HABITAT SELECTION BY ELK BEFORE AND AFTER WOLF REINTRODUCTION IN YELLOWSTONE NATIONAL PARK

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Abstract: Prey species are thought to select habitats to obtain necessary resources while also avoiding predation. We examined whether habitat selection by elk (Cervus elaphus) changed following the reintroduction of wolves (Canis lupus) into Yellowstone National Park in 1995. Using conditional fixed-effects logistic regression to build habitats-selection models, we compared seasonal habitat selection by elk based on weekly elk radiolocations taken in 1985–1990 (without wolves) and 2000–2002 (with wolves). Fire-related habitat changes and climate likely interacted with wolf avoidance in shaping habitat selection by elk. In summer, when wolf activity was centered around dens and rendezvous sites, elk apparently avoided wolves by selecting higher elevations, less open habitat, more burned forest, and, in areas of high wolf density, steeper slopes than they had before wolf reintroduction. In winter, elk did not spatially separate themselves from wolves. Compared to the pre-wolf period, elk selected more open habitats in winter after wolf reintroduction, but did not change their selection of snow water equivalents (SWE) or slope. Elk appear to select habitats that allow them to avoid wolves during summer, but they may rely on other behavioral antipredator strategies, such as grouping, in winter. This study provides evidence that wolves can alter seasonal elk distribution and habitat selection, and demonstrates how the return of wolves to Yellowstone restores important ecosystem processes.

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Key words: Canis lupus, Cervus elaphus, elk, habitat selection, predation risk, resource selection functions, wolf, Yellowstone National Park.

In predator–prey systems, habitat selection by prey species may require making tradeoffs between the acquisition of resources (e.g., forage, mates, shelter) and avoidance of predators (Werner and Anholt 1993). To reduce the risk of predation, prey theoretically make behavioral decisions to decrease the probabilities of encounter, attack, and capture, and the time spent vulnerable to predation ( Lima and Dill 1990). Antipredator behaviors by prey include distancing themselves from a predator, keeping vigilant to detect predators, and using habitat structure to hide from predators or to evade pursuing predators once attacked (Bergerud et al. 1984, Elgar 1989, Kie 1999). Predator-induced habitat selection can have population-level consequences if predator avoidance detracts from foraging or reproduction (Sinclair and Arcese 1995, Sutherland 1996:157–166, Lima 1998). However, habitat selection also can stabilize predator–prey systems by giving prey spatial or temporal refuges from predators (Huffaker et al. 1963, Pimental et al. 1963, Taylor and Pekins 1991). Habitat shifts and predator avoidance by individual prey can buffer demographic declines due to predation, thus facilitating the persistence of the prey population ( Lima 1998).

Habitat selection by elk has been well documented in North American populations (reviewed in Slovik et al. 2002). Elk are habitat generalists, once distributed throughout much of the continent (O’Gara and Dunders 2002). Although primarily grazers, elk also browse during fall and winter. They use forest edges for thermal and hiding cover, often use sagebrush habitats for calving, and select slopes of low to moderate steepness, particularly those with south-facing aspects (Houston 1982, Slovik et al. 2002). Elk are long-legged cursors, adapted to sustained running over uneven, open terrain to outdistance predators (Geist 2002).

Studies of wolf–ungulate interactions have found that ungulates avoid areas of high wolf density, especially during calving season, presumably to reduce their risk of predation (Mech 1977, Edwards 1983, Stephens and Peterson 1984, Ferguson et al. 1988, Dekker et al. 1995). Escape habitats that elk use when disturbed by predators include rivers, edges of cliffs, sloped terrain, tree

Predation risk can vary among individuals depending on age and body condition, as shown in several studies in which wolves selectively killed old and young prey (Carbyn 1983, Kunkel et al. 1999, Smith et al. 2003a). Ungulates are particularly vulnerable to predation during severe winters when snow accumulation and crust formation make locomotion difficult and forage inaccessible (Parker et al. 1984, Tellier and Kelsall 1984, Jédzajewski et al. 1992, Huggard 1993, Mehl et al. 2001). Some studies have suggested that ungulate avoidance of wolf predation, whether accomplished by moving to areas of low wolf density or by spending more time vigilant, costs them foraging opportunities (Edwards 1983, Furguson et al. 1988, Laundré et al. 2001).

The reintroduction of wolves into Yellowstone National Park (YNP), Wyoming, in 1995 after a 70-year absence (Bangs and Fritts 1996) has been a major perturbation to the region and to elk in particular (Smith et al. 2003a). Before wolf reintroduction, predation upon elk calves by grizzly bears (Ursus arctos), black bears (U. americanus), and coyotes (C. latrans) accounted for nearly 90% of predator-caused mortalities and 40% of total mortalities of calves (Singer et al. 1997). For adult elk, in contrast, bears, coyotes, and cougars (Felis concolor) are minor sources of mortality, none of which are believed to reduce the adult segment of the elk population substantially (Murphy 1998, Knight et al. 1999, Crabtree and Sheldon 1999). As YNP's most abundant ungulate, elk now serve as a vital food source for wolves, constituting 92% of wolf kills (Smith et al. 2004a).

The YNP wolf population has grown rapidly from 31 individuals in 1995 to 174 individuals in 2003 (Smith et al. 2004b), yielding a high wolf density of 50 wolves/1,000 km² (Smith et al. 2003a). With wolves restored to the system, elk in Yellowstone now face substantially greater predation pressure, which could prompt them to alter their habitat selection patterns. To examine this possibility, we tested for differences in habitat selection by radio-collared elk before versus after wolf reintroduction.

STUDY AREA

Yellowstone National Park covers an area of 8,991 km² in the northwest corner of Wyoming and on adjacent lands in Montana and Idaho. Elevation varies from 1,500 to 3,300 meters. Precipitation at low elevations averages 25 cm annually, 30–35% of which falls as snow. High elevations receive roughly 180 cm of precipitation per year, of which 70% is snow (Farnes et al. 1999).

