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SUMMER HOME RANGE FIDELITY IN ADULT FEMALE ELK (CERVUS

ELAPHUS) IN NORTHWESTERN COLORADO

by

April M. Brough

A thesis submitted in partial fulfillment of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

James N. Long Major Professor Mary M. Conner Committee Member

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UTAH STATE UNIVERSITY Logan, Utah

2009

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ABSTRACT

Summer Home Range Fidelity in Adult Female Elk (*Cervus elaphus*) in Northwestern Colorado

by

April M. Brough, Master of Science

Utah State University, 2009

Major Professor: James N. Long Department: Wildland Resources

Understanding the degree of spatial fidelity of individuals within a species increases our ability to manage appropriately. Elk (*Cervus elaphus*) is a highly managed species in the Intermountain West, but there is little research evaluating summer home range fidelity of individual elk. We evaluated fidelity of 72 adult female elk to individual summer-fall home ranges in the White River study area in northwestern Colorado during two consecutive summers. Based on individual kernel-estimated utilization distributions, we used (1) the Volume of Intersection (VI) statistic and (2) interannual distances between centers of mass to compare summer range overlap and distribution. We also examined the role of landcover in summer habitat selection by elk from three distinct perspectives: landscape, individual, and philopatric. While many previous habitat studies included landscape analysis, few incorporate individual analysis and none contain a philopatric assessment, to our knowledge. We found adult female elk in the White River Study area exhibit fidelity to individual home ranges. VI values indicated that 93% of the elk showed some home range overlap, with a median value of 0.42 (SE = 0.02, n = 72). Between-year center-ofmass distances ranged from 183 m to 34,170 m ($\bar{x} = 3819$, SE = 619, n = 72), while within-year maximum distances between location points ranged from 4,320 m to 31,680 m ($\bar{x} = 13,958$, SE = 628, n = 72). Our landcover results indicated elk can be characterized as both generalists and specialists. While elk occurred across a very diverse landscape, we found a preference for *Aspen-Mixed Conifer*, *Aspen*, and *Dry-Mesic Spruce-Fir* landcover types, and a general avoidance of *Agriculture*, *Sagebrush Steppe*, *Subalpine Meadow*, and *Grassland*. We also found a high degree of similarity in landcover composition between years for individual elk.

Elk home range fidelity could impact habitat management, specifically with respect to browsing and successful aspen (*Populus tremuloides*) regeneration. Incorporation of the philopatric perspective into future elk behavior and habitat selection studies could make results more rigorous and expand understanding of landscape-level results.

(67 pages)

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CHAPTER I

INTRODUCTION

Elk (*Cervus elaphus*) are important ungulates in the Intermountain West and are managed for hunting recreation, aesthetics, species diversity, and habitat health. The extensive literature on elk includes studies of herd population, social dynamics, animal health, animal movement, herbivory, and habitat selection. Improved understanding of elk increases our ability to achieve a broad range of management objectives related to elk and their habitat. In an effort to further our understanding of elk as a species, this study examines two aspects of elk behavior: (1) philopatry, described as fidelity of an individual to a specific area, and (2) landcover type associations within habitat selection

Philopatry is often discussed in terms of home range fidelity, or site fidelity. Understanding philopatry is important; as we improve our understanding of the spatial fidelity of individuals, we may more effectively manage critical habitats to sustain wildlife species. One example of philopatry among ungulates is that of 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 Jr. et al. 2003). This intergenerational, matriarchal mosaic of home ranges is referred to as the Rose Petal effect (Mathews 1989 dissertation). In elk research, many studies address general herd fidelity to a use area, however few investigate the fidelity of an individual elk to an individual range.

Elk habitat selection is a topic represented in an extensive literature, ranging from general to very specific. The benefits of greater understanding in this area are similar to

those of understanding philopatry. Also similar to the fidelity literature, most studies conducted so far have been performed with elk anonymity; elk were not analyzed for individual actions, but all actions by elk were analyzed together.

The focus of this study is the individual animal; we examine both philopatry and landcover associations from the under-appreciated perspective of the individual elk. The data set from this study is unique in sample size and repeated measure. Seventy-two adult female elk in the White River Study area in northwestern Colorado were radiocollared and repeatedly located during two consecutive summers. Each elk was identifiable as an individual, and treated as such. We first evaluated the fidelity of individual elk to its individual summer-fall home range. To evaluate spatial fidelity, we assessed overlap of summer-fall home ranges for the 72 elk across 2 consecutive summers. Based on individual kernel-estimated utilization distributions, we used (1) the Volume of Intersection (VI) statistic and (2) interannual distances between centers of mass to compare summer range overlap and distribution. Fidelity could affect the current approach to elk management in the form of herbivory management or habitat selection modeling. For the second part of our study, we evaluated elk habitat selection from three distinct perspectives: (1) habitat selection by the elk population in general; (2) habitat selection by individual elk; and (3) consistency of habitat selection by individual elk across two summers. We refer to these three perspectives as (1) the Landscape Level, (2) the Individual Level, and (3) the Philopatric Perspective. We used relative abundance and similarity indices to assess elk use of the various landcover types. The characterization of elk as either habitat generalists or specialists may be dependent on the level of analysis, and we examined this idea throughout our landcover analyses. If

characterization does vary by level, it could have important implications for methods and approaches to both research and management of elk.

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CHAPTER II

SUMMER-FALL HOME RANGE FIDELITY OF ADULT FEMALE ELK IN NORTHWESTERN COLORADO¹

ABSTRACT

Understanding the degree of spatial fidelity of individuals within a species increases our ability to manage appropriately. Elk (Cervus elaphus) is a highly managed species in the Intermountain West, but there is little research evaluating summer home range fidelity of individual elk. We evaluated fidelity of 72 adult female elk to individual summer-fall home ranges in the White River study area in northwestern Colorado during 2 consecutive summers. Based on individual kernel-estimated utilization distributions, we used (1) the Volume of Intersection (VI) statistic and (2) interannual distances between centers of mass to compare summer range overlap and distribution. We found adult female elk in the White River Study area exhibit fidelity to individual home ranges. VI values indicated that 93% of the elk showed some home range overlap, with a median value of 0.42 (SE = 0.02, n = 72). Between-year center-of-mass distances ranged from 183 m to 34,170 m ($\bar{x} = 3819$, SE = 619, n = 72), while within-year maximum distances between location points ranged from 4,320 m to 31,680 m ($\bar{x} = 13,958$, SE = 628, n =72). Elk home range fidelity could impact habitat management, specifically with respect to ungulate browsing and successful aspen (*Populus tremuloides*) regeneration.

