 13,958, SE = 628, n = 72), with a median of 13,024 m. The within-year maximum distances were, on average, 3.7 times greater than the COM distances (t_{71} = 13.15, P $\leqslant$ 0.001).

Chi-squared analysis indicated that a significant difference existed between within-year hunting and no-hunting maximum distance calculations (χ21 = 12.25, P $\leqslant$ 0.001) such that maximum
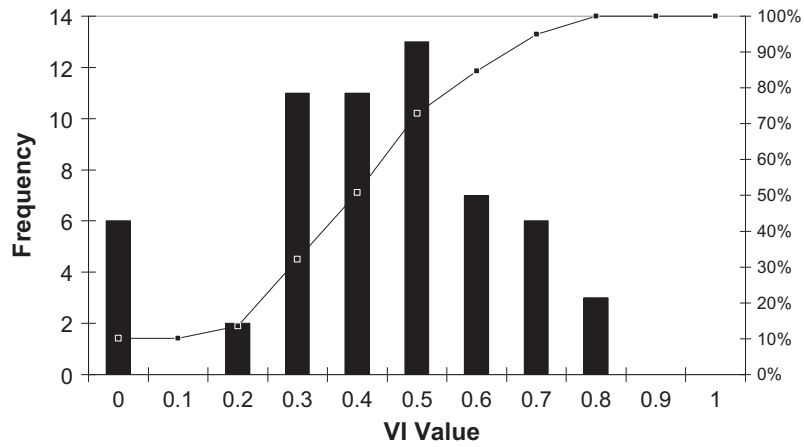
Fig. 2. Distribution of volume of intersection (VI) values for adult female elk in the White River area of Colorado during July 15–Oct 15, separated for 1996 and 1997. VIs were based on utilization distributions calculated with a kernel estimator. Solid line represents the cumulative distribution function of VI.
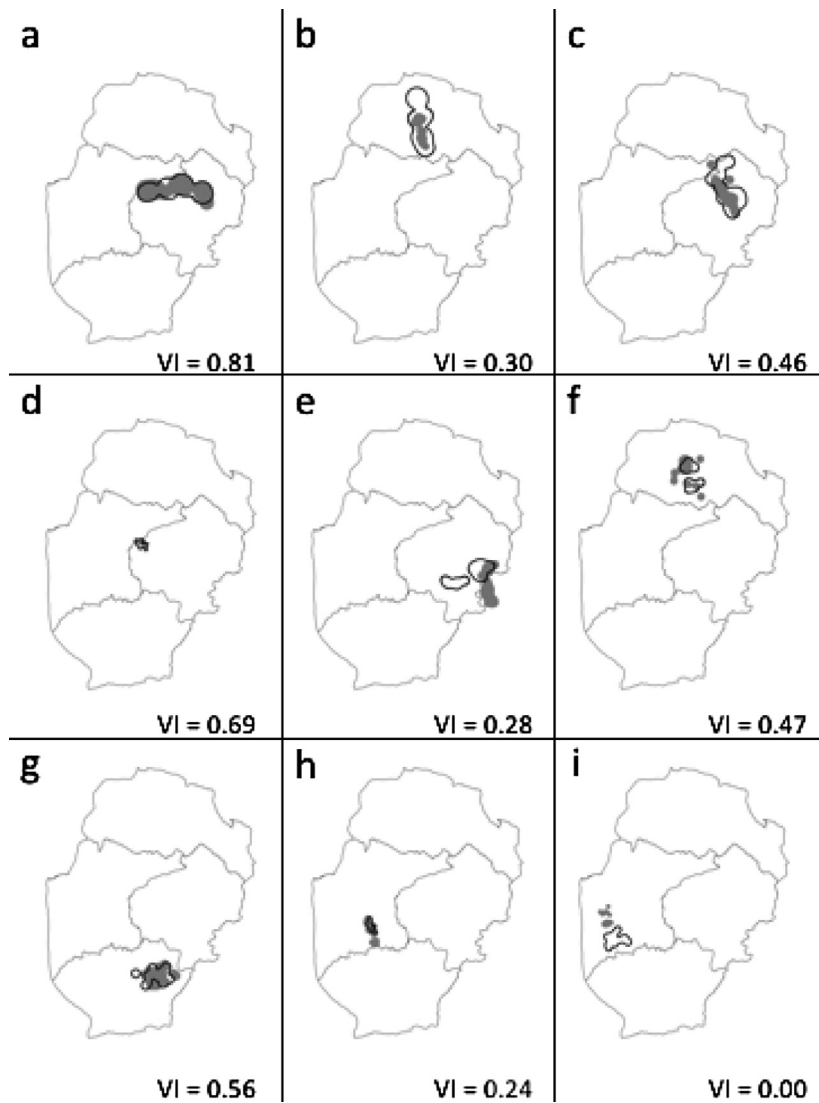