The Northern Range, which serves as the wintering grounds of the Northern Yellowstone elk herd, spans the Lamar River and Yellowstone River watersheds and covers an area of 1,500 km² (Lemke et al. 1998). This area sits within the lower elevations of the park and adjacent land north of the park, where the climate is milder and drier than in other regions of the park (Houston 1982). The vegetation is primarily steppe or shrub steppe (big sagebrush, Artemisia tridentata; Idaho fescue, Festuca idahoensis) with some stands of conifers (mostly Douglas-fir, Pseudotsuga menziesii) and aspen (Populus tremuloides; Despain 1990).

Continuous conifer forests (Engelmann spruce, Picea engelmannii; subalpine fir, Abies lasiocarpa; lodgepole pine, Pinus contorta; whitebark pine, Pinus albicaulis) dominate the higher elevations on the Buffalo Plateau (north of the park) and in the interior and eastern portions of the park (Despain 1990) where the Northern herd summers (Houston 1982:4).

In 1988, severe drought conditions led to the most extensive fires in the park's recorded history: 36% of YNP was burned (Despain et al. 1989, Singer et al. 1989). The fires briefly stimulated increases in the protein levels and digestibility of forage, but in the first 2 years after the fires, elk did not show a preference for burned over unburned areas (Romme et al. 1995, Norland et al. 1996). However, secondary effects of the fires on elk habitat selection may emerge as successional changes in vegetation take place (Norland et al. 1996). Elk may show greater use of burned forest as an herbaceous understory develops in these areas (Singer and Harter 1996, Turner et al. 1999).

During our current study from 2000 to 2002, drought prevailed again in the northern Rocky Mountains (National Climatic Data Center 2003). Because drought adversely affects forage productivity, dry conditions could drive elk to use higher elevations that receive relatively more precipitation.

METHODS

Data Collection

We used helicopter net-gunning to capture adult cow elk in the winters of 2000–2002 (Cook et al. 2004). To ensure a good representation of the herd, we aerially surveyed elk distribution within 1 day prior to capture. Then when targeting elk for capture, we distributed radiocollars proportionally.
among elk groups throughout the Northern Range. However, we did not capture elk outside of park boundaries. Each elk was fitted with a VHF radiocollar equipped with a mortality beacon.

We collected data between 21 June 2000 and 1 November 2002, comprising 3 summers and 2 winter seasons with wolves present in YNP. We attempted to locate each radiocollared elk once per week by airplane. We recorded positions in Universal Transverse Mercator (UTM) coordinates in North American Datum 1983 using a Garmin Global Positioning System (GPS) unit. When marking elk locations, an effort was made to visually identify the collared animal, or at least its group. Telemetry error ranged from an estimated 24 m (SE = 4) for locations in which the collared individual was visually identified (69% of summer locations and 65% of winter locations) to 86 m (SE = 13) for locations in which no elk were seen and the position was determined solely from the radio signal (15% of summer locations and 3% of winter locations; Mao 2003).

For comparison to these elk locations with wolves present, we used locations of radiocollared elk monitored before wolf reintroduction. These individuals were tracked aerially from January 1985 to April 1987 (7 cows) and January 1987 to April 1990 (21 cows). The first set of cows was captured in clover traps in 1985 and 1986 in the Stephens Creek and Eagle Creek areas of the lower Northern Range as part of a study examining movements and distribution of elk relative to hunting zones (Vore 1990). We used data on only those cows that migrated into the park for comparison to the current sample of elk. The second set of cows was captured for a separate study in 1987 using clover traps placed in the middle and upper sections of the Northern Range (Singer 1988, Vales and Peek 1996). We subsampled these data to eliminate consecutive locations <5 days apart for all individuals.

In addition, because the cow elk data from the pre-wolf period did not fully represent 2 of the herd segments (Quadrant/Mt. Holmes and Buffalo Plateau), we included locations of radiocollared calves monitored from 1987 to 1990 (66 calves total, 65 having summer data, 39 with winter data; Singer et al. 1997, Smith et al. 1998) as a substitute for cow locations. Only those calves that survived at least their first summer were included in the analysis. Consecutive calf locations spaced <5 to 7 days apart were discarded. We classified all locations from the pre-wolf period as either pre-fire or post-fire, based on the date of the location relative to the date of the nearest burn that occurred in the 1988 fires. Most of these locations were taken using aerial telemetry and plotted manually on 1:24 topographic maps. We estimated error to be <1 km.

The season for each location was designated as summer, winter, or migration, based on whether the elk was on its summer home range (i.e., not on the Northern Range), winter home range (i.e., on the Northern Range), or in between. The summer and winter locations of 6 nonmigratory elk that summered on or near the Northern Range were distinguished using the median dates of transition between summer and winter ranges shown by the migratory elk. Spring migration generally occurred in late May and fall migration occurred in mid-October to early November (S. B. Evans, University of Minnesota, unpublished data). Elk locations taken during migration periods were not used in the analysis of habitat selection. All locations were recorded during daylight hours, usually between 0700 and 1300. This analysis therefore only addresses habitat selection by elk during these times of the day.

Habitat Availability

The spatial extent of habitats available to individuals was defined by seasonal herd segment areas. Houston (1982:34) described herd segments as "elk with similar affinities for specific range areas and similar patterns of movement in response to changing environmental conditions." A herd segment area thus approximates the area over which an elk might reasonably travel between successive relocations taken at approximately a weekly interval. This spatial scale also is appropriate for YNP because a fairly large extent of >10 km diameter, such as the area of a seasonal herd segment, is necessary to capture the variability in landscape features of YNP (Boyce et al. 2003).

We did not consider an extent larger than the herd segment area because elk show strong fidelity to their home ranges (Craighead et al. 1972, Shoesmith 1979), so selection of a herd segment area from the available parkwide landscape is likely to be dictated more by learned migration routes and familial associations (Shoesmith 1979) than by resources and habitat types. In addition, because there were insufficient numbers of locations per elk to adequately define individual home ranges (requiring ≥50 locations per animal; Leban et al. 2001), we could not pursue analysis at a scale smaller than the size of the herd segment.

To define herd segments, we grouped elk locations into several geographic regions. Summer elk locations were assigned to 1 of 5 herd segments.
based on similarities in migration routes and geographic summer ranges. Winter elk locations were partitioned into 4 regions of the Northern Range delineated by topographic features (e.g., river canyons and mountain ranges) and similarities in distributions among individuals. The areas available for use by the seasonal herd segments were then defined by 95% kernel home ranges generated from these groupings of elk locations (Figs. 1, 2). Elk locations falling outside of the kernels were discarded from further analysis.