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INTRODUCTION

Fidelity of an individual to a specific area, or philopatry, is commonly studied by wildlife ecologists. Philopatry is often discussed in terms of home range fidelity, or site fidelity. Philopatric behavior is believed 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). Understanding philopatry is important; as we improve our understanding of the spatial fidelity of individuals, we may more effectively manage critical habitats to sustain wildlife species.

Philopatric behavior is exhibited by diverse species (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 that of 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 Jr. et al. 2003). This intergenerational, matriarchal mosaic of home ranges is referred to as the Rose Petal effect (Mathews 1989 dissertation).

Elk (*Cervus elaphus*) are an important ungulate in the Intermountain West and are managed for hunting recreation, aesthetics, species diversity, and habitat health. Shortterm and long-term studies demonstrate herd fidelity to seasonal ranges (Knight 1970, Craighead et al. 1973, Hershey and Leege 1982, Irwin and Peek 1983, Edge et al. 1987, Benkobi et al. 2005) and specific patterns of habitat use (McCorquodale 2003, Millspaugh et al. 2004, Anderson et al. 2005). Many of these studies utilize locations of radio-collared elk. Although all of these studies describe elk space use, none specifically addresses individual home range fidelity.

We evaluate the fidelity of each elk to its individual summer-fall home range, specifically focusing on adult female elk in the migratory White River herd of the northwestern Colorado. To evaluate spatial fidelity, we assessed overlap of summer-fall home ranges for 72 elk across 2 consecutive summers. We note that these data were originally collected for a study to assess the impacts of hunting on elk movement to private land in the late summer. Because individual fidelity could be impacted by changes in hunting seasons, we describe the original study and explain how we addressed hunting impacts in the methods section.

STUDY AREA

The White River study area was located in northwestern Colorado and covered approximately 4,540 km² (Fig. 1). Land ownership was 34% private and 66% public with public land managed by the Bureau of Land Management (BLM) or the United States Forest Service (USFS). 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). Public land uses included diverse hiking and camping recreation, timber sales, domestic livestock grazing, hunting, and limited surface coal mining.

Elevation ranged from 1,600 to 3,700 m. The central and eastern portions of the study area contained high elevation sub-alpine and alpine areas commonly used by elk

during 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). Elevations declined from east to west, with elk winter ranges located in the western portions of the area in the lower White River.

At the Marvine Ranch location (elev. 2,379 m) long-term mean temperatures for July and January were 14°C and -8°C; mean annual precipitation was 70 cm, and average total snowfall was 527 cm (Marvine Ranch Station, WRCC 2006). At the Meeker location (elev. 1,903 m), 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, WRCC 2006). Precipitation in 1996 did not vary greatly from the 100year average. However, the precipitation in 1997 increased substantially during July – October 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.

Vegetation in the higher montane/subalpine zones (>2,600 m) was composed of Engelmann spruce (*Picea engelmanni*), subalpine fir (*Abies lasiocarpa*), and aspen (*Populas tremuloides*) interspersed with meadows. Vegetation at mid-elevations of 2,000 m - 2,600 m included aspen woodlands, Gambel oak (*Quercus gambelii*) shrubland, and woodlands of pinion pine (*Pinus edulis*) and juniper (*Juniperus scopulorum*). Sagebrush steppe, grasslands, and agriculture were prevalent at elevations lower than 2,000 m. Aspen covered 23% of the study area and was primarily located between 2,000 m and 3,400 m (USGS National Gap Analysis Program 2004, CDOW 2005).

Elk in the White River population were 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 September, and began migrating back to winter ranges in October (USDA, 2002). For 1996 and 1997, population estimates for the 4 GMUs in the study area were 25,000-30,000 elk (CDOW, unpublished data). More detailed descriptions of the study area and elk population can be found in Conner et al. (2001), Freddy (1987), and Boyd (1970).

METHODS

Data Collection

Conner et al. (2001) captured and radio-collared 80 adult female elk (\geq 2 years old) in the White River study area in July 1996 (Fig. 1) 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 (Conner et al. 2001). 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 cows located during both summers. Between 20 July and 10 October, each cow was relocated twice a week (every 2-4 days) between the hours of 0700 and 1500 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 radiocollars (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 early in the south area (24 August) and 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).

Data Analysis

We obtained 20-23 relocations per cow 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 (Seaman and Powell 1996, Seaman et al. 1999, Kernohan et al. 2001). Although we had lower than the recommended 30 observations per animal we used the fixed kernel estimator to provide the least-biased estimates of home ranges (Seaman et al. 1999). We represented home ranges by calculating 95% utilization distributions (UDs) using the Animal Movement ArcView Extension (Hooge and Eichenlaub 2000) in ArcView (version 3.3).

To evaluate interannual fidelity of individual cows to a home range, we calculated the overlap between the 1996 and 1997 UDs for each cow using the Volume of Intersection (VI) index statistic (Seidel 1992, Millspaugh et al. 2004). 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, with 1 representing maximum overlap. A VI value equal to zero indicated that none of the area used by the cow in

1996 (as represented by the 1996 UD) overlapped with the area used in 1997. A VI value equal to 1.00 indicated that the cow 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 (Millspaugh et al. 2004, Fieberg and Kochanny 2005) in ArcInfo Workstation (version 9.1). We considered any non-zero VI value as indicative of summer-fall home range fidelity (McCorquodale 2003).

As an additional metric of home range fidelity, we calculated the distance between centers of mass for the 1996 and the 1997 UD for each elk and the maximum distance across the home range. We first calculated the center of mass for each UD using the Center of Mass extension (v.1.b, Jenness 2006) in ArcView 3.3. We then calculated the Euclidean distance between the 1996 and 1997 centers for an individual elk using ArcMap (version 9.1). A distance equal to 0 signified that the center of mass of the 1997 UD was in exactly the same location as the center of mass of the 1996 UD, indicating that the elk was returning to the same location interannually. A large distance between centers of mass 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 centers of mass as being small or large. That is, if the maximum within-year distance was less than the center-of-mass (between year) 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 for the hypothesis:

H₀: Mean within-year maximum distance \leq mean between-year center-of-mass distance.

H_A: Mean within-year maximum distance > mean between-year center-of-mass 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 used ArcMap (version 9.2) to calculate the mean center and distance between centers. We compared hunting and non-hunting data using 2×2 contingency tables that were analyzed by chi-square (testing for difference between two medians) due to the range and standard deviation of some of the data sets. 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:

H₀: Non-hunting median within-year maximum distance \leq hunting median within-year maximum distance.