Fig. 3. Example utilization distributions (UDs) for 1996 (filled polygons) and 1997 (hollow polygons) for nine adult female elk in the White River area of Colorado. Volume of Intersection (VI) values are displayed for each elk. (b)–(h) were fairly typical of UD shape, size and relative location in this study while (a) and (i) were selected to illustrate the diversity of UDs. Data are from radio telemetry locations collected July-October in 1996 and 1997.
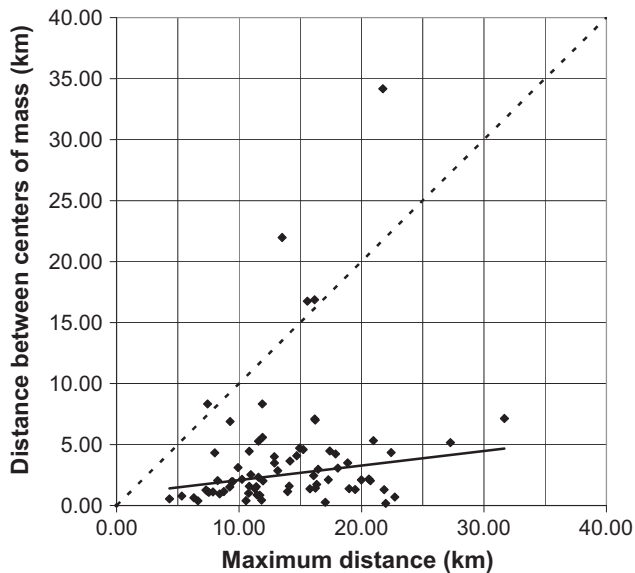
Fig. 4. Distances between 1996 and 1997 centers of mass (COM) versus maximum distance between points within a given year (linear regression does not include elk with VI = 0). The dashed line indicates where the center of mass and maximum distance between points is equal; points above the line indicate female elk for which the distance between the center of mass between years was greater than the maximum distance between points within years, while points below indicate maximum distance between points was greater.

distances decreased when hunting locations were excluded. Distances between the 1996 and 1997 COM (calculated without points collected during hunting season) ranged from 110 m to 32,876 m (mean = 3796, SE = 605, n = 72), with a median of 2076 m. Exclusion of hunting location points did not substantially alter distances related to COM. No significant difference existed between hunting and no-hunting COM distance calculations ($\chi^2_1 = 0.03$, P = 0.867). The between-year median distance in COM for all 72 elk (2108 m) was only 16% as large as the within-year median maximum distance across an elk home-range (∼13,024 m).