We assumed that each elk had a priori knowledge of its portion of the summer or winter range, and that it could travel throughout its home-range area within the time elapsed between relocations. We generated points randomly placed within these home-range polygons (20 per summer elk point, 13 per winter elk point) to represent locations available to elk, and we matched these random points to corresponding elk locations spatially (within each polygon) and temporally (by season and also within seasons by time-specific Geographic Information System [GIS] layers: see below).

Habitat Characteristics

We used GIS coverages of vegetation type, habitat openness, elevation, slope, wolf density index, and snow water equivalent (SWE: Farnes and Romme 1993) to obtain data on habitat characteristics at used and available locations (Tables 1, 2). We used 2 vegetation maps representing plant cover types before and after the 1988 fires (Dixon 1997, Matson et al. 1999). For mosaic vegetation pixels (i.e., >1 vegetation type), we randomly chose 1 of the first 2 listed vegetation types. We then consolidated the vegetation types into broad categories: grasslands, shrublands, other nonforest (rock, talus, lithic ridges, streams and ponds, etc.), burned conifer, unburned conifer, and aspen. Willow (Salix spp.) habitats were not well mapped on
Table 1. Availability of vegetation typesa on the northern Yellowstone elk herd’s summer and winter ranges in Yellowstone National Park, 1985–2002.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Summer range (%)</th>
<th>Winter range (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>12</td>
<td>15</td>
</tr>
<tr>
<td>Shrubland</td>
<td>11</td>
<td>40</td>
</tr>
<tr>
<td>Other nonforest</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Aspen</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Burned conifer</td>
<td>28b, 27c</td>
<td>0c, 6c</td>
</tr>
<tr>
<td>Unburned conifer</td>
<td>70b, 45c</td>
<td>42b, 34c</td>
</tr>
</tbody>
</table>

a Minimum mapping resolution was approximately 2 ha (Dixon 1997); although, the cell size of the Geographic Information System grid layer was 25 m.

b Before 1988 fires.

c After 1988 fires.

the Northern Range, so willow could not be considered as a separate vegetation type; instead it was included in the shrublands category (Mattson et al. 1999). Habitat openness was calculated for each grid cell as the percentage of nonforested pixels within a 400-m radius, which was the median distance at which humans approaching on foot would elicit a fleeing response in YNP elk (Cassirer et al. 1992). Elevation was taken from a 30-m Digital Elevation Map (DEM), and slope in degrees was derived from the DEM.

Wolf density index maps, represented by kernel utilization distributions (Worton 1989, Hooge and Eichenlaub 1997) were made using weekly radiolocation data of collared wolves. Radiocollars were maintained on 27%, 34%, and 25% (32, 45, and 37 wolves) of the YNP wolf population in 2000, 2001, and 2002 (Smith et al. 2001, 2003b; Smith and Guernsey 2002). Collars were distributed among wolf packs in proportion to pack size, so that wolf radiolocations were representative of the distribution of the YNP wolf population.

The wolf density index is a unit-less measure of relative wolf predation risk. Separate wolf maps were made for early (May–Jun), mid (Jul–Aug), and late (Sep–Oct) summer, and winter (Nov–Apr) for each year (2000–2002; Fig. 3). The index was calculated for each pixel as:

$$\text{Wolf density index} = \left(101 - \text{Kernel value}\right) \times \frac{N_w}{10},$$

where $N_w$ was the number of wolves on the landscape (estimated as 69, 90, and 88 adult wolves in early and midsummers 2000–2002; estimated as 126, 139, and 158 adults and pups in late summers 2000–2002 and winters 2000–2001 and 2001–2002: D. W. Smith, National Park Service, unpublished data). This factor adjusts the wolf density index to account for (1) annual variation in wolf population size, and (2) seasonal variation in wolf distribution and movements while pups develop from nonhunting dependents in early and midsummer into more active predators in late summer and winter. The wolf density index ranges from low (6.9) to high (1,580) values, representing a maximum wolf density of 50 wolves/1,000 km² on the Northern Range in winter (Smith et al. 2003a).

Snow maps, measuring SWE in cm, were made using the Yellowstone snow model (Wockner et al. 2002). A snow map was made for each day on which the cumulative change in SWE since the previously mapped snow day was ≥1.2 cm at either the Mammoth, Tower Falls, or Lamar snow stations. Farnes et al. (1999) estimated that accumulations of 2.5 to 5.0 cm of SWE can prompt elk to move to areas of lower snow, so snow maps made at an interval of <2.5 cm of SWE should be sufficient to detect responses of elk to changes in SWE.

To assess moisture conditions during the foraging growing season, we calculated the mean Keetch-Byram Drought Index (KBDI: Keetch and Byram 1968) values for the first 750 Growing Degree-Days (GDD) of each year. Most forage production occurs during these first 750 GDD (Farnes et al. 1999). We averaged the KBDI within each of 5 weather stations distributed throughout the elk summer range (Tower Falls, Canyon, Yellowstone Lake, Parker Peak, and Old Faithful) and then took the mean of these values across stations but within years. We compared the mean KBDI for each year with the 1961–1990 mean KBDI for these stations reported by Farnes et al. (1999) using paired t-tests. The

Table 2. Continuous variables used to predict habitat selection by elk in Yellowstone National Park, 1985–2002. Median, minimum, and maximum values are based on random (available) points.

<table>
<thead>
<tr>
<th>Variable</th>
<th>GIS® grid cell size (m)</th>
<th>Summer range</th>
<th>Winter range</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Median</td>
<td>Min</td>
</tr>
<tr>
<td>Openness (%)</td>
<td>25</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>30</td>
<td>2,477</td>
<td>1,639</td>
</tr>
<tr>
<td>Slope (degrees)</td>
<td>30</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Wolf density index</td>
<td>100</td>
<td>142.2</td>
<td>6.9</td>
</tr>
<tr>
<td>SWE® (cm), 1985–1990</td>
<td>100</td>
<td>100</td>
<td>3.4</td>
</tr>
<tr>
<td>SWE® (cm), 2000–2002</td>
<td>100</td>
<td>100</td>
<td>4.4</td>
</tr>
</tbody>
</table>

a Snow Water Equivalent.

b Geographic Information System.
years 1988, 2000, and 2001 were expected to be drought years. KBDI data were not available for summer 2002, so moisture levels for this growing season could not be assessed.

