

## DISTRIBUTION AND ABUNDANCE OF SNOWSHOE HARES IN YELLOWSTONE NATIONAL PARK

KAREN E. HODGES,\* L. SCOTT MILLS, AND KERRY M. MURPHY

Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA (KEH, LSM)

Centre for Species at Risk and Habitat Studies, University of British Columbia Okanagan, 3333 University Way, Kelowna, BC V1V 1V7, Canada (KEH)

Yellowstone Center for Resources, Yellowstone National Park, WY 82190, USA (KMM)

Snowshoe hares (*Lepus americanus*) are widespread in boreal and montane forests of North America, vary in their temporal dynamics, and are major drivers in their food webs. In Yellowstone National Park, Wyoming, hare abundance, distribution, and temporal dynamics are unknown, yet Yellowstone contains a large area within their southern range that is relatively unfragmented by human activities. The 1988 Yellowstone fires have led to extensive regenerating stands, a seral condition that elsewhere supports relatively high numbers of hares. To examine snowshoe hare dynamics in the park from 2002 to 2007, we surveyed stands within 7 cover types and estimated abundance for a subset of sites. Both livetrapping data and fecal pellet count surveys showed that snowshoe hares are rare in Yellowstone. More than 36% of surveyed stands did not support any hares. Mature forest cover types were more likely to have hares than were stands regenerating after the 1988 fires, but very few stands supported high numbers; 96% of stands had <0.5 hares/ha. Three stands that burned in 2003 had hares before the fire, but none afterward. Hare numbers fluctuated modestly over time, but patterns were not indicative of a cycle. Taken altogether, our results indicate that snowshoe hares in Yellowstone are rare, patchily distributed, and apparently acyclic, important findings both for understanding hare dynamics and for implications for the Yellowstone food web that includes the federally Threatened Canada lynx (*Lynx canadensis*).

Key words: fire, habitat, *Lepus americanus*, lodgepole pine, snowshoe hare, Yellowstone National Park

The forests in Yellowstone National Park in northwestern Wyoming are legacies of the region's volcanic and fire history. The volcanic history has created areas with different parent rock, which weathers into nutrient-poor rhyolitic and nutrient-rich andesitic soils that support different plant communities (Hansen et al. 2000). The recent fire history is dominated by the 1988 fires that burned approximately 250,000 ha, about 36% of the park. More recently, the 2003 fire year was the 2nd largest in the last century (~11,280 ha burned—National Park Service 2007). These events have produced a mosaic of interspersed nonforested areas, mature forest, and recently burned forests. The regenerating forests vary from <1,000 to >50,000 saplings/ha (Kashian et al. 2004; Turner et al. 2004), which de facto means they vary widely in their suitability for wildlife.

Our interest is in how snowshoe hares (*Lepus americanus*) respond to this mosaic landscape. Snowshoe hares undergo striking population cycles in boreal forest (Hodges 2000a; Keith 1990; Krebs et al. 2001; Wolff 1980). Most snowshoe hare populations in the southern part of their range have lower numbers than in the north (i.e., <1 hare/ha versus peak densities of 4–6 hares/ha in boreal forest). Some southern populations fluctuate, although often with lower peak abundances and lower amplitudes (Hodges 2000b; Malloy 2000). In some locations, hare populations may be stable at lower densities, which is thought to occur because of habitat fragmentation that contributes to high predation by generalist predators (Keith 1990; Murray 2000; Wirsing et al. 2002; Wolff 1981).

Because of its position and size, Yellowstone is included in the proposed designation of critical habitat for the federally Threatened Canada lynx (*Lynx canadensis*—United States Fish and Wildlife Service 2008), despite the small numbers of lynx in the park (Murphy et al. 2006). Lynx are obligate predators of snowshoe hares, so the distribution and abundance of snowshoe hares within the park is of direct

\* Correspondent: karen.hodges@ubc.ca

relevance to its lynx population. Historic lynx records in Yellowstone documented lynx mostly near spruce–fir forests, and surveys for lynx during 2001–2004 confirmed only 3 or 4 individuals, generally in areas dominated by andesitic soils (Murphy et al. 2006). These sparse lynx records suggest that snowshoe hares also are uncommon and patchily distributed in Yellowstone.