4. Discussion

We found that individual adult female elk strongly exhibit inter-annual fidelity to summer-fall home ranges, which we associate with philopatric social behavior. Although there was considerable variation in UD size, UD shape, and VI value, 93% of the 72 elk returned in 1997 to at least some portion of the exact area they occupied in 1996. Furthermore, all 72 elk returned to the same vicinity occupied during the previous year. Each of the 67 females that had a non-zero VI value exhibited a COM distance of less than 8 km. There was low support for the null hypothesis (H1$_O$) that within-year maximum distance was less than between-year COM distance (P = 0.074). Rather, while variable, the within-year median maximum distance across an elk home-range (∼13,024 m) was substantially larger than the between-year median distance in COM (2108 m), providing support for hypothesis H1$_A$. Collectively, these results suggest adult female elk are philopatric to their summer-fall home range. However, the analysis and results do not address home-range fidelity during the winter when elk are thought to be less philopatric. Our results are similar to the findings of Webb et al. (2011), wherein elk were found to have strong core home-range fidelity, even in the face of human development. Such a strong, predictable pattern of home-range fidelity in adult female elk suggest they are not nomadic during the growing season, when young aspen are vulnerable to herbivory, and this might

lend itself to a sub-population-level approach to management that targets adult females in areas where reduced browsing pressure is desired to regenerate aspen.

As further support for elk home range fidelity, the chi-squared tests underscored a contrast in space use when hunting period was excluded from analyses. The original study found that hunting season start dates influenced elk movement in the White River study area (Conner et al., 2001). Our study corroborated this result, as the maximum distance traveled by an elk within the summer-fall of a given year decreased when the hunting locations were excluded from analysis, supporting hypothesis H2$_O$. Interestingly, we found no significant change in the between-year COM distance when hunting season locations were excluded (no support for H3$_O$ or H3$_A$). This indicates that although hunting pressure forces greater overall movement by an elk within a given year, the home-range center remained fixed, suggesting home-range fidelity even under disturbance scenarios. This result also confirms that the purposeful manipulations of hunting season during 1996 and 1997 likely did not alter elk home-range fidelity.

The VI calculation was generally illustrative of the degree of fidelity for an individual elk. While we made a distinction between non-zero (93%) and zero values (7%) in this study, visual inspection of UDs for elk with VI values equal to zero indicated even these elk were still returning to the same general vicinity, which was also indicated by COM values (Fig. 3). Similarly, elk that exhibited VI values that might be considered "low" (e.g., VI = 0.24 in Fig. 3h) still offered substantial support for home-range fidelity. Another ambiguity arose from UD size. As expected given the nature of the VI formula, small UDs with a high degree of overlap produced the same VI value as large UDs with a high degree of overlap (e.g., Fig. 3d and g, respectively). Without some estimate of distance between home-range location from year to year, the degree of overlap is not fully interpretable.

It is also apparent that a given VI value can represent various ecological situations. Interpreting VI values independent of COM or a similar complementary spatial analysis may lead to misinterpretation of ecological relevance. For example, UDs that were similar in size but offset in location (e.g., Fig. 3e) could produce the same VI value as UDs that were "concentric" yet varied in size (e.g. Fig. 3b). The difference in the location of overlap could hold important information; if the non-overlap section were to fall on different habitat than the overlap section, it might imply that fidelity is based on social dynamics rather than dependency on certain habitat conditions. If the non-overlap section fell on similar habitat, it might imply fidelity to that specific habitat type, with the size of the UD simply fluctuating as conditions in the study area fluctuate, e.g., climatic variability or habitat suitability *sensu* (Seidel and Boyce, 2016). For example, the reduction in UDs, on average, from 1996 to 1997, was concurrent with a substantial increase in late-season precipitation, suggesting elk had to cover less distance to find forage. Therefore, while the VI communicates percent overlap between UDs it lacks relative location information, and should be supplemented with additional analysis on home range location, such as we provided with COM. Regardless, VI and COM results in this study strongly indicated that adult female elk exhibit home-range fidelity during the summer-fall season.

5. Management implications

We found strong evidence for spatial fidelity of adult female elk to individual summer-fall home ranges in the White River, Colorado, USA. One possible application of our results is the incorporation of the elk fidelity concept in addressing the effects of elk herbivory on the silvicultural regeneration of aspen and subsequent recruitment. Because elk space use is predictable relative to other large herbivores (e.g., bison), local hunting is more likely

to have a negative impact on local densities. For example, removal of a group of adult female elk (sub-population) occupying a specific area, rather than large-scale population reduction, may be sufficient to allow vegetation recruitment to the canopy. That is, the selective removal of relatively few, specifically identified female elk, from an area where aspen regeneration harvests are proposed, may create a 'window of opportunity' (Sage et al., 2003). This idea has been demonstrated for female white-tailed deer (as described by the Rose Petal theory) by researchers in the eastern United States. The selective removal of groups of female deer led to dramatic increases in the success of vegetation regeneration and recruitment efforts (Campbell et al., 2004; Oyer and Porter, 2004; Sage et al., 2003) although results were limited in areas with exceptionally high deer populations (Miller et al., 2010). Although elk social dynamics are not identical to white-tailed deer, and elk typically occupy larger home-ranges, we have demonstrated that site fidelity occurs. Limitations might exist because we lack knowledge of how many elk use, or overlap in their use of, a specific area. However, the fidelity concept suggests targeted removal would at least temporarily open up habitat space, reduce browsing pressure, and the opportunity for successful establishment and recruitment of aspen. How long the 'window of opportunity' would remain open is another uncertainty that could be addressed with future research focused on the selective removal of elk in areas where elk herbivory causes vegetation degradation.

Incorporating a sub-population-level elk management approach (removing only females, targeted directly) based on their summer-fall home-range fidelity presupposes that the individuals chosen occupy summer-fall ranges dominated by aspen. Furthermore, individual elk that occupy the potential harvest area during summer-fall would need to be identified before operations occurred, regardless of when the animals were removed. That is, because of site fidelity, females determined to occupy an area during summer-fall could be removed when prudent. It is important to remember, removing targeted elk might not alleviate the browsing problem if other ungulates (domestic or native) are present. Regardless, the selective removal of philopatric elk represents another potential tool to help decrease the risk of aspen regeneration/recruitment failure. Even if elk only use the aspen-dominated type for a portion of the year, precluding them may be the difference between sufficient or failing aspen regeneration/recruitment. Similarly, our finding that elk UDs were smaller during years of moisture excess (i.e., higher browse availability) suggests targeted removal could be more effective in wet years. Finally, the 'window of opportunity' likely only needs to be open for a few years (e.g., 2–4 years) to ensure suckering aspen achieves heights greater than ~2 m, after which they become much less likely to be browsed (DeByle and Winokur, 1985).

In addition to contemporary application in calculating elk harvesting targets in particular areas, results from this study could find application in elk management models. Elk fidelity could be included as a predictor in models of elk habitat or space use. Current work has included habitat type, stage and configuration, topography, and other landscape characteristics to predict elk habitat use, space use, or spatial distribution (e.g., Creel et al., 2005; Edge et al., 1987; Irwin and Peek, 1983; Kie et al., 2005; Stubblefield et al., 2006). By including the site fidelity concept into these models, we would gain additional insight into both the social behavior and environmental factors influencing elk habitat and space use.

Future studies of philopatry in elk, in the White River or elsewhere, could take advantage of new global positioning system (GPS) technology, and potentially monitor elk over all seasons and for multiple years. Had GPS been deployed in our study during the late-90s we might be able to detect site fidelity during other important seasons (e.g., winter, spring) when elk are likely at least partially relying on aspen for forage. Furthermore, monitoring multiple locations over multiple years in rapidly changing landscape would allow an assessment of the putative effects of changing vegetation demographics, as aspen distribution on the Colorado landscape is likely increasing (Thompson et al., 2010), and this, in turn, may increase suitable elk habitat and variability in spatial dynamics. With the reintroduction of wolves and increasing energy development in Colorado, it will be important for future studies of elk side fidelity to be conducted.

Acknowledgements

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