Habitat-selection Models

We built models of habitat selection for the pre- and post-wolf periods by comparing used and available habitats to obtain Resource Selection Functions (RSF; Manly et al. 2002). RSFs are equations that predict the relative probability of use, taking the form:

$$w(X) = \exp(\beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n),$$

where $w(X)$ is the RSF value, $\beta$s are the estimated coefficients, and $X$s are habitat variables (Manly et al. 2002).
Table 3. A priori candidate models for summer habitat selection by elk in Yellowstone National Park for pre-wolf (1985–1990) and post-wolf (2000–2002) periods. For each model, −2* log-likelihood (−2LL), number of parameters (K), difference in AICc compared to lowest-scoring model (Δj), and AICc weight (wj) are given.

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Model structureb</th>
<th>−2LL</th>
<th>K</th>
<th>Δj</th>
<th>wj</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-wolf:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NW-1</td>
<td>VEG</td>
<td>8532</td>
<td>5</td>
<td>261.7</td>
<td>0.0</td>
</tr>
<tr>
<td>NW-2</td>
<td>ELEV + VEG</td>
<td>8242</td>
<td>7</td>
<td>155.8</td>
<td>0.0</td>
</tr>
<tr>
<td>NW-3</td>
<td>SECURITY + VEG</td>
<td>8331</td>
<td>9</td>
<td>119.2</td>
<td>0.0</td>
</tr>
<tr>
<td>NW-4</td>
<td>ELEV + SECURITY + VEG</td>
<td>8258</td>
<td>11</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Post-wolf-NW:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NW-1</td>
<td>VEG</td>
<td>11158</td>
<td>5</td>
<td>188.3</td>
<td>0.0</td>
</tr>
<tr>
<td>NW-2</td>
<td>ELEV + VEG</td>
<td>11026</td>
<td>7</td>
<td>59.5</td>
<td>0.0</td>
</tr>
<tr>
<td>NW-3</td>
<td>SECURITY + VEG</td>
<td>11103</td>
<td>9</td>
<td>141.2</td>
<td>0.0</td>
</tr>
<tr>
<td>NW-4</td>
<td>ELEV + SECURITY + VEG</td>
<td>10958</td>
<td>11</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>W-1</td>
<td>WOLF + VEG</td>
<td>11141</td>
<td>7</td>
<td>179.2</td>
<td>0.0</td>
</tr>
<tr>
<td>W-2</td>
<td>WOLF + ELEV + VEG</td>
<td>11020</td>
<td>9</td>
<td>62.0</td>
<td>0.0</td>
</tr>
<tr>
<td>W-3</td>
<td>WOLF + SECURITY + VEG</td>
<td>11085</td>
<td>11</td>
<td>130.7</td>
<td>0.0</td>
</tr>
<tr>
<td>W-4</td>
<td>WOLF + ELEV + SECURITY + VEG</td>
<td>10953</td>
<td>13</td>
<td>2.9</td>
<td>0.2</td>
</tr>
<tr>
<td>W-ii</td>
<td>WOLF + ELEV + WOLF*ELEV + VEG</td>
<td>11020</td>
<td>10</td>
<td>63.6</td>
<td>0.0</td>
</tr>
<tr>
<td>W-iii</td>
<td>WOLF + SECURITY + WOLF*SECURITY + VEG</td>
<td>11081</td>
<td>13</td>
<td>130.5</td>
<td>0.0</td>
</tr>
<tr>
<td>W-iv</td>
<td>WOLF + ELEV + WOLF<em>ELEV + SECURITY + WOLF</em>SECURITY + VEG</td>
<td>10944</td>
<td>16</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

b VEG = Vegetation categories; ELEV = Elevation + Elevation²; SECURITY = Openness + Openness² + Slope + Slope²; WOLF = Wolf Density Index + Wolf Density Index².

to estimate the βs, we used conditional fixed-effects logistic regression, also known as discrete choice, matched case-control, McFadden's choice, or paired logistic regression (StataCorp 2001:200–215). Conditional fixed-effects logistic regression allows one to account for differing availabilities of habitats among observations by matching used locations to a "choice set" of random locations (Arthur et al. 1996, McCracken et al. 1998, Cooper and Millsbaugh 1999, Compton et al. 2002). Choice sets are specific to the individual and to the space and time at which the individual was observed (McCracken et al. 1998). In this analysis, conditional fixed-effects logistic regression ensured that changes in vegetation following the 1988 fires, and variation in wolf distribution and snowfall by year and season, were taken into account when comparing used to available habitat. We assigned a choice set of random locations to each elk location spatially based on the seasonal herd segment area of the individual elk, and temporally to the maps of vegetation, wolf index, and snow water equivalent corresponding to the date of the elk location.

We used the corrected Akaike's Information Criterion (AICc; Burnham and Anderson 1998) to rank a priori candidate models (Tables 3, 4). Candidate models were chosen to evaluate the alternative hypotheses that: (1) elk select habitat based on vegetation type, habitat openness, snow, elevation, and/or slope (candidate models NW-1 through NW-4); (2) elk avoid wolves, in addition to selecting for other habitat characteristics (candidate models W-1 through W-4); and (3) avoidance of wolves by elk is tempered by their selection for other habitat characteristics (candidate models W-1i through W-4i).

We only considered linear interactions between the wolf density index and the other continuous variables. Because of collinearity in the post-wolf dataset between elevation and SWE (r = 0.62), elevation was not included as a predictor in the winter models.

We conducted post hoc exploration to refine the top a priori
models. When a quadratic relationship between the logit of the RSF and a predictor variable gave an optimum that fell near or beyond the range of possible values of a predictor variable, we tested whether a linear term would provide a better fit (based on AICc) than including the additional squared term. We also examined whether some interaction terms could be discarded from the set of a priori models (Anderson and Burnham 2002). Models were evaluated using k-fold cross-validation, with Spearman’s rank correlation coefficient (rho) as the test statistic (k = 5, n = 10; Boyce et al. 2002, 2003).

We report 3 models for each season: the highest scoring pre-wolf and post-wolf models that have the same predictor variables (non-wolf [NW] models without the wolf density index term, henceforth called “pre-wolf” and “post-wolf:NW” models), and the top-ranking post-wolf model that includes the wolf density index term (full post-wolf-W model). We assessed changes in habitat selection between the pre-wolf and post-wolf periods by comparing β coefficients between the “non-wolf” models for each predictor variable. For linear relationships, we tested for differences in βs using a t-test (Brown and Rothery 1993:227). For quadratic relationships, we tested for differences in optimal values between the pre-wolf and post-wolf models using a Z-test, assuming a Gaussian distribution around each optimum. The optimal value for a predictor variable X based on setting the first derivative of the regression equation with respect to X equal to zero is:

$$X_{max} = \frac{-\beta_1}{2\beta_2},$$

where $X_{max}$ is the optimum, $\beta_1$ is the estimated coefficient for the linear term, and $\beta_2$ is the estimated coefficient for the squared term. The SE for $X_{max}$ was calculated using error propagation of the SEs of the $\beta$s (Stuart and Ord 1994:351, eq. 10.17):

$$SE(X_{max}) = |X_{max}| \sqrt{ \frac{\sigma_{\beta_1}^2}{\beta_1} + \frac{\sigma_{\beta_2}^2}{\beta_2} + \frac{2 \sigma_{\beta_1} \sigma_{\beta_2}}{\beta_1 \beta_2} + \text{cov}(\beta_1, \beta_2)},$$

Finally, we examined the post-wolf-W model to describe the distribution of elk relative to wolves and the selection of habitat components by elk across a range of relative wolf densities.

RESULTS

Ninety-three adult cow elk were captured and radiocollared during the post-wolf-reintroduction period: 45 in March 2000, 28 in February 2001, and 20 in February 2002. Thirteen elk were excluded from analysis because they died within 2 weeks after capture, had collar malfunctions that did not permit radiotracking, or otherwise had few (<7) relocations. The remaining 80 elk were each relocated an average of 12 times/season/year (SE = 0.26), yielding 1,560 summer and 1,590 winter locations. The mean time interval between successive locations for an individual was 12 days (SE = 0.11).

The pre-wolf data consisted of 431 summer locations and 738 winter locations of radiocollared cow elk, and 724 summer locations and 322 winter locations of radiocollared calves. Preliminary analysis showed that there was no difference in models derived from the pre-wolf data on cows only, calves only, or cows and calves combined, thus justifying the use of calf locations as a proxy for cow locations. Based on mean KBDI, the first 750 GDD of 1985–1987, 1989, and 2000 were similar to the long-term average moisture levels (Mao 2003). The growing season of 1988, the year in which the massive fires occurred, was drier than the long-term average, whereas that of 2001 was wetter than the long-term average (Mao 2003).

Summer Habitat-selection Models

Model Selection.—The best a priori summer models based on AICc were the full models that included terms for vegetation types, elevation, habitat openness, and slope in the NW models, as well as additional terms for wolf density and interactions between wolf density and elevation, openness, and slope in the W model (Table 3). The a priori pre-wolf model no. NW-4, which had both a linear and squared term for habitat openness, predicted maximum selection for habitat openness of 95%, whereas its post-wolf counterpart predicted a maximum at 2% openness, suggesting that linear terms were sufficient. When we conducted post hoc refinement of the best a priori models, we found that using only the linear term for openness made a large improvement on the pre-wolf model no. NW-4 based on AICc, although only a minor improvement on the post-wolf model no. NW-4 (Table 5). Modifying the best a priori post-wolf-W model, no. W-4i, we found that using a linear wolf density term and only including 1 interaction term, slope×wolf density, made a negligible improvement (Table 5). Although only 1 of these post hoc models greatly improved on its matching a priori model, we selected all 3 post hoc models as the overall best summer models based on the principle of parsimony.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pre-wolf habitat selection</th>
<th>Post-wolf-NW habitat selection</th>
<th>Post-wolf-W habitat selection</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>β</td>
<td>SE</td>
<td>P</td>
</tr>
<tr>
<td>Shrubland</td>
<td>-0.09</td>
<td>0.10</td>
<td>0.387</td>
</tr>
<tr>
<td>Other nonforest</td>
<td>-1.30</td>
<td>0.33</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Burned foresta</td>
<td>-0.86</td>
<td>0.16</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Unburned foresta</td>
<td>-0.24</td>
<td>0.11</td>
<td>0.026</td>
</tr>
<tr>
<td>Openness</td>
<td>0.013</td>
<td>0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Elevation</td>
<td>0.026</td>
<td>0.003</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Elevation²</td>
<td>-5.27E-06</td>
<td>5.33E-07</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Slope</td>
<td>0.010</td>
<td>0.012</td>
<td>0.427</td>
</tr>
<tr>
<td>Slope²</td>
<td>-0.0014</td>
<td>0.0004</td>
<td>0.001</td>
</tr>
<tr>
<td>Slope * wolf density</td>
<td>3.19E-05</td>
<td>1.41E-05</td>
<td>0.024</td>
</tr>
<tr>
<td>Wolf density</td>
<td>-0.00048</td>
<td>0.00201</td>
<td>0.223</td>
</tr>
</tbody>
</table>

- Post hoc model modified from a priori prewolf summer model no. NW-4.
- Post hoc model modified from a priori postwolf summer model no. NW-4.
- Post hoc model modified from a priori postwolf summer model no. W-4.
- Burned aspen + burned conifer.
- Unburned aspen + unburned conifer.
- Relative to AICc of the best a priori candidate model.

The selected pre-wolf and post-wolf-NW summer models predicted elk use based on vegetation, a linear relationship with habitat openness, and quadratic relationships with elevation and slope (Table 5). The selected post-wolf-W model included a negative linear wolf density term and a negative interaction between slope and wolf density (Table 5). All of the models predicted elk locations well, according to k-fold cross validation (Table 5).

Pre-wolf and Post-wolf Model Comparisons.—Elk selected less open habitat in summer during the post-wolf period compared to the pre-wolf period (t = -7.79, P < 0.01). Specifically, elk selected more burned forest habitat (relative to grasslands) after wolf reintroduction compared to the pre-wolf period (t = 5.72, P < 0.01). Elk selected higher elevations after wolf reintroduction (optimum at 3,434 m [SE = 184.41] than before ( optimum at 2,451 m [SE = 19.7]; Z = 5.30, P < 0.01). Within the range of actual elevations in YNP (1,500–3,300 m), the post-wolf model’s partial RSF with respect to elevation approximated a linear increasing function, i.e., selection was predicted to be greatest for the highest elevations. The optimal slope in the post-wolf-NW model (8 degrees [SE = 2.21]) did not differ from that of the pre-wolf model (3 degrees [SE = 3.5]; Z = 1.02, P > 0.05). However, the post-wolf-W model had a significant positive interaction between slope and wolf-density index (Table 5, Fig. 4). Elk also selected areas of low wolf density, shown by the negative β for wolf density index (Table 5).

Winter Habitat-selection Models

Model Selection.—The best a priori winter models were full models that included terms for vegetation, SWE, openness, and slope in the NW models, as well as additional wolf density and interaction terms in the W model (Table 4). No post hoc refinement was needed for the pre-wolf and post-wolf-NW models (Table 6). Modifying the struc-

Fig. 4. Selection of slope by elk during summer in the post-wolf-reintroduction period, Yellowstone National Park, 2000–2002. Solid lines are partial Resource Selection Functions (RSF) values with respect to slope predicted by the summer post-wolf-W model at wolf density index levels ranging from zero to 1,600 (light to dark lines). The dashed line is the partial RSF with respect to slope predicted by the summer post-wolf-NW model.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pre-wolf habitat selection</th>
<th>Post-wolf-NW habitat selection</th>
<th>Post-wolf-W habitat selection</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\beta$</td>
<td>SE</td>
<td>$P$</td>
</tr>
<tr>
<td>Shrubland</td>
<td>-0.09</td>
<td>0.10</td>
<td>0.387</td>
</tr>
<tr>
<td>Aspen$^d$</td>
<td>0.13</td>
<td>0.27</td>
<td>0.636</td>
</tr>
<tr>
<td>Shrubland</td>
<td>0.16</td>
<td>0.11</td>
<td>0.132</td>
</tr>
<tr>
<td>Other nonforest</td>
<td>-0.68</td>
<td>0.25</td>
<td>0.001</td>
</tr>
<tr>
<td>Burned conifer</td>
<td>-0.64</td>
<td>0.30</td>
<td>0.033</td>
</tr>
<tr>
<td>Unburned conifer</td>
<td>0.14</td>
<td>0.13</td>
<td>0.272</td>
</tr>
<tr>
<td>Openness</td>
<td>0.044</td>
<td>0.005</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Openness$^2$</td>
<td>-3.83E-04</td>
<td>3.98E-05</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Slope</td>
<td>0.028</td>
<td>0.013</td>
<td>0.035</td>
</tr>
<tr>
<td>Slope$^2$</td>
<td>-0.0016</td>
<td>0.0004</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Snow</td>
<td>-0.13</td>
<td>0.01</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Snow $^a$</td>
<td>-0.13</td>
<td>0.01</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Wolf density</td>
<td>0.0033</td>
<td>0.0004</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Wolf density$^2$</td>
<td>-0.14E-04</td>
<td>2.38E-07</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$-2LL$</td>
<td>5977</td>
<td>8483</td>
<td>8373</td>
</tr>
</tbody>
</table>
| $\Delta$$^a$ | 0       | 101.4 | -0.4 | 0.92 (p<0.002) | 0.96 (p<0.002) | 0.93 (p<0.002)

$^a$ A priori pre-wolf winter model no. NW-2.
$^b$ A priori post-wolf winter model no. NW-2.
$^c$ Post hoc model modified from a priori post-wolf winter model no. W-2i.
$^d$ Burned + unburned aspen.
$^e$ Relative to the AICc of the best a priori candidate model.

The selected winter pre-wolf and post-wolf-NW models predicted elk use based on vegetation, quadratic relationships with habitat openness and slope, and a negative linear relationship with snow (Table 6). The selected post-wolf-W model included a quadratic relationship with wolf density and negative interactions with slope and snow (Table 6). Kfold cross validation showed that all of these models predicted elk locations well (Table 5).

Pre-wolf and Post-wolf Model Comparisons—Elk selected for more open habitat in winter in the post-wolf reintroduction period (optimum at 71% openness [SE = 3.4]) compared to the pre-wolf period (optimum at 57% openness [SE = 1.4]; $Z = 3.72, P < 0.01$). Relative to selection of grasslands, selection of shrublands ($t = -2.12, P < 0.05$) and other nonforested habitats ($t = -2.05, P < 0.05$) was lower after wolf reintroduction than before. There was no difference in the effect of snow between the 2 time periods ($t = 0.36, P > 0.05$); in both cases, elk selected low SWE (Table 6). Selection of slope did not differ ($Z = 0.25, P > 0.05$); in both time periods, elk selected an optimum of 9 degrees slope (SE = 2.2, pre-wolf; SE = 0.9, post-wolf). In the post-wolf-W model, the optimal wolf density index (given median available values of 12 degrees slope and 4.4 cm SWE: Table 2) was 994. Negative interactions were found between slope and wolf density, and between snow and wolf density (Table 6, Figs. 5 and 6).

![Fig. 5. Selection of slope by elk during in the post-wolf-reintroduction period, Yellowstone National Park, 2000–2002. Solid lines are partial Resource Selection Functions (RSF) values with respect to slope predicted by the winter post-wolf-W model at wolf density index levels ranging from zero to 1600 (light to dark lines). The dashed line is the partial RSF with respect to slope predicted by the winter post-wolf-NW model.](image-url)
Fig. 6. Selection of snow water equivalent (SWE) by elk during winter in the post-wolf reintroduction period Yellowstone National Park, 2000–2002. Solid lines are partial Resource Selection Functions (RSF) values with respect to SWE predicted by the winter post-wolf-W model at wolf density index levels ranging from zero to 1,600 (light to dark lines). The dashed line is the partial RSF with respect to SWE predicted by the winter post-wolf-NW model.

DISCUSSION

Patterns of habitat selection by the Northern Yellowstone elk herd changed between 1985–1990 and 2000–2002. Aside from effects due to wolves, some of these changes may be a result of post-fire succession and other environmental factors. In fact, wolves, fire, and climate likely have interactive effects on the behavior and fitness of ungulates (Carbyn 1983, Jędrzejewski et al. 1992, Huggard 1993, Kunkel and Pletscher 2001, Mech et al. 2001). Changes in elk population size also could alter animal distributions through density-dependent habitat selection (Fretwell and Lucas 1970). However, because elk density remained near carrying capacity throughout our study (winter densities of 12 elk/km² in 1985–1990 vs. 9 elk/km² in 2000–2002, based on elk population counts reported by Taper and Gogan [2002] and N. Varley, University of Alberta, personal communication), we suspect that intraspecific competition is unlikely to have declined enough to produce a density-dependent change in habitat selection.

At the weekly timescale of this study, elk avoided areas of high wolf density in the summertime. However, during winter elk selected areas of moderately high wolf density; i.e., they did not spatially separate themselves from wolves, indicating that winter habitat selection by wolves closely mirrored habitat selection by elk at this scale. Instead, avoidance of wolves in winter must take place on a shorter timeframe or at a smaller spatial scale than we measured; e.g., an encounter-by-encounter basis (see MacNulty 2002 for details on wolf–elk encounters and attacks in YNP).

Changes in Summer Habitat Selection

Following wolf reintroduction, elk have shifted toward selection of less open habitats, specifically more burned forest, in summer. Contrary to the notion that predator avoidance comes at the cost of foraging (Lima and Dill 1990), elk in YNP may benefit in both respects by selecting burned forest habitats. Herbaceous understory has increased in burned forests following opening of the canopy by fire (Turner et al. 1999), so elk may be making use of the available forage. Present-day selection for burned forest (12 to 14 years after the 1988 fires) contrasts with the earlier finding by Norland et al. (1996) that in the first 2 years after the fires, no change in summertime habitat selection by elk occurred. However, as those authors predicted, changes in habitat selection did occur later as long-term succession of burned forests began to take place.

Furthermore, unlike elk, wolves in Yellowstone avoid burned forest (Yellowstone Wolf Project, unpublished data). Burned forests in YNP are abundant with fallen timber (Tinker and Knight 2000), which can be an obstacle to locomotion (Parker et al. 1984). Wolves search for prey by traveling long distances and making chance encounters (Mech 1970). Usually they must run down their prey (Mech 1970), so chasing an elk through downed timber could prove challenging. Overall, it may be energetically unprofitable for wolves in Yellowstone to travel and hunt in burned forest. Elk, on the other hand, may use Yellowstone’s complex habitat structure of downed timber and young lodgepole pines as hiding cover. In contrast, Kunkel and Pletscher (2001) hypothesized that in Glacier National Park understory vegetation was disadvantageous to prey because wolves use such vegetation as stalking cover when they hunt. Differences in habitat structure and composition between the 2 parks, such as density and arrangement of understory vegetation, may result in wolves and their prey having variable strategies of using vegetation as stalking, hiding, or escape cover.

In addition, if an elk does encounter wolves in burned forest, the presence of downed timber may enhance its ability to defend itself. On the Northern Range (N. Varley, University of Alberta, personal communication) and in Jasper National Park, Alberta (Schmidt and Gunson 1985,
Dekker et al. (1995), elk have been observed backing up against trees or the edge of a cliff to block wolves from attacking from behind. Wolves are less successful at attacking a prey that stands its ground, apparently because of the high risk of injury due to kicking (Mech 1970, MacNulty 2002). MacNulty (2002) found that elk in YNP defended themselves by standing their ground in over 50% of encounters with wolves, mostly recorded in winter, but it is not well known how elk respond to wolf encounters in the summer under very different climate and habitat conditions, nor is it known how elk react to predators in burned forest habitat. Nevertheless, by choosing habitats that wolves do not favor, elk can reduce their rate of encounter with wolves.

In the post-wolf-reintroduction period, elk selected higher summer elevations compared to the pre-wolf period. Drought did not appear to influence this change. The summer growing seasons of 2000 and 2001 were similar to or wetter than the pre-wolf summers of 1985–1989. Nevertheless, with much of the summer range converted into burned forest, which lacks canopy cover to shade the understory, summer forage may dry faster than it did before the 1988 fires. A change in plant phenology resulting indirectly from the fires could cause elk to move to higher elevations in search of moister forage and cooler temperatures.

Movements to higher elevations in summer also allow elk to reduce the probability of encountering wolves during the pup-rearing season. Wolves in YNP den at lower elevations in April while the elk herd is still on the Northern Range (Thurston 2002). However, elk leave the Northern Range and migrate to the summer range beginning in mid-May (Craighead et al. 1972; S. B. Evans, University of Minnesota, unpublished data). Between May and August, although adult wolves may travel widely to hunt, they must return to the dens and rendezvous sites to feed the pups (Mech 1970, Thurston 2002). Elk that summer at higher elevations distance themselves from wolf activity centers, thus reducing their predation risk (e.g., Bergerud et al. 1984).

Changes in Winter Habitat Selection

Following wolf reintroduction, elk selected more open habitats in winter. Because wolf density within YNP is highest on the Northern Range (Smith et al. 2003a), the wolf predation risk for elk is higher in winter than in summer. Yet elk did not avoid wolves during winter on the week-to-week basis on which data were collected in this study. One possibility is that on the largely nonforested landscape of the Northern Range, now that wolves have been restored to the system, more elk may be using grouping as an anti-predator strategy (Dehn 1990, Jędrzejewski et al. 1992, Hebblewhite and Pletscher 2002). During the period after wolf reintroduction, elk group sizes were larger in areas of higher wolf density, even after accounting for differences in vegetation cover (Mao 2003). Of course, larger groups attract more wolves (Hebblewhite and Pletscher 2002), and elk may form groups for reasons other than predation risk, e.g. when forage is distributed patchily (Heard 1992, Clarke et al. 1995) or when social interactions occur (Franklin and Lieb 1979, Shoemsmith 1979, Bender 1996).

Regardless of the immediate mechanism causing elk to aggregate, grouping allows elk to (1) dilute wolf predation risk, essentially by using their fellow group members as hiding cover (Hamilton 1971) and (2) detect approaching wolves more readily (Pulliam 1973). In very large groups, such as the aggregations of as many as 700 elk that we observed, dilution is believed to be more important than detection in reducing per capita predation risk (Dehn 1990). The grouping strategy may be especially useful for elk on the open landscape of the Northern Range where they cannot use dispersion or tree cover for hiding.

Trophic cascades promoting the growth of willow and aspen (Romme et al. 1995, Singer et al. 1998, Ripple et al. 2001, White et al. 2003) could result from a reduction in the elk population by wolves (e.g., Boyce 1993) or from distributional shifts and increased movements of elk avoiding wolves (e.g., Mitchell and Lima 2002). However, in this study, elk showed no significant change in selection of aspen, which was highly preferred during winter in both pre- and post-wolf-reintroduction periods. After wolf reintroduction, elk selected shrublands less often than grasslands. The shrublands category included willow, but because willow is not well mapped on the Northern Range, selection of willow could not be measured. Very low elk density (e.g., 3 elk/km² or lower) may be required before a significant reduction in herbivory on these species can be observed (White and Feller 2001). With elk density on the order of 10 elk/km² (Lemke et al. 1998) and YNP wolf population beginning to level off (Smith et al. 2003a), wolf predation alone may not be able to alter elk demography and herbivory patterns sufficiently to achieve willow and aspen release. Other factors including

**Interactions between Selection of Wolf Density and Other Habitat Features**

Although there were no overall differences in selection of slope or SWE before vs. after wolf reintroduction, selection of these habitat features did vary depending on wolf density. Elk tended to select low wolf-density areas in summer, but those elk that did occur in areas of high wolf density selected steeper slopes. Using sloped terrain gives an ungulate a better vantage point from which to watch for predators (Byers 1997, Kunkel and Pletscher 2001). Wolves (Carroll et al. 2003) and wolf kills (Bibikov 1982, Kunkel and Pletscher 2001) tend to occur on shallower slopes, suggesting that ungulates are easier to kill there. Having a higher center of gravity than wolves, ungulates may be more likely to stumble if they run downslope and they may lose momentum once reaching the bottom of a hill (Bibikov 1982). In contrast, ungulates that move upslope may be less likely to be attacked by wolves because they may be in a better position to defend themselves by kicking downward, or because wolves may be able to detect that prey which are fit enough to climb a slope would be difficult to kill (Bibikov 1982). Cassirer et al. (1992) reported that a common response of elk to disturbance by skiers was to move upslope onto ridges. Elk probably respond in a similar manner when disturbed by wolves and other predators. Although almost none of our radiolocations of elk occurred during actual encounters with wolves, a higher encounter rate in areas of high wolf density could result in the observation that elk select steeper slopes in those places.

During winter, elk in areas of higher wolf density selected less steep slopes, contrasting with the summertime. This finding is unlikely to be an anti-predator strategy and instead points to the greater predation risk elk face in winter. On a weekly timescale elk could not avoid wolves, so selection of low slope in winter coinciding with high wolf density may reflect the similarities in habitat selection by elk and wolves at this scale (e.g., Kunkel and Pletscher 2001), rather than avoidance strategies by elk.

Elk also selected lower SWE in higher wolf-density areas. Most large mammals, elk and wolves included, prefer areas of low snow accumulation for ease of locomotion (Tefler and Kelsall 1979, Houston 1982:139, Parker et al. 1984, Kunkel and Pletscher 2001, Slovkin et al. 2002). Deep and crusty snow limits both movement and foraging for grazers (Tefler and Kelsall 1979), but can be beneficial to wolves, which achieve a higher kill rate under such conditions (Nelson and Mech 1986, Mech et al. 2001, Smith et al. 2004a). This suggests that the probability of an elk being killed is greater in deeper snow than in shallow snow, so although elk may encounter wolves more often in low snow areas, their probability of capture should be lower where movement is easier and where flight and defense are both possible. Prey can tolerate risky habitats if their probability of escape outweighs the probabilities of encounter and attack (Lima 1992).

**Tradeoffs and Seasonal Strategies of Habitat Selection**

The ability of elk to avoid wolves by selecting different habitats is seasonally dependent in YNP, largely because of the migratory nature of the Northern herd and their use of vastly different summer and winter ranges. Because each seasonal range presents elk with different availabilities of habitats and resources from which to choose, elk show different responses to wolf predation risk between the 2 seasons.

On the summer range, where forage is abundant, elk can use habitats that allow them to avoid wolf predation, and they may not need to make a trade-off between food and safety. Elk disperse throughout an expansive summer range, and they can avoid wolves by choosing particular habitat structures and terrain features that reduce their risk of wolf predation. During winter, however, in addition to high wolf density, elk face severe weather conditions, greater competition due to higher elk density, less nutritious forage, and loss of fat reserves and body weight (Houston 1982, Cook 2002). In fact, mortality during winter accounts for nearly all of the annual cow elk mortality in this herd (S. B. Evans, University of Minnesota, unpublished data). Winter is a time of subsistence feeding at best, so elk may choose not to trade foraging for spatial avoidance of wolves, and instead they may wait until a wolf encounter occurs before expending energy to avoid predation.

**MANAGEMENT IMPLICATIONS**

Motivation for wolf recovery in Yellowstone by the National Park Service and the U.S. Fish and Wildlife Service was partly to restore the ecologi-
cal processes afforded by wolf predation (U.S. Fish and Wildlife Service 1987, Ray et al. 2005). Speculation on the effects of wolves prior to their release in the park was necessarily based on patterns of predation in systems with different complements of prey (Boyce 1993). Our results document that the presence of wolves alters the seasonal pattern of distribution and habitat use by elk, results that are corroborated by movement paths used by elk when wolves are present (Fortin et al. 2005). Because elk are the most abundant ungulates in the park, this redistribution of elk significantly alters the spatial and temporal patterns of herbivory and nutrient cycling (Frank and Evans 1997, Frank 1998). Furthermore, our observations reinforce other studies that have demonstrated that ecological processes are being altered by wolves (Wilmers and Getz 2005). Clearly, restoring wolves to Yellowstone was fundamental to meeting the ecological-process management function of national parks (Yellowstone National Park 1997, Boyce 1998).

ACKNOWLEDGMENTS
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