Snowshoe hares use both mature closed-canopy forest and regenerating stands of various species (reviewed in Hodges 2000a, 2000b), including lodgepole pine (*Pinus contorta*), the dominant species regenerating in Yellowstone (Kashian et al. 2004; Turner et al. 2004). Snowshoe hares frequently achieve their highest local densities in regenerating stands (Ferron and St-Laurent 2008; Fox 1978; Koehler 1990; Mowat and Slough 2003; Paragi et al. 1997), suggesting that hares ought to respond favorably to the regeneration after the extensive 1988 fires in Yellowstone. This correlation of hare density and regenerating stands is thought to be driven by a favorable response of hares to understory cover. One caveat here is that substantially more is known about how snowshoe hares respond to forestry activities (Fisher and Wilkinson 2005; Griffin and Mills 2003; Hodges 2000b) than how they respond to stand-replacing fires with natural regeneration (but see Mowat and Slough 2003).

Against the uncertainties about spatial distribution, temporal variation, and the impacts of postfire regeneration on snowshoe hare abundance in Yellowstone National Park, we tested the following hypotheses: hares are more common in postfire regenerating stands than in mature stand types, hare density is positively correlated with amount of understory cover, and hare dynamics are relatively stable in this ecosystem.

## MATERIALS AND METHODS

We used geographic information system habitat layers for Yellowstone National Park to identify common forest cover types that might support snowshoe hares. We excluded nonforested cover types because snowshoe hares do not use them, except for an occasional willow (*Salix*) thicket (Hodges 2000b). We sampled 7 stand types: spruce–fir (*Picea engelmannii*–*Abies lasiocarpa*), 3 seral stages of lodgepole pine (*Pinus contorta*; LP0, LP2, and LP3), Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and willow-riparian (Despain 1990). LP0 lodgepole stands were regenerating postdisturbance, usually within 0–40 years postfire. In our case, we chose LP0 stands that had burned in the 1988 fires because by far the majority of LP0 in Yellowstone arose from this 1 fire season. LP2 stands (150–300 years old) were closed-canopy lodgepole stands; understory trees may be lodgepole or other species. LP3 stands (>300 years old) had canopies that were a mix of lodgepole, spruce, and fir, often with well-developed understories. We did not sample LP1 stands (40–150 years) because this cover type was uncommon in Yellowstone. The 3 remaining cover types (Douglas-fir, aspen, and willow-riparian) were domi-

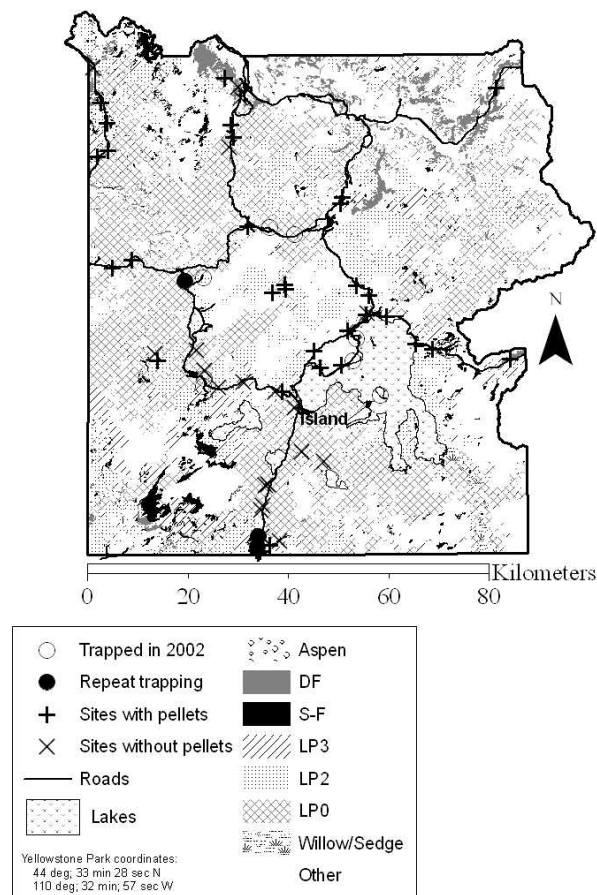


FIG. 1.—Map of Yellowstone National Park, Wyoming, showing areas where we sampled for snowshoe hares (*Lepus americanus*) during 2002–2007.

nated by the species named; we selected mature Douglas-fir and aspen stands. Willow-riparian sites occurred along streams or rivers, and often did not contain trees.

Our goal was to sample 5–20 sites in each cover type, with rarer types sampled less often than common ones, in as many different areas across the park as possible (Fig. 1). We used 20 ha as our primary sampling area (for larger stands, we situated our study sites within the larger stand), but in 3 instances we used 10-ha sites when 20-ha sites were not locally available (2 willow-riparian and 1 LP0). To reduce field costs, we preferentially selected sites that were near roads or convenient hiking trails, but we included a buffer strip of at least 50 m between each site and roads. There is no evidence in the literature that snowshoe hare populations are affected by roads. Our results can be extrapolated reliably across the park because, except for the reduction of vegetation in a maximum 11-m-wide safety zone adjacent to each side of paved 2-lane roads, our sites are otherwise representative of other areas within the park. We also examined our data from sites both close and distant from roads and found no differences in presence or relative abundance of hares (analyses not shown).

From 2002 to 2007, we used 2 approaches to sample relative abundance and distribution of snowshoe hares within these stand types in Yellowstone National Park. In 2002, we

used mark–recapture livetrapping to obtain population estimates on 13 sites selected to sample the 4 most common habitat types thought capable of supporting snowshoe hares in Yellowstone: LP0 (4 sites), LP2 (3 sites), LP3 (3 sites), and spruce–fir (3 sites, including 1 on Frank Island in Yellowstone Lake). The other 3 habitat types (aspen, Douglas-fir, and willow-riparian) were not trapped primarily because they were much less common in Yellowstone; furthermore, previous literature from the southern part of their range has suggested these types seldom support high abundances of snowshoe hares (Hodges 2000b). From 2003 to 2007, we trapped 3 of the 2002 sites to describe changes in snowshoe hare abundance over time.

Second, we used fecal pellet counts as an index of relative abundance (Hodges and Mills 2008; Krebs et al. 2001; Mills et al. 2005) on 68 sites (Fig. 1; 55 nontrapped sites and 13 trapped sites). Thirty-one sites were surveyed a single time, whereas the remaining sites were surveyed for 2–6 years to assess annual variability in relative abundance. We were unable to sample our target number of 5 each of the willow-riparian, aspen, and Douglas-fir sites because these stand types were rare, often occurred in small patches, were sometimes mapped inaccurately, and some potential sites were inaccessible.

In 2003, the 7,305-ha East Fire provided a fortuitous natural experiment, by burning 3 sites we had previously sampled (2 with livetrapping and pellets, and 1 with pellets). We resampled these sites with pellet counts to assess the short-term impact of the fire on snowshoe hare numbers.

*Livetrapping snowshoe hares.*—Trapping sessions spanned 3–5 nights in July or August. We used Tomahawk live traps (18 × 18 × 51 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin) placed in an 8 × 10 array with 50-m spacing. We baited traps with alfalfa and apple, set them in early evening, and checked them near dawn. Snowshoe hares were weighed and ear-tagged (Monel #3), and we took a 3-mm tissue punch from an ear for future genetic analysis. We also recorded sex and the length of the right hind foot. Snowshoe hares were handled for 2–5 min and released at the point of capture. These procedures were approved by the Animal Care Committees at the University of Montana (2001–2005) and University of British Columbia (2006–2007), and were in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

We estimated snowshoe hare abundance with the Lincoln–Petersen estimator adjusted for sample size (Chapman 1951; Mills et al. 2005; Seber 1982), an approach that is reasonably unbiased for small numbers of captures (Davis et al. 2003). Because the number of captured snowshoe hares per site was uniformly <10, we were unable to use program CAPTURE or MARK (Manning et al. 1995).

*Fecal pellet plots.*—We used 5.08 × 305-cm pellet plots (2 inches × 10 feet—Krebs et al. 1987, 2001). The 20-ha sites were sampled with 80 plots, whereas the three 10-ha sites were sampled with 50 plots. These sample sizes are more than adequate to detect reliably whether snowshoe hares are absent

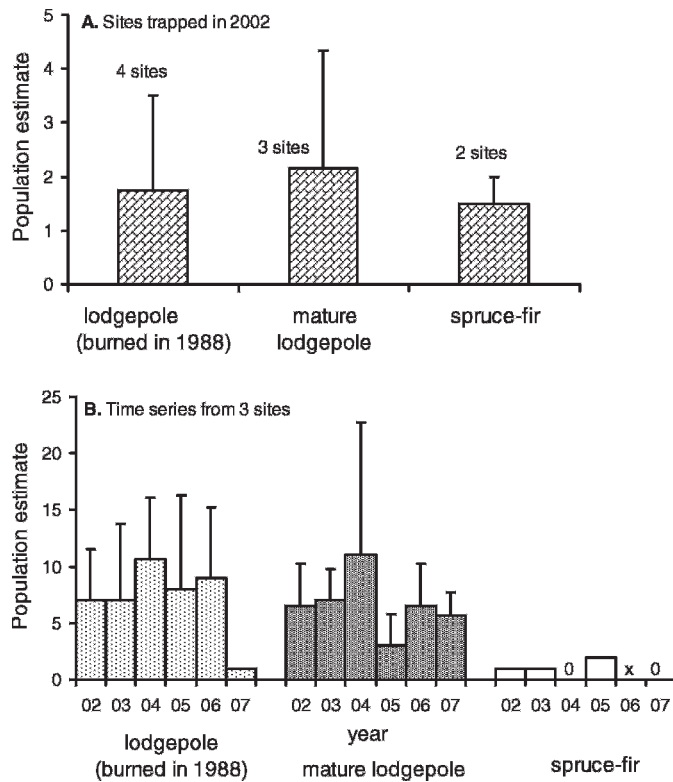
or functionally scarce (<0.3 hares/ha), at low abundance (0.3–0.7 hares/ha), or of moderate to high abundance (>0.7 hares/ha—Hodges and Mills 2008; Mills et al. 2005). We used a geographic information system to delineate the study stands, scattered random points within each stand, then worked in Excel (Microsoft Inc. 2005) to develop efficient travel routes and provide bearings and distances between points. Specifically, we graphed the points, manually ordered them in a route that looked logistically reasonable, then calculated the bearings and distances from point to point. In the field, we used a global positioning system to locate the 1st point to within 5 m, and thereafter used 100-m ropes and compass bearings to locate subsequent points. We marked plots with a nail and string; the nail marked the starting point and we laid the string out due north, then used a ruler to establish the width of each plot. We counted all intact pellets that were more than one-half inside the plot boundary. On the study sites that were livetrapped, pellet plots were offset 5 m from the points delineated for the 8 × 10 trap array. During 2007, the field crew included all pellets touching an edge of the transect rather than pellets that were more than one-half inside. We therefore corrected the 2007 estimates by recalculating the area sampled to include a boundary strip of one-half pellet diameter, using a pellet diameter of 8.4 mm (Zahratka and Buskirk 2007), then converting densities back to the area of the original plot.

During 2003, Yellowstone National Park staff independently conducted modified pellet plot surveys at 15 sites near lynx hair-snares that they deployed in remote areas of the park (Murphy et al. 2006), 13 east of Yellowstone Lake (southeastern Yellowstone) on a 3.2-km grid, and 2 near Tower Junction (north-central Yellowstone). The crews counted 25 pellet plots spaced 20 m apart along 1 transect. If pellets were present and the crews had time, they conducted a 2nd transect of 25 plots. This design is adequate to identify if hares are functionally scarce, but is less accurate at estimating pellet density when pellets are present (Hodges and Mills 2008). No vegetation data were collected, but stand type was identified. We did not use these data in our statistical analysis because of the different methodology, but we presented the results here to extend the patterns observed elsewhere in the park.

*Vegetation surveys.*—Overstory and understory cover are the vegetative attributes most clearly and consistently linked with snowshoe hare abundance, with understory frequently more predictive than overstory (Hodges 2000a, 2000b). As indicators of overstory, we recorded canopy closure and the density and species of overstory trees. As indicators of understory, we estimated the density and species of saplings, quantified horizontal cover with cover boards, and recorded an index of downed wood.

For stands surveyed for fecal pellets of snowshoe hares, we recorded overstory at 10 points and understory at 30 points. The sites sampled for vegetation were randomly chosen from the points chosen for pellet plots. The density of overstory trees was estimated with variable radius sampling using a

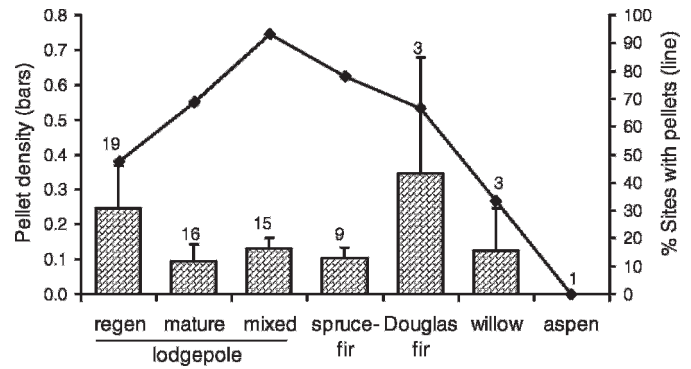




**FIG. 2.**—Population estimates of snowshoe hares (*Lepus americanus*) in Yellowstone National Park, Wyoming, derived from livetrapping. A) Population estimates from 12 mainland sites livetrapped in 2002. Values are the mean and 1 SE of population estimates across sites. Each trapping site trapped an area of ~25 ha. The number of sites trapped is given by each bar. No hares were captured on 3 mixed-canopy LP3 sites. B) Estimates from 3 sites for 2002–2007; each column provides an estimate for a single year, and error bars are 95% confidence limits. The spruce–fir site had no hares in 2004 or 2007, and was not trapped in 2006.

Spiegel relaskop (Forestry Suppliers Inc., Jackson, Mississippi) and a basal area factor of 10. If needed, we used a basal area factor of 5 or 20 to obtain a target of ~8–15 trees per sampling point. We recorded species and diameter at breast height (DBH) of each tree >7.5 cm DBH identified by the relaskop and then calculated the basal area (m<sup>2</sup>/ha—Avery and Burkhart 1994). To estimate the density of saplings (trees >0.5 m tall and <7.5 cm DBH), we used a 2-m-radius circle and classified trees, by species, into 1 of 3 height classes: 0.5–1.5 m, 1.5–3.0 m, and >3 m. We estimated canopy closure via a GRS densitometer (Forestry Suppliers Inc.). Horizontal cover was estimated at 6 m from observers using a 0.5 × 2-m cover board divided into blocks of 0.25 m<sup>2</sup> to gauge the percent covered in 0.5-m height increments. Our index of downed logs (>8 cm diameter) was the number encountered along a 6-m transect.

For the forest stands we livetrapped, we sampled vegetation systematically 100 m apart along 2 of the internal rows of the grid (e.g., 3rd and 6th). That design provided 10 locations for vegetation sampling, with each central point used for the overstory estimates and three 10-m transects laid out at 120° angles used for downed wood and understory cover. Saplings



**FIG. 3.**—Average snowshoe hare (*Lepus americanus*) pellet density in Yellowstone National Park, Wyoming, in relation to forest stand type. The bars show pellet density (pellets/0.155-m<sup>2</sup> plot). We used the average pellet density/site for sites that were surveyed in multiple years. The number of stands sampled is given above each bar.

were measured in 2-m subplots centered at the midpoint of each transect.

**Statistical analyses.**—For sites surveyed in multiple years, we used the average pellet count as our response variable; we obtained similar results using the 1st count or the median count. We used analysis of variance (ANOVA) to compare vegetative attributes and hare abundance estimates among stand types. To relate pellet count data to habitat variables, we used logistic regression, because 36% of our sampled sites had no fecal pellets. We then used linear regression for all sites that had pellets to see if any of the habitat variables were related to pellet density. We used a Mantel test to examine whether distance between sites was related to pellet density, i.e., if high-density sites were clustered together.

## RESULTS

Snowshoe hares occurred at low abundances in our study locations within Yellowstone National Park. In 2002, only 4 of 12 mainland sites we livetrapped had snowshoe hares (Fig. 2A). Abundances did not differ among stand types, averaging 0–2.2 individuals per ~20-ha trapping grid ( $F = 0.33$ ,  $d.f. = 3, 11$ ,  $P = 0.80$ ). We also trapped in mature spruce–fir habitat on Frank Island in Yellowstone Lake and caught no hares there either.

The 3 sites trapped from 2002 to 2007, chosen for continued trapping because they had hares, had no clear temporal trends in hare abundance (Fig. 2B). The LP0 site supported a population of 7.0–10.7 hares from 2002 to 2006, but we caught only 1 hare in 2007. Hare numbers averaged 6.6 in the mature lodgepole stand, and the confidence intervals overlapped through time. The spruce–fir site had only 0, 1, or 2 individuals captured each year.

Our pellet results also indicated that snowshoe hares were rare in Yellowstone (Fig. 3). Although Douglas-fir and LP0 had the highest average pellet counts ( $\bar{X} \pm SE$ : