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Wapiti Home Range and Movement Patterns in a Sagebrush Desert

Abstract

Daily movement descriptions have not been available for wapiti (*Cervus elaphus*) using sagebrush (*Artemisia tridentata*) and cropland. Thus, we quantified home ranges and daily movement patterns of radio-collared wapiti in a sagebrush-cropland mosaic in southeastern Idaho. Wapiti in our study had the largest home-range sizes and traveled the longest daily distances of 14 and 8 investigations, respectively. Annual, minimum-convex-polygon home-range areas for nonmigratory wapiti in our study ranged from 544 to 555 km^2. Summer, minimum-convex-polygon home-range areas ranged from 79 to 593 km^2. Summer, harmonic-mean core areas ranged from 26 to 148 km^2. Mean-minimum-daily distance traveled by marked wapiti from June through August was 8.8 km (SE = 0.8, n = 59). Large home-range sizes have been correlated with low precipitation; however, juxtaposition of habitat components in our study area also contributed to long daily movements and large home-range areas. During the summer, daytime bedsites were in native rangeland, while nighttime relocations were in cropland. We speculate that the most important (interrelated) factors behind the large wapiti movements in the INEL area were aridity, juxtaposition of habitat components, habitat requirements, and human disturbance.

Introduction

North American wapiti management has been based largely on information collected in montane habitats. In light of wapiti range expansions in semi-arid habitats during the last 2 decades, information on ecology of wapiti in these areas is needed. Wapiti now occupy treeless habitats in the Red Desert in Wyoming, the Arid Lands Ecology Reserve in south-central Washington, the Idaho National Engineering Laboratory (INEL) in southeastern Idaho, and the Great Basin of south-central Oregon. Baseline biological information is needed by managers if non-montane wapiti populations are to be effectively managed. For example, understanding wapiti home-range patterns and movements is necessary for strategic harvest planning (Boyce 1989:13) and for effective handling of crop damage complaints.

Our data is important because movement and home-range information on wapiti in sagebrush-steppe has been rare. Plus, cropland use has not been reported for wapiti using sagebrush-steppe (McCorquodale et al. 1986, McCorquodale 1987, McCorquodale et al. 1989). Home-range descriptions have been available only from south-central Washington, which was at the northwestern edge of the sagebrush-steppe (McCorquodale et al. 1989). Depending upon information from one location may be problematic because there may be factors of interest that were different for that site. Our information complements data from south-central Washington because there were substantial differences in water availability and in sagebrush:grass biomass ratio between these 2 areas. The Washington site had a perennial stream, while surface water in the INEL area was limited to artificial sources, including irrigated cropland. The sagebrush:grass biomass ratio was lower in Washington.

Wapiti colonized the INEL area by the mid-1980s (Moritz 1988). This colonization coincided with increased water availability via Bureau of Land Management (BLM) guzzlers and severe winters. Two wapiti herds, each roughly 80 animals, had formed by 1989 (Strohmeyer 1992). Cropland damage complaints increased with wapiti numbers. Our objective was to describe home ranges and daily movements.

Study Area

The study area encompassed private, public, and INEL lands. Most of the private lands were cropland. Public lands included BLM, United States Forest Service, and state lands. The INEL covered 2,305 km^2 in southeastern Idaho and was established in the 1950s to test nuclear reactors. Public access was restricted while livestock grazing

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was limited to the INEL's periphery. Hunting on INEL land was limited to depredation hunts which extended 0.8 km inside the NE border in the Mud Lake area.

Elevations ranged 1454-1554 m (Harniss and West 1973). The rolling topography was broken by volcanic craters and cones. Precipitation peaked in December-January and May-June. From May 1989 to August 1991, mean annual precipitation was 20.3 cm, and mean July and January temperatures were 32.3 C and -1.6 C, respectively (R. Mitchell, U.S. Dep. of Energy., unpubl. data). Surface water was restricted to artificial sources: guzzlers, cropland irrigation, and waste-water ponds near INEL facilities.

Adjacent croplands were primarily alfalfa with some potato, wheat, barley, oats, and rapeseed. About 87% of the INEL was sagebrush-steppe, with the rest being grassland and juniper (*Juniperus* spp.) woodland (McBride et al. 1978). The juniper woodlands were concentrated in the Lemhi mountain foothills and the Cedar Butte Lava area. Common grasses were bluebunch wheatgrass (*Agropyron spicatum*), needle-and-thread (*Stipa comata*), and Indian ricegrass (*Oryzopsis hymenoides*).

Methods

Female and male wapiti were captured by helicopter net-gunning and each animal was radio-collared and ear-tagged. We relocated marked wapiti from April 1989 through August 1991, visually verifing relocations when possible. No more than 2 relocations were recorded every 24 hours per individual to minimize temporal dependence between relocations (Swihart and Slade 1985).

Diurnal aerial relocations were obtained from fixed-wing aircraft using Loran-C devices (Boer et al. 1989). Nocturnal, aerial relocations were made with a helicopter-mounted infrared system which allowed visual verification of wapiti. Accuracy of the Loran-C systems used were not tested, but Patric et al. (1988) found mean error in location accuracy for such devices to be 1.0 km (0.1 SE, n = 18).

We plotted ground relocations in Universal Transverse Mercator System (UTM) coordinates. Ground relocations were obtained weekly during winter and biweekly during summer (once diurnally, once nocturnally). Nocturnal telemetry work in winter was limited to weeks coinciding with a full moon. Croplands were surveyed for presence of wapiti during June when marked wapiti use was intermittent.

No triangulation errors occurred for ground, cropland relocations because marked animals were either seen or their nocturnal presence was verified by fresh tracks and feces. We estimated triangulation error for ground, non-cropland relocations by comparing triangulations to subsequent, corresponding visual relocations. We randomly selected 75 relocations that had both triangulation and visual information. We defined the error between a triangulation and respective visual relocation as the distance between the visual relocation and the center of the polygon formed by intersecting bearings. The mean of this distance was 0.3 km (0.04 SE, n = 75).

The harmonic--mean estimator in Program Home Range (Ackerman et al. 1990) best quantified our home-range areas. However, we also reported minimum-convex-polygon (MCP) areas because they have been the most commonly reported. We estimated seasonal home ranges for each marked wapiti having ≥20 relocations. Timing of migrations, changes in group sizes, and timing of cropland use led us to define seasons as: summer = July-September, fall = October-December, winter = January-March, and spring = April-June.

We quantified minimum-daily movement patterns during June, July, and August by calculating distances between consecutive daytime and nighttime relocations. Only relocations occurring <1 day apart were used. We defined daily distance, the distance moved in a 24-hour period, to be twice the respective day-night distance because a 24-hour period involved animals moving from shrub-steppe (day) to cropland (night) to shrub-steppe (day).

Statistical Analyses

A factorial analysis of variance tested differences among seasonal home-range areas and among daily distances. We tested pairwise comparisons with population marginal means because sample sizes were unequal (Searle, Speed, and Milliken 1980). Power calculations followed Desu and Raghavarao (1990:58-9). The 95% harmonic-mean areas were not transformed. A natural logarithmic transformation normalized the MCP areas and the daily distances; however, we reported untransformed means and standard errors. The repeated measures (multiple relocations of marked individuals) in the daily distances were removed by using the mean distance for a given animal-month-year varied largely because of legal harvest of marked bulls. Marked wapiti were relocated 1403 times. Sixty-one percent of daytime, ground relocations and 88% of daytime, aerial relocations were visually verified. Cropland relocations totalled 356, of which 354 were verified either visually or with fresh wapiti fecal material and tracks.

Annual Home Ranges

Distribution of the Mud Lake-Argonne (MA) herd was almost exclusively on INEL land (Figure 1). This herd wintered in the central portion of INEL land near the Argonne facility then summered in the Mud Lake area. We consider these animals to be nonmigratory because their shifts in home-range use were gradual (>2 months) and

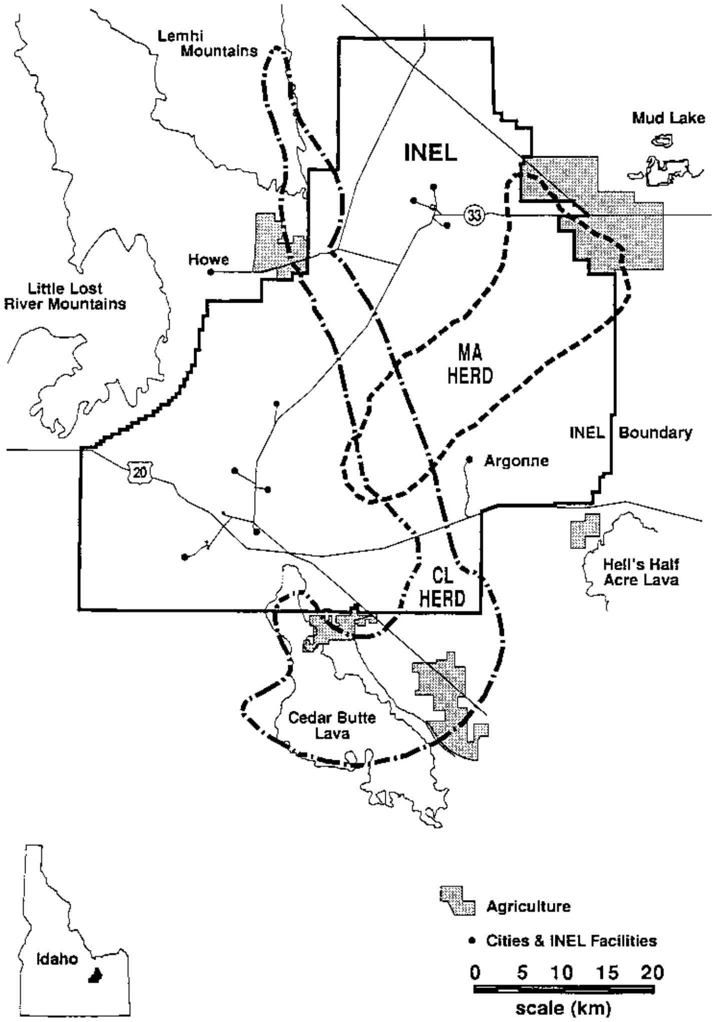

Figure 1. Annual Cedar-Lemhi (CL) and Mud Lake-Argonne (MA) wapiti herd distributions in the Idaho National Engineering Laboratory (INEL) area. Marked males having distributions that only partially overlapped with the cow-calf herds were not drawn.

the distance between their winter and summer areas was about 9 km. We calculated annual home-range areas for 3 MA wapiti (2 males, 1 female). For these areas, the number of relocations per individual ranged from 91 to 152. Their mean MCP area was 551 km^2 (3.6 SE, $n = 3$).

In contrast, the Cedar-Lemhi (CL) herd spent much of its time on non-INEL land, using the central portion of the INEL only when migrating between the wintering area, Lemhi mountains, and the summering area, Cedar-Butte-Lava area. Time spent by CL wapiti during migrations varied from 2 days (fall) to 3 weeks (spring). Annual home-range sizes for CL wapiti were not calculated because the distance between the edges of their summer and winter areas was about 40 km.

Seasonal Home Ranges

The number of calculable home-range areas for marked individuals varied with season (Table 1). No winter home-range sizes were calculated because the number of relocations per individual was <20 for all animals. The highest numbers of relocations per individual occurred in the summer. Twelve of the 14 summer home-range areas had >30 relocations/individual. All spring and fall home-range areas had ≤31 relocations/individual. Spring and fall home ranges for CL wapiti were awkward to quantify because movement between the Cedar Butte Lava area and the Lemhi Mountains occurred at these times. Fall home ranges of CL wapiti were especially troublesome because movement between the Cedar Butte Lava area and the Lemhi mountains occurred more than once for some animals and patterns of individuals were not consistent between years. Thus, spring and fall home ranges for CL wapiti refer to the area, either Lemhi Mountains or Cedar Butte Lava, where most of a given marked animal's time was spent.

The MCP home-range areas had interaction between seasons and herds ($F = 9.2$; 2, 16 df; $p = 0.002$). Fall, MA areas were the largest for all season-herd combinations ($p \leq 0.02$). Summer and spring areas were not different between herds ($p \geq 0.2$). Summer areas were larger ($p \leq 0.01$) than spring and fall areas for CL wapiti. The log transformation created asymmetrical confidence intervals causing variation in power. Thus, power for detecting a 50 km^2 (effective size) difference between 2 home-range areas, was about 0.2 at upper confidence interval boundaries and was 0.5-0.6 at lower confidence interval boundaries. Similarly, power for detecting a 100 km^2 difference between 2 areas varied from 0.5-0.6 to >0.9 at upper and lower confidence interval bounds, respectively.

TABLE 1. Seasonal home range size by herd, gender, and method for wapiti in the Idaho National Engineering Laboratory area, 1989-1991. Sample size was the number of individual wapiti.

Category	Sample size	Range (km^2)	Mean (km^2)	SE
Minimum Convex Polygon Home Range				
Mud Lake-Argonne				
fall	3	438-480	466	14
winter[a]	0	—	—	—
spring	2	143-198	170	28
summer	5	114-220	165	22
Cedar-Lemhi				
fall	3	65-116	91	15
winter[a]	0	—	—	—
spring	4	61-130	95	14
summer	9	79-593	245	55
95% Harmonic Mean Home Range				
Mud Lake-Argonne				
fall	3	246-274	257	9
winter[a]	0	—	—	—
spring	2	116-218	167	51
summer	5	47-479	335	78
Cedar-Lemhi				
fall	3	132-177	149	14
winter[a]	0	—	—	—
spring	4	115-250	170	31
summer	9	133-332	265	21
Harmonic Mean Core Area[b]				
Mud Lake-Argonne				
fall	3	0-105	57	31
winter[a]	0	—	—	—
spring	2	0- 0	0	0
summer	5	93-148	128	10
Cedar-Lemhi				
fall	3	41- 55	46	4
winter[a]	0	—	—	—
spring	4	0- 82	46	18
summer	9	26- 86	70	7

[a] Not quantified because number of relocations per individual <20.

[b] A 0.0 value for a core area indicates Program Home Range did not detect a core area for at least one individual.

Differences among the 95% harmonic-mean home-range areas were not significant ($F = 1.8$; 16 df; $p = 0.16$). This conclusion may be an error because power was low. Power for detecting a 50 km^2 difference (effective size) between 2 home-range areas, was 0.25. Power for detecting a 100 km^2 difference between 2 areas was 0.73.

Harmonic-mean core areas had interaction between season and herd ($F = 6.9$; 2,16 df; $p = 0.007$). Summer core areas for MA wapiti were the largest ($p \leq 0.005$) for all herd-season combinations. Spring core areas for MA wapiti were smaller ($p = 0.04$) than their fall core areas. Spring core areas for MA wapiti were also smaller ($p = 0.01$) than summer core areas for CL wapiti. Power for detecting a 20 km^2 difference (effective size) between 2 core areas, was 0.5. Power for detecting a 35 km^2 difference between 2 core areas was 0.9.

Daily Distances

Spatial differences in wapiti movement patterns contributed to differences in daily distances traveled. CL males had home ranges that only partially overlapped with that of CL females. Home ranges of MA males overlapped with that of MA females, but MA males often moved independently of MA females. For example, infrared, helicopter scans of Mud Lake-area croplands in July showed MA wapiti, including some males, would be in 1 grain field while several all-male groups of 1-3 animals would be scattered across alfalfa fields.

Daily distances were different among herd-month-gender combinations ($F = 8.7$; 1,33 df; $p = 0.006$). Daily distances traveled by CL males increased ($p = 0.01$) from July to August (Table 2). Increases in daily distances traveled by MA females and MA males from June to August were not significant ($p \geq 0.2$). The decrease in daily distances traveled from July to August by CL females was also not significant ($p \geq 0.9$). Again, the log transformation created asymmetrical confidence intervals causing power to vary. Thus, power for detecting a 2.0 km difference (effective size) between two mean distances was 0.1 and 0.3 at upper and lower confidence boundaries, respectively. Power for detecting a 5.0 km difference between two mean distances was 0.5 and 0.8 at upper and lower confidence boundaries, respectively.

TABLE 2. Daily distances by herd, month, and gender for wapiti during June-August in the Idaho National Engineering Laboratory area 1989-1991. Sample size was the number of unique animal-month-year combinations.

Category	Sample size	Mean (km)[b]	SE[c]
Overall	59	8.8	0.8
Herd-Month-Gender[a]			
CL-June-female	0	—	—
CL-June-male	0	—	—
CL-July-female	13	9.6	2.0
CL-July-male	3	8.4	4.1
CL-August-female	13	4.9	0.9
CL-August-male	4	17.3	3.3
MA-June-female	2	7.5	0.8
MA-June-male	1	4.4	—
MA-July-female	5	8.2	1.1
MA-July-male	7	9.1	1.0
MA-August-female	4	10.4	2.6
MA-August-male	7	10.2	1.2

[a] MA = Mud Lake-Argonne herd; CL = Cedar-Lemhi herd.

[b] — = No data available.

[c] — = Not calculable.

Cropland Use

Intermittent cropland use by marked wapiti began in June. Track surveys in the Mud Lake area showed wapiti used cropland nightly in groups of 5-10 animals. Track surveys in the Cedar Butte Lava area also showed nightly cropland use by wapiti. Marked wapiti from both herds exhibited a distinct circadian pattern from July through September. Daytime bedsites were in native rangeland, while nighttime relocations were in cropland. MA wapiti entered and exited cropland in darkness, while CL wapiti often entered cropland before sunset and exited after sunrise. No daytime cropland relocations for MA wapiti occurred, while CL wapiti were occasionally relocated in cropland during rainy days. Crops used by wapiti changed over the summer. Wheat, oats, and barley were crops used until the end of July when these crops were dried for harvest. Wapiti began using alfalfa at this time. Alfalfa use became intermittent in October, ceasing with freezing nighttime temperatures. Daytime and nighttime areas were generally the same for marked wapiti from October through May.

Discussion

Annual, MCP home-range sizes for MA wapiti, 551 km^2, were larger than that for other non-migratory wapiti and red deer (*Cervus elaphus*) herds in non-arid environments which ranged 3-112 km^2 (Catt and Staines 1987, Craighead et al.

1973, Edge et al. 1985, Edge et al. 1986, Franklin et al. 1975, Franklin and Lieb 1979, Jeppesen 1987, Waldrip and Shaw 1979). The annual, MCP home-range area for wapiti in the Washington sagebrush-steppe, 162 km^2, was also smaller than that for MA wapiti (McCorquodale et al. 1989).

The MCP estimate for summer home-range sizes for wapiti in the sagebrush-steppe of Washington, 95 km^2 (McCorquodale et al. 1989), was smaller than that for wapiti in the INEL area, 165 km^2 and 245 km^2 for MA and CL wapiti, respectively (Table 3). Summer home-range sizes for wapiti and red deer in non-arid environments were also smaller, 1-31 km^2, than that for wapiti in sagebrush-steppe (Boer 1989; Catt and Staines 1987; Craighead et al. 1973; Edge et al. 1985; Edge et al. 1986; Franklin et al. 1975; Franklin and Lieb 1979; Georgii 1980a,b; Irwin and Peek 1983; Jenkins and Starkey 1982; Jeppesen 1987; Martinka 1969; Waldrip and Shaw 1979; Wallace 1991).

Mean daily distances travelled by wapiti during the summer in the INEL area were high in comparison with other investigations (Table 4). Wapiti in the Washington sagebrush-steppe travelled 2.2 km/day from June through August (McCorquodale et al. 1989), while Jackson Hole wapiti travelled 3.2 km from 16 July to 15 September (Martinka 1969). Wapiti in Arizona's White Mountains also travelled less during the summer, 7.5 km/day (Wallace 1991), than wapiti in the INEL area.

Thus, wapiti in the INEL area had the largest home-range sizes and longest daily distances of all investigations examined. Of course, it is important to keep in mind that these comparisons are more qualitative than quantitative in nature because of methodological differences. Confounding influences in home-range comparisons include home-range calculation method, number of relocations per home range, time period, and gender composition.

TABLE 3. Summary of summer, MCP home range areas for adult wapiti and red deer from 14 investigations. Reported measures of variation are not listed because they could not be standardized across the investigations.

Area (km^2)	Period	Elk[a]	Habitat	Source
1[b]	Jun-Sep	fr	spruce-fir-beech	Georgii 1980
2	1 Jul-15 Sep[c]	fr	spruce	Catt and Staines 1987
3[d]	Jun-Aug[c]	h	beech-redwood	Franklin et al. 1975
3	Mar-Sep[c]	fr	conifer-moorland	Jeppesen 1987
4	Apr-Nov	mr	spruce-fir-beech	Georgii 1980
4	1 Jul-15 Sep[c]	mr	spruce	Catt and Staines 1987
6	Apr-Aug	f	prairie-oak	Waldrip and Shaw 1979
8	16 Jun-8 Sep	f	cedar-hemlock	Irwin and Peek 1983
10	21 Jun-23 Sep	f	lodgepole pine	Craighead et al. 1973
11[e]	5 Jun-15 Sep[c]	f	spruce-hemlock	Jenkins and Starkey 1982
12	Jun-Sep	f	spruce-fir-alpine	Bear 1989
12	6 May-15 Sep	m	conifer	Martinka 1969
12	6 May-15 Sep	f	conifer	Martinka 1969
16	Jun-Sep	m	spruce-fir-alpine	Bear 1989
20	Jun-Aug	f	conifer-chaparral	Wallace 1991
31	Jun-Aug	f	conifer-chaparral	Wallace 1991
95	Jun-Aug	f	shrub-steppe	McCorquodale et al. 1989
118	Jun-Aug	m	shrub-steppe	McCorquodale et al. 1989
165	Jul-Sep	h	sagebrush	This study
245	Jul-Sep	h	juniper-lava	This study

[a] fr = female red deer, mr = male red deer, h = wapiti herd, f = female wapiti, m = male wapiti.

[b] Quadrat procedure.

[c] Home range size calculations involved periods other than summer.

[d] Boundaries based on vegetation types.

[e] 95% probability ellipse.

TABLE 4. Comparisons of daily distances travelled by adult wapiti and red deer from 8 investigations.

Daily Distance (km)	Variation[a]	Method[b]	Sampling Period	Elk[c]	Habitat	Source
0.2	—[d]	mp	May	f	lodgepole pine	Craighead et al. 1973
1.2	—[d]	mp	June	f	lodgepole pine	Craighead et al. 1973
1.4	0.1	cr	annual	f	conifer	Edge and Marcum 1985
2.2	0.2	cr	summer	h	shrub steppe	McCorquodale et al. 1989
2.4	—	mp	fall	h	beach-redwood	Bowyer 1981
2.5	—[d]	mp	Aug	f	lodgepole pine	Craighead et al. 1973
3.0	0.4	cr	fall	h	shrub-steppe	McCorquodale et al. 1989
3.2	1.0-5.6	cr	16 July-15 Sep	f	conifer	Martinka 1969
3.2	0.2	mp	winter	h	conifer-chaparral	Wallace 1991
3.3	1.1-9.4	cr	6 May-15 July	f	conifer	Martinka 1969
3.5	0.6	cr	spring	h	shrub steppe	McCorquodale et al. 1989
4.0	0.5	mp	annual	fr	conifer-moorland	Jeppesen 1987
4.0	0.3	mp	spring	h	conifer-chaparral	Wallace 1991
4.2	—[d]	mp	Oct	f	lodgepole pine	Craighead et al. 1973
6.5	0.5	mp	fall	h	conifer-chaparral	Wallace 1991
7.5	0.3	mp	summer	h	conifer-chaparral	Wallace 1991
7.1	1.3	m2	June-Aug	f	juniper-lava	This study
12.6	3.6	m2	June-Aug	m	juniper-lava	This study
8.9	1.2	m2	June-Aug	f	sagebrush	This study
9.5	0.8	m2	June-Aug	m	sagebrush	This study

[a] Variations were either standard errors or ranges; — = unavailable.

[b] Distances were calculated from the following: cr = consecutive relocations, mp = multiple points over 24 hours, and m2 = day-night relocations <24 hours apart.

[c] fr = female red deer, h = wapiti herd, f = female wapiti, m = male wapiti.

[d] Data were from one animal.

Likewise, the quality of daily-distance estimates are affected by the gender composition and length of time periods between the relocations used.

Why do wapiti in the INEL area travel so much? Aridity may be a factor. Annual precipitation and annual, MCP home-range areas have been previously suggested to be related (McCorquodale et al. 1989). We agree with McCorquodale et al.'s (1989) point that while annual home-range area is highly correlated with annual precipitation, this relationship is not linear. That is, home-range size is influenced by multiple factors including forage availability, juxtaposition of resources, physiological state, cover quality, ambient temperature, habitat requirements, abundance of insects, difficulty of travel, population density, plant phenology, human disturbance, and social relationships (Craighead et al. 1973; Georgii 1980a,b; Jenkins and Starkey 1982; Irwin and Peek 1983; Edge et al. 1985; McCorquodale et al. 1989). For example, while it is true that the INEL area is more arid than the Washington sagebrush-steppe, human disturbance may be more of a constraint at the Washington site. We found wapiti home ranges did not conform to the INEL's boundaries; however, McCorquodale et al. (1989) found wapiti home ranges roughly matched the size and shape of an area free from human disturbance.

The key to explaining the large summertime movements of wapiti in the INEL area lies in understanding the motivation for the circadian pattern between the cropland and sagebrush habitats. Obviously, surface water was important. However, it was not the sole motivator, because in certain areas the wapiti were equally close to cropland and guzzlers that were in native vegetation.

Perhaps the key motivator is nutrition. This is unlikely, since the nutritional quality of the native forage was sufficient to meet elk maintenance requirements (J. C. Mosley, Univ. Id., unpubl. data). A worthwhile study would be to better separate the forage versus water needs of the INEL wapiti by manipulating crop types and irrigation regimes.

Juxtaposition of resources also provided an incomplete explanation (of at least differences between the CL and MA herds) because inspection of topographic maps indicated distances between vegetation types used during the day and nearest cropland were similar; however, human-related disturbances differed between the wapiti herds. These disturbances appeared to affect at least the timing of cropland use. When MA wapiti were hunted during the summer, they limited the time they spent in cropland to early morning hours (roughly 0200-0400). This contrasts with the CL wapiti which were not subjected to depredation hunts and would enter cropland during daylight hours.

Jeppesen (1987) found similar circadian patterns among red deer in Denmark in a mosaic of conifer plantations, moorland, and grassland. Red deer bedded diurnally in forest cover and fed nocturnally in more open vegetation types. Jeppesen (1987) attributed this pattern as an adaptation to human disturbance which included hunting. This is also an appropriate hypothesis for wapiti in the INEL area because human access to INEL land was restricted creating a disturbance-free zone. Unfortunately, we were unable to quantify the human disturbance adjacent to INEL land. Still, human disturbance is also not the sole motivator because there were times when the CL wapiti were not being disturbed while on cropland, yet they maintained a circadian pattern.

A heat-stress hypothesis may be the best explanation. Heat stress increases maintenance requirements (Young 1988:461) and may cause ruminants to seek cover during the day and shift their grazing behavior to nighttime. Wapiti in the Washington sagebrush-steppe were noted to water at night and daily distances calculated with multiple relocations within a 24-hour period were comparable to those in the INEL area (McCorquodale, Pacific Northwest Lab., pers. commun.).

In conclusion, the most important (interrelated) factors causing the relatively large home-range areas found in our study are aridity, juxtaposition of habitat components, and human disturbance. Moreover, a heat-stress hypothesis best explains the circadian pattern of daily movements observed during the summer. This implies wapiti in any hot and arid environment would exhibit a similar pattern.

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