H_A: Non-hunting median within-year maximum distance > hunting median within-year maximum distance.

and

H₀: Non-hunting median between-year center-of-mass distance \leq hunting median between-year center-of-mass distance.

H_A: Non-hunting median between-year center-of-mass distance > median hunting between-year center-of-mass distance.

RESULTS

The distribution of VI values (Fig. 2) indicated that 93% of the elk (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 cows had zero overlap, even these 5 cows were located within the same general area during both years (e.g., Fig. 3i). We show some UDs that were fairly typical of UD shape, size and relative location (Fig. 3b – 3h), while others were selected to illustrate the diversity of UDs (Fig. 3a and 3i).

UD area also varied widely among cows (e.g. Fig. 3c and Fig. 3d). For example, areas of the 1996 UDs ranged from 821 – 28,092 ha ($\bar{x} = 7,185$, SE = 619, n = 72). Similarly, areas of the 1997 UDs ranged from 726 – 46,254 ha ($\bar{x} = 6,356$, SE = 809, n = 72). Areas for 1996 and 1997 were not significantly different ($t_{71} = 2.83$, P = 0.006). While some cows had similar UD sizes between years (e.g., Fig. 3a), other cows exhibited large variation in range size with the larger UD occurring in either 1996 or 1997 (e.g., Fig. 3b and Fig. 3h, respectively).

Distances between the 1996 and 1997 centers of mass ranged from 183 m to 34,170 m ($\bar{x} = 3,819$, SE = 619, n = 72), with a median of 2,108 m. Distances between

centers of mass (CM) were negatively associated with VI overlap (CM = $5.5 - 6.7 \times$ VI; intercept both non-zero; $P \le 0.001$). Within-year maximum distances between location points (occurring in either 1996 or 1997) ranged from 4,320 m to 31,680 m ($\bar{x} = 13,958$, SE = 628, n = 72), with a median of 13,024 m. The within-year maximum distances were greater than the center-of-mass distances ($t_{71} = 13.15$, $P \le 0.001$, Fig 4.).

Exclusion of hunting location points did not substantially alter distances related to center of mass. Distances between the 1996 and 1997 centers of mass (calculated without points collected during hunting season) ranged from 110 m to 32,876 m ($\bar{x} = 3,796$, SE = 605, n = 72), with a median of 2,076 m. Within-year maximum distances decreased when hunting locations were excluded, ranging from 3,447 m to 27,782 m ($\bar{x} = 10,511$, SE = 556, n = 72), with a median of 9,094 m. Chi-squared analysis indicated that a significant difference existed between hunting and no-hunting maximum distance calculations ($\chi^2_1 = 12.25$, $P \le 0.001$), between hunting maximum distance $(\chi^2_1 = 96.69, P \le 0.001)$, and between no-hunting maximum distance and no-hunting center-of-mass distance existed between hunting and no-hunting center-of-mass distance ($\chi^2_1 = 96.69, P \le 0.001$). No significant difference existed between hunting and no-hunting center-of-mass distance calculations ($\chi^2_1 = 0.03, P = 0.867$).

The distribution of location points varied greatly among cows, ranging from highly clustered to more uniformly dispersed, and from single to multiple activity centers. Because 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).

DISCUSSION

Our data are consistent with the hypothesis that individual adult female elk exhibit interannual fidelity to summer-fall home ranges, which we associate with philopatric behavior. Although there was considerable variation in UD size, UD shape, and VI value, 93% of the 72 cows returned to the same vicinity in 1997 that they occupied in 1996. Each of these 67 cows had a non-zero VI value and a centers-of-mass distance less than 8 km. The between-year median distance in centers of mass for all 72 elk (2,108 m) was only 16% as large as the within-year median maximum distance across a home range for an elk within a given year (13,024 m). These facts, taken together with the fact that there was low support for the null hypothesis that within-year maximum distance was less than between-year center-of-mass distance (P = 0.074), corroborates the hypothesis that adult female elk are philopatric to their summer-fall home ranges.

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. 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. Interestingly, we found no significant change in the between-year center of mass distance under similar inspection. This indicates that although hunting pressure forces greater movement by an elk within a year, the center of an elk's home range remains in the same location, suggesting home range fidelity even under disturbance.

In our analyses, variations in UDs might have been amplified by the low number of data points per cow per summer. Although we minimized bias by using the least squares cross validation fixed kernel estimator, 20-23 points is lower than the recommended 30 points. Fewer data points cause the fixed kernel estimator to oversmooth and overestimate the UD shape and size (Seaman et al. 1999). A greater number of locations would decrease the buffer portion of the UD calculated, as well as enhance the ability to detect and discard location points that were merely excursions (based on statistical analysis). Overall, more locations would produce more accurate VI values that could either increase VI values due to increased core overlap, or decrease VI values due to the removal of erroneous buffer overlap.

Although having more data points might reduce variation in UDs and VI values, we suspect some of the observed variation in home ranges is real. As environmental and social dynamics shift, we expect variations in elk utilization of home ranges within the broad constraint of home range fidelity. In general, we found substantial differences in home range size and shape between cows in the same year (e.g., Fig. 3a and Fig. 3d), as well as between years for an individual cow (e.g., Fig. 3b). We note that these differences could be due to a variety of environmental or social factors.

The VI calculation was generally illustrative of the degree of fidelity, although it was somewhat ambiguous in some circumstances. For example, we made a distinction between non-zero (93%) and zero values (7%) in this study. However, visual inspection of UDs for elk with VI values equal to zero, indicated even these elk were still returning to the same general vicinity. Similarly, elk associated with 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 Fig. 3g, 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 center-of-mass or 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.

Although the VI calculation offers a useful way to communicate percent overlap between UDs, VI by itself lacks relative location information. Therefore, we recommend those using the VI calculation supplement this tool with additional analysis on home range location, such as centers of mass, to verify and enhance interpretation of VI results.

MANAGEMENT IMPLICATIONS

We found evidence of spatial fidelity of adult female elk to individual summerfall home ranges in the White River, Colorado, which could influence habitat management plans. One possible application is the incorporation of the elk fidelity concept in addressing the effects of elk herbivory. For example, removal of a group of elk occupying a specific area, rather than large scale population reduction, may be sufficient to allow vegetation regeneration. In this vein, spatial fidelity of female whitetailed deer (as described by the Rose Petal theory) was exploited by researchers in the eastern United States; by selectively removing groups of female deer they dramatically increased the success of vegetation regeneration efforts (Sage et al. 2003, Campbell et al. 2004, Oyer and Porter 2004). However, elk social dynamics may preclude an identical strategy for elk. In particular, it is not known how many elk use or overlap in their use of a specific area, or if all elk were removed from an area, how long the area would remain free of elk. Still, elk fidelity could prompt future research in selective removal for areas where elk herbivory is purported to cause vegetation degradation.

Results from this study could also find application in 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., Irwin and Peek 1983, Edge et al. 1987, Creel 2005, Kie et al. 2005, Stubblefield et al. 2006). Inclusion of site fidelity into these models may provide additional insight into factors influencing elk habitat or space use because these variables may be due to individual elk behavioral philopatry as well as environmental factors.

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Figure 1. The White River study area.



Figure 2. Distribution of volume of intersection (VI) values for White River adult female elk during July 15 – Oct 15, separate for 1996 and 1997. VIs were based on utilization distributions calculated with a kernel estimator.



Figure 3. Utilization distributions (UDs) for 1996 (filled polygons) and 1997 (hollow polygons) for 9 White River adult female elk. Volume of Intersection (VI) values are displayed for each elk. Figures 3b – 3h were fairly typical of UD shape, size and relative location while Figures 3a and 3i were selected to illustrate the diversity of UDs.



Figure 4. Distances between 1996 and 1997 centers of mass versus maximum distance between points within a given year (linear regression does not include elk with VI = 0).

CHAPTER III

LANDCOVER TYPES IN ELK SUMMER USE AREAS: AN ANALYSIS FROM A PHILOPATRIC PERSPECTIVE²

Abstract

We examined the role of landcover in summer habitat selection by 72 adult female elk from three distinct perspectives: Landscape, Individual, and Philopatric. While many previous habitat studies included landscape analysis, few incorporate individual analysis and none contain a philopatric assessment, to our knowledge. Our results indicated elk can be characterized as both generalists and specialists, with certain traits becoming more apparent at the various analysis levels. While elk occurred across a very diverse landscape, we found a preference for *Aspen-Mixed Conifer* (P = 0.0003), *Aspen* (P = 0.0158), and *Dry-Mesic Spruce-Fir* (P = 0.0003) landcover types, and a general avoidance of *Agriculture* (P = 0.0000), *Sagebrush Steppe* (P = 0.0020), *Subalpine Meadow* (P = 0.0000), and *Grassland* (P = 0.0001). We also found a high degree of similarity in landcover composition between years for individual elk; similarity index results ranged from 0.25 to 0.98 ($\bar{x} = 0.80$, SE = 0.01). Incorporation of the philopatric perspective into future elk behavior and habitat selection studies could make results more rigorous and expand understanding of landscape level results.

1. Introduction

Elk (*Cervus elaphus*) is iconic in the Intermountain West and is managed for species diversity, big game, aesthetics, and forest health. The extensive literature on elk

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includes studies of herd population, social dynamics, animal health, animal movement, herbivory, and habitat selection. Improved understanding of elk increases our ability to achieve a broad range of management objectives related to elk and their habitat.

The topic of elk habitat selection alone has prompted extensive literature, with study scopes ranging from broad landscape levels (e.g., Kie et al., 2005) to strictly dietary emphases (e.g., Cook et al., 1996). For the most part, studies have been performed with elk anonymity; elk were not analyzed for individual actions, but all actions by elk were analyzed together (e.g., Stubblefield et al., 2006). In general, elk are described as opportunistic or generalists, with some noted habitat preferences such as minimal human disturbances, roads, and predators; high levels of forest edge; and presence of aspen stands, meadows, and mature closed-canopy forests (Anderson et al., 2005; Creel, 2005; Edge, 1987; Hanley, 1983; Irwin and Peek, 1983; Larkin et al., 2004; McCorquodale, 2003; Stubblefield et al., 2006).

Our insight into elk habitat selection stems from the results of a recent elk movement study. Brough et al.(see Chapter II) observed philopatric behavior by elk in the White River study area in northwestern Colorado; adult female elk demonstrated strong fidelity to their individual summer use areas. The data set from this study is unique in sample size and repeated measure: 72 adult female elk were radiocollared and repeatedly located during two consecutive summers. Each elk was identifiable as an individual, and treated as such. When we combined these elk movement data with landcover data for the White River study area, we were able to evaluate elk habitat selection from three distinct perspectives: (1) habitat selection by the elk population in general; (2) habitat selection by individual elk; and (3) consistency of habitat selection by individual elk across two summers. We refer to these three perspectives as (1) the Landscape Level, (2) the Individual Level, and (3) the Philopatric Perspective. While we acknowledge many factors undoubtedly contribute to habitat selection, here our objective is to describe the association between landcover types and elk summer use areas. We suspect that the characterization of elk as either habitat generalists or specialists may be dependent on the level of analysis, and examine this idea throughout our landcover analyses. If characterization does vary by level, it could have important implications for methods and approaches to both research and management of elk.

2. Methods

2.1. Study Area

The White River study area is located in the Rocky Mountains of northwestern Colorado, and covers approximately 4,540 km² (Fig. 5). It consists of 4 Colorado Division of Wildlife (CDOW) game management units (GMU): 12, 23, 24, and 33. Land in the study area is privately (34%) or publicly owned (66%). Public land is managed by either the Bureau of Land Management (BLM) or the United States Forest Service (USFS).

Elevation ranges from 1,600 to 3,700 m. The central and eastern portions of the study area are high plateaus, divided by the White River valley. The northern and western portions tend to be gently sloped hills, descending to the lower elevations. Sharp cliffs and canyons predominate in the southern portion. USFS land uses include recreation, timber sale, domestic livestock grazing, and hunting. Some surface coal mining occurs adjacent to the northwest boundary of the study area.

Climate variations are associated with the topographic variations of the study area. Precipitation is fairly constant throughout the year, with peaks in the spring and fall (Western Regional Climate Center [WRCC], 2006). In higher elevations, the mean temperatures for July and January are 16°C and -6°C; mean annual precipitation is 52 cm, with an average total snowfall of 446 cm (Marvine Station, WRCC, 2006). At lower elevations, the mean temperatures for July and January are 19°C and -6°C; mean annual precipitation is 42 cm, with an average total snowfall of 177 cm (Meeker Station, WRCC, 2006).

Precipitation in 1996 did not vary greatly from the 100-year average. However, the precipitation in 1997 increased substantially July – October, with as much as 14 cm in September, compared to the September mean of 4 cm (Table 1). Temperatures during both study years were close to the 100-year averages.

Vegetation in the study area is varied. Stands of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and aspen occur with interspersed meadows in the higher montane/subalpine zones, typically >2,600 m. Vegetation at midelevations of 2000 m – 2600 m includes aspen woodlands, Gambel oak shrubland, or pinyon pine and juniper woodlands. Sagebrush steppe, grasslands, and agriculture are prevalent at elevations lower than 2000 m. Aspen covers 23% of the study area, existing mostly from 2000 m to 3400 m (Colorado Division of Wildlife, 2005; United States Geological Survey [USGS] National Gap Analysis Program, 2004).

2.2. Study Species

The White River elk are migratory. Spring migration from winter to summer

range occurs Apr 15 – Jun 20, with calving occurring May 15 – Jun 20. Elk occupy summer range Jun 16 – Oct 14. The study area consists mainly of summer range. Fall migration back to winter range occurs Oct 15 – Nov 30 (United States Department of Agriculture [USDA], 2002). For 1996 and 1997, population estimates for the 4 GMUs in the study area were 20,000-30,000 elk (Darby Finley, Colorado State University (CSU), personal communication). More detailed descriptions of the study area and elk herd can be found in Conner et al. (2001) and Boyd (1970).

2.3. Data Collection

In a collaborative effort by CSU and CDOW, 80 adult female elk (\geq 2 years old) were captured and radio-collared in the White River study area in July 1996 (Conner et al., 2001). Capture sites were randomly chosen locations distributed throughout the study area. Although some constraints existed due to private land access and time, a reasonably representative sample was obtained, with 2 cows being captured at some locations. Locations were collected during the summers of 1996 and 1997. For the current study, we only used data for the 72 cows located during both summers. Between 20 July – 10 October, each cow was relocated twice a week (every 2-4 days) between the hours of 0700 and 1500. Locations were obtained from a fixed-wing aircraft. Mean telemetry plus Global Positioning System (GPS) error was 333 m (95% CI = 265–401), based on 24 blind tests conducted on randomly located radiocollars. A detailed description is given in Conner et al. (2001).

We digitized a USGS map of the area (1:100,000) to provide an ArcMap layer defining study area boundaries. We obtained a seamless Digital Elevation Model (DEM)

of the area with a pixel resolution of 30 m x 30 m. Our analysis of vegetation was based on a landcover classification raster from the Southwest Regional Gap Analysis Project (SWReGAP, USGS National Gap Analysis Program, 2004). Pixel resolution was 30 m x 30 m. The study area contained 50 unique SWReGAP landcover types. Of the 50 landcover types present in the study area, 14 occurred on at least 1% of the study area (Table 2). So as to provide meaningful ecological interpretations, we focused on these 14 landcover types in our analysis. Detailed descriptions of landcover types are provided in the SWReGAP Landcover Legend Description database (USGS National Gap Analysis Program, 2004).

2.4. Data Analysis

In our 3-tiered analysis, we investigated relationships between elk location and landcover. As part of our comparisons, we contrasted "occupied" and "available" areas. An "occupied" area was the geographical area occupied by an elk, which we defined as a buffered point (BP) shapefile regardless of analysis level. The "available" area was the geographical area available to an elk, which, depending on the level of analysis, we defined as either the entire study area or as a utilization distribution (UD) shapefile. We discuss the generation of these GIS shapefiles below.

2.4.1. GIS Shapefiles

A given BP shapefile represented the occupied area for an individual elk in a given year. We created BP shapefiles by buffering elk location points, a method also used by McCorquodale (2003). Each elk had 20-23 location points in a given summer, resulting in two BP shapefiles for each elk: one consisting of buffered 1996 locations and

one consisting of buffered 1997 locations. We used a 333-m buffer radius, which was based on the mean telemetry plus GPS error (Conner et al., 2001). Using the BP shapefiles as masks on the SWReGAP raster enabled us to define the landcover occupied by an individual elk in a given year.

A given UD shapefile represented the area available to an individual elk in a given year. We calculated UD shapefiles with a fixed kernel estimator, using least squares cross validation (LSCV) in ArcView 3.3 (ESRI). Each elk had two UD shapefiles: one calculated from 1996 locations and one calculated from 1997 locations. The LSCV 95% fixed kernel home range estimator was more appropriate for estimating summer use areas in our study than other common estimators (such as minimum convex polygon or adaptive kernel) because of required sample size, utilization calculation, nonparametric distribution, and sensitivity to outliers (Seaman and Powell, 1996; Seaman et al., 1999; Kernohan et al., 2001). We consider it appropriate to characterize the area available to an elk as her UD rather than the entire study area due to the philopatric behavior of female elk in the study area, as well as the diversity of topography, climate, and vegetation across the study area (Brough et al., in review). Using the UD shapefiles as masks on the SWReGAP raster enabled us to define the landcover potentially available to an elk in a given year. Thus we could compare the habitat that an individual elk selected (in the BP shapefile) to the habitat which we considered available to her (in the UD) for either 1996 or 1997.

2.4.2. Relative Abundance

Because UDs varied in size, we used relative landcover abundance type to

facilitate comparison of landcover occupation between elk, rather than an absolute pixel count of landcover. We first used the BP and UD shapefiles as masks to extract yearly landcover rasters for each elk from the SWReGAP landcover raster. We then calculated the relative abundance (RA) of each landcover type within each raster as the number of pixels of landcover type divided by the total number of pixels in the raster, multiplied by 100. RAs were calculated for all 50 landcover types in each of the 288 landcover rasters (2 yearly BP landcover rasters and 2 yearly UD landcover rasters for each of the 72 elk). We also calculated RAs of landcover types in the study area in general.

2.4.3. Landscape-Level Analysis

This level of analysis investigated habitat selection (i.e. landcover occupation) by the entire study population (72 adult females) across the entire landscape. We specifically compared the RAs of landcover types in all elk-occupied areas (within a given year) to the respective RAs in the entire study area. To obtain RAs in elk-occupied areas, we merged all BP shapefiles from one year (eliminating double count of overlap areas), resulting in a merged 1996 BP shapefile and a merged 1997 BP shapefile. We used these merged BP shapefiles as masks on the landcover raster and obtained RAs for each SWReGAP landcover type for both rasters. An RA_{merged} > RA_{study area} indicated that the elk population occupied this landcover type to a greater extent than it occurs on the landscape. An RA_{merged} < RA_{study area} indicated that the elk population occupied this landcover type to a lesser extent than it occurs on the landscape, and an RA_{merged} \approx RA_{study area} indicated neither general preference nor avoidance of that landcover type by the elk.

We also performed a Principal Components Analysis (PCA) to examine patterns in landcover occupation by the elk population. We performed the PCA using the RAs from the individual 1996 BP rasters; however we only included the landcover types that had an RA >1% in the merged 1996 BP raster to aide realistic ecological interpretation of the results. Because our abundance data were relative rather than absolute, we used a composition approach for our PCA calculations (Khattree and Naik, 2000). We performed the PCA using a covariance matrix (SAS Institute, 2003), and then evaluated the resulting components for explanatory ecological trends of occupied landcover types.

2.4.4. Individual-Level Analysis

The focus of this level of analysis was apparent habitat selection patterns by individual elk, rather than the population as a whole; we based our comparison on areas occupied by, and available to, individuals. Here we compared the RA of a landcover type in an individual BP shapefile to the respective RA in the respective UD shapefile (e.g., comparing the *Aspen* RA in an elk's 1996 BP shapefile to the *Aspen* RA in her 1996 UD). We tied this analysis back to the landscape level by plotting the RA_{BP} vs RA_{UD} comparisons for all 72 elk for a given landcover type in a given year and performing linear regression analysis. If elk (as seen through individuals) occupied a landcover type to a greater extent than it occurred in their respective UD shapefiles, the slope of the regression would be greater than one (i.e. b>1). Alternatively, slopes less than or equal to one would suggest landcover occupation less than or equal to its representation in the UDs. We used a log-log scale due to skewness and to reduce variance and diminish the weight of extreme outliers. Because not every BP shapefile contained every landcover type (i.e., RA = 0 for some elk), we offset all values by adding 1, enabling us to use the log-scaling (Hamilton, 1992). We used the t-statistic to test for significant differences in slope. We performed these calculations for all 50 landcover types; however, we only discuss results for the 10 landcover types that occurred on more than 1% of the merged 1996 BP shapefile. These 10 landcover types are a subset of the 14 landcover types that occurred on more than 1% of the study area, and are of greatest ecological relevance to elk habitat selection (Table 2).

We emphasize the difference between the analysis of individual elk distributions discussed here and the landscape level analysis above. In the landscape analysis, we combined all elk occupation data prior to analysis and compared it to landcover data from the entire landscape. In this individual analysis, we compare the individual occupation data from each elk to the available landcover data in her unique UD. In the linear regression, we are looking for patterns of individual selection across the population, rather than patterns of a combined population selection.

2.4.5. Philopatric Perspective

We believe this level of analysis is unique to our study. Prompted by the philopatric behavior of female elk in this population, we examined individual landcover occupation patterns in successive summers. Even though elk in the study area exhibited high fidelity to an individual summer use area, areas varied greatly in size, shape, and nature of non-overlap (Brough et al., in review). A comparison of landcover occupation offers insight into whether elk were simply returning to a specific geographic location or if they also displayed affinity or avoidance for specific landcover types in subsequent years. A high landcover similarity index value between years would be consistent with landcover composition as a possible factor in summer use area selection.

We tested for landcover similarity between years for each elk by comparing the landcover composition of her 1996 BP shapefile to the landcover composition of her 1997 BP shapefile, using the Bray-Curtis modification of the Sorenson index (Magurran, 1988):

$$C_N = \frac{2\sum_{1}^{j} \min(a, b)}{(N_a + N_b)}$$

where N_a is the total landcover abundance occurring in the BP shapefile in 1996, N_b is the total landcover abundance occurring in the BP shapefile in 1997, *j* is the total number of landcover types occurring in the BP shapefile in either 1996 or 1997, and min(a,b) is the lower of the 2 RAs (1996 vs. 1997) for landcover types occurring in the BP shapefiles. For our study, both N_a and N_b were equal to 100 due to our use of relative abundance values rather than absolute abundance values. A similarity index value of 0 would indicate a completely different landcover composition in the 1996 and 1997 BP shapefiles; an index value of 1 would indicate an identical landcover composition between years.

3. Results

3.1. Landscape Level

3.1.1. RA Comparison

The RAs of landcover types in the study area and merged 1996 and 1997 BP shapefiles are presented in Table 2. We calculated RAs for each of the 50 unique SWReGAP landcover types; however, in order to focus on meaningful ecological relationships, we only report RAs for the 14 landcover types that occur on at least 1% of the study area (Table 2). By comparing the RAs for the merged BP shapefiles to those for the study area, we found the general elk population occupied *Aspen, Dry-Mesic Spruce-Fir, Mesic Spruce-Fir, and Aspen-Mixed Conifer* to a greater degree than these types occur on the landscape. In contrast, the population occupied *Gambel Oak, Agriculture, Sagebrush Steppe, Pinyon-Juniper,* and *Big Sagebrush* to a lesser extent than these types occur on the landscape. The population appeared to occupy *Mesic Meadow* to the same degree that it occurred on the landscape.

3.1.2. PCA Analysis

We plotted each elk (in terms of her unique combination of landcover RAs) using two PCA components as the axes: Component 1 reflects differences in landcover types that are associated with elevation (shown as Factor 1 in Fig. 6), and Component 2 appears to be associated with the RA of the *Aspen* landcover type in elk BP shapefiles (Factor 2 in Fig. 6). Component 1 corresponds with the elevation gradient across the study area. High values on this axis correspond with low-elevation summer use areas (BP shapefiles), which have higher percentages of lowland cover types, such as *Gambel Oak* *Woodland* and *Sagebrush Steppe*. Low axis values correspond with high-elevation summer use areas (BP shapefiles), which have higher percentages of high elevation cover types, such as *Dry-Mesic Spruce-Fir* and *Subalpine Meadow*. Component 1 accounts for 60% of the total variation in elk occupation of landcover type. Component 2 suggests *Aspen* abundance in the BP shapefiles is an important habitat factor with axis values directly proportional to the abundance of *Aspen* in BP shapefiles. Component 2 accounts for 14% of the total variation in elk occupation of landcover type.

Components 1 and 2 account for 74% of the total variation in elk occupation of landcover types. When viewed from the perspective of the Component 1 axis, the distribution of data along the Component 2 axis seems to suggest a correlation between elevation and *Aspen* abundance; *Aspen* abundance was minimized for elk with low and high Component 1 values (high and low elevations, respectively), and peaked for elk with mid-range values (Fig. 6). We used SWReGAP landcover data to investigate the distribution of *Aspen* across the study area with respect to elevation (Fig. 7). The elevational range of the study area is 1400 - 4000 m (Fig. 7a). The elevational range of the BP shapefiles is 2100 - 3500 m. *Aspen* occurs within the study area at 2000 - 3400 m (Fig. 7b). *Aspen* is available through the majority of the BP shapefiles' elevational range, with the greatest abundance occurring from 2600 - 2800 m (Fig. 7). It might appear that elk occupation of the *Aspen* landcover type is simply an artifact of elevation; however, this is not consistent with our analysis of individual elk.

3.2. Individual Level

Elk occupied specific landcover types to greater and lesser extents than the

landcover types occurred in their respective UD shapefiles. Graphs of Aspen, Gambel Oak, and Agriculture are shown to illustrate (Fig. 8 - 10). Seven of the ten landcover types for which we tested for linearity had slopes significantly different than 1 (Table 3). Three of the seven significant landcover regressions had slopes greater than one (b>1), indicating that elk occupied these landcover types to a greater extent than they occurred in the UD shapefiles. These three landcover types were Aspen-Mixed Conifer (P = (0.0003), Aspen (P = 0.0158), and Dry-Mesic Spruce-Fir (P = 0.0003). Four landcover regressions had slopes significantly less than one (b<1), indicating that elk occupied these types to a lesser degree than they occurred in the UD shapefiles. These four landcover types were Agriculture (P = 0.0000), Sagebrush Steppe (P = 0.0020), Subalpine Meadow (P = 0.0000), and *Grassland* (P = 0.0001). The remaining three landcover types, which were prevalent in the BP shapefiles but whose regressions did not have slopes significantly different from one (b=1), suggesting neither selection nor avoidance, were Gambel Oak (P = 0.1147), Mesic Spruce-Fir (P = 0.1132), and Mesic Mixed-Conifer (P = 0.1147) 0.4855).

3.3. Philopatric Perspective

Similarity index results ranged from 0.25 to 0.98, with a mean value of 0.80 and a standard error of 0.01. A similarity value of zero indicates that the landcover composition, explicitly type and abundance, in an elk's 1996 BP shapefile and her 1997 BP shapefile is completely different. A value of one indicates that the landcover composition of an elk's BP shapefile is identical in the two years. The six lowest similarity values corresponded to the six cow elk with the lowest degree of fidelity,

having little or no overlap between 1996 and 1997 BP shapefiles (Brough et al., Chapter II). Similarity index values among these six elk (mean = 0.56, SE = 0.06) were significantly different than similarity index values for the remaining high fidelity elk (P < 0.001).

We also tested the similarity data for a relationship with elevation. Based on the elevational landcover trend we found in our PCA results (Component 1), we hypothesized that if an elk changed elevation between 1996 and 1997, her similarity index value would be smaller than typical. We found a weak, but significant, relationship between change in elevation between years and decreased similarity between landcover types (P < 0.0002).

4. Discussion

Our results provide insight into the association between vegetation and elk habitat selection. We observed a dualistic nature in elk and believe they can be characterized as both habitat generalists and specialists. Specific aspects of these two characterizations become more prominent depending on the level of analysis.

The widely held view of elk as habitat generalists is understandable, considering that the Landscape level of analysis is the most frequent in the literature; we believe it to be correct as well. The White River study area is an extremely diverse landscape with great topographic relief and 50 different landcover types. The fact that elk appear to fully occupy the study area suggests a great deal of flexibility in their use of habitat. Our PCA results support the generalist characterization, reminding us of the great degree of variation in summer use area landcover composition due to elevation. At the same time, we also found evidence of specialist behavior at the Landscape level, such as the general preference for aspen and a population avoidance of pinyon-juniper. At this level of analysis, we encounter many unknowns; we make conclusions based on averages and means, while individual behavior that could influence our understanding and management of elk is easily masked and possible results in erroneous interpretations.

Further clarification can be found at the individual level, which allows us to examine how individual animals react to local availability instead of a broad and potentially vague study area. Whereas outliers could be the reason for supposed preference at the landscape scale, data for individuals allow us to directly look for a common trend among elk by examining individual behavior. Individual results can then be combined (as done in the linear regression analysis) to provide insight into general patterns in elk behavior. Here we can more confidently conclude elk preferences and identify, investigate, and postulate concerning individual deviations from the population behavior. This confidence comes from the ability to see the inner workings of what takes place at the landscape level. For example, at the individual level we gain insight into the apparent elk affinity for aspen; the general preference observed at the landscape level is not simply the result of elk seeking out portions of the study area that are rich in aspen. Rather, they appear to be seeking out portions of their own UDs (i.e., their own neighborhood) that have aspen.

Although the individual level of analysis gives us additional insight, incorporating the philopatric level provides even more. From the previous fidelity study we know that elk return to the summer use areas. The unique information that our results provide is that once the elk return to their summer use area, they use the landcover in the same manner. Not only is area consistent, but use of the landcover in the area is consistent. This type of information is only available through individual tracking and accounting from year to year. The philopatric level of analysis also shed light on the elevation variation highlighted by the landscape level analysis. By examining repeated years of individual's landcover use, we were able to determine that while elevation dictates what landcover is available (and thereby introduces landcover composition variations) individual use patterns are still very similar. This was most apparent in the six individuals that experienced the largest elevational changes. These six elk had essentially no overlap between years. One plausible cause of relocation for these elk is disturbance, either natural or introduced (e.g., hunting). Another explanation could be dispersal, as mandated by elk social patterns. Regardless of cause, the relocation illuminates a most interesting point: these elk still maintained relatively high landcover composition similarity index values (mean = 0.56) given the diversity of the study area, despite being lower than high-fidelity animals (mean = 0.80). This could insinuate that while an elk may be forced to relocate, she retains some of her previous landcover use patterns in her new area.

The combination of these three levels of analysis illustrate how a dualist nature can exist in elk. We suggest that in accordance with the current view elk are generalists in determining their local area or summer use area. Perhaps the establishment of this fidelity area is based on matriarchal lines, as observed in other ungulates. McLoughlin et al. (2008) suggest habitat use patterns may be conferred to offspring from their mothers based on learning, and that the females in the study exist in very stable matrilineal groups. Millspaugh et al. (2004) also suggested matriarchal social organization as a possible key to movement dynamics. If so, alternative management approaches such as selective removal might possibly be incorporated into elk herbivory management. Additionally we believe that elk are specialists in their use of the resources within that area. We emphasize that the clarity in this diagnosis would not be attainable at the landscape level alone, and that further investigation at the individual level and, even more importantly, philopatric level are needed to better understand and thereby manage elk.

5. Conclusion

Our results suggest that elk can reasonably be characterized as both habitat generalists and specialists and that the appropriate characterization is dependent on the level of analysis; while elk are opportunists, they exhibit preference behavior. This duality in nature became apparent in our analyses: while we observed that adult female elk in the White River study area occur across the entire landscape (indicating a generalist nature), we also found elk prefer certain landcover types (indicating a specialist nature). The less common use of Individual analysis, combined with the unique Philopatric perspective, allowed a more robust and complete understanding of elk behavior in regards to landcover occupation. Future elk behavior and habitat selection studies should take advantage of the more rigorous approaches seen in the individual and philopatric levels, utilizing the ability to evaluate elk habitat occupation of individuals and the ability to compare individuals from year to year.

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Table 1White River total monthly and annual average precipitation at lower elevations for the years of
study (1996, 1997) contrasted against the106-year averages (Western Regional Climate Center
2006, Meeker Station).

Voor(o)	Total Monthly Average Precipitation (cm)												Total Annual Average
rear(s)	Jan	Feb	Mar	Apr	Мау	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Precipitation (cm)
1996	4.95	5.51	2.90	4.83	3.00	2.62	5.16	1.35	4.45	6.81	6.68	3.35	51.59
1997	4.22	2.26	1.14	9.58	4.75	2.26	6.27	8.36	13.97	6.63	2.84	1.83	64.11
1900-2006	2.79	2.59	3.43	4.39	3.76	3.07	3.48	4.52	3.99	3.73	3.00	2.87	41.63

Table 2Relative abundances of SWReGAP landcover types in the White River study area and in the
Buffered Point (BP) shapefiles. Relative abundance was calculated as the pixels of landcover type
divided by the total number of pixels in either the study area or the combined buffered point
shapefiles, displayed as a percentage. Detailed descriptions of landcover types are given in the
SWReGAP Landcover Legend Description Database (SWReGAP 2007).

SWReGAP Landcover Type	Relative Abundance in Study Area (%)	Relative Abundance in Combined 1996 Buffered Point Shapefiles (%)		
Rocky Mountain Aspen Forest and Woodland	23	42		
Rocky Mountain Gambel Oak-Mixed Montane Shrubland	16	15		
Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	11	13		
Agriculture	9	2		
Inter-Mountain Basins Montane Sagebrush Steppe	8	6		
Rocky Mountain Subalpine Mesic Spruce-Fir Forest and Woodland	6	8		
Colorado Plateau Pinyon-Juniper Woodland	6	0		
Inter-Mountain Basins Big Sagebrush Shrubland	4	0		
Inter-Mountain West Aspen-Mixed Conifer Forest and Woodland Complex	4	5		
Southern Rocky Mountain Montane-Subalpine Grassland	3	2		
Rocky Mountain Subalpine Mesic Meadow	2	2		
Rocky Mountain Subalpine-Montane Riparian Shrubland	2	< 1		
Rocky Mountain Montane Mesic Mixed Conifer Forest and Woodland	1	2		

Table 3Statistical results indicating extent of elk occupation of specific landcover types with respect to
landcover type abundance on the landscape. A slope equal to 1 indicates elk occupy landcover
type to the same extent it occurs on the landscape. A slope greater than 1 indicates elk occupy the
type to a greater extent than it occurs on the landscape, and a slope less than one indicates elk
occupy the type to a lesser extent than it occurs on the landscape.

SWReGAP Landcover Type	Slope	Standard Error	t Value	Р	
Agriculture	0.59	0.04	-9.83	0.0000	
Inter-Mountain Basins Montaine Sagebrush Steppe Inter-Mountain West Aspen-Mixed Conifer Forest and Woodland Complex Rocky Mountain Aspen Forest and Woodland	0.79 1.27 1.14	0.07	-3.21 3.82 2.47	0.0020	
Rocky Mountain Aspen Forest and Woodland Rocky Mountain Gambel Oak-Mixed Montane Shrubland Rocky Mountain Montane Mesic Mixed Conifer Forest and Woodland	0.93	0.04	-1.60	0.1147	
Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland Rocky Mountain Subalpine Mesic Meadow	1.13 0.72	0.03 0.04	3.78 -7.90	0.0003	
Rocky Mountain Subalpine Mesic Spruce-Fir Forest and Woodland Southern Rocky Mountain Montane-Subalpine Grassland	1.09 0.80	0.06 0.05	1.60 -4.27	0.1132 0.0001	



Figure 5. The White River study area in northwestern Colorado, consisting of Colorado Division of Wildlife (CDOW) Game Management Units (GMUs) 12, 23, 24, and 33



Figure 6. PCA results with landcover type vectors

Percent Study Area (by Elevation Range)



Percent Aspen in Study Area (by Elevation Range)



Figure 7. Histogram of elevational distribution (a) of the study area and (b) of *Aspen* in the study area



Figure 8. Linear regression plots of relative abundance in UD versus relative abundance in BP for *Aspen*



Figure 9. Linear regression plots of relative abundance in UD versus relative abundance in BP for *Gambel Oak*





Figure 10. Linear regression plots of relative abundance in UD versus relative abundance in BP for *Agriculture*

CHAPTER IV

CONCLUSION

We examined two aspects of elk behavior in this study: philopatry and habitat selection. With respect to the first topic, we found individual adult female elk to exhibit interannual fidelity to summer-fall home ranges. In regards to the second emphasis, we concluded that elk can be characterized as both habitat generalists and specialist, depending on the level of analysis.

Elk spatial fidelity could influence habitat management plans. One possible application is the incorporation of the elk fidelity concept in addressing the effects of elk herbivory; elk fidelity could prompt future research in selective removal for areas where elk herbivory is purported to cause vegetation degradation. Results from this study could also find application in management models. Elk fidelity could be included as a predictor in models of elk habitat or space use.

Our habitat selection results suggest that the approach of examining elk as individuals from a philopatric perspective allows a more robust and complete understanding of elk behavior in regards to landcover occupation. Future elk behavior and habitat selection studies that utilize this unique approach are likely to offer richer descriptions of the broad and diverse behavior of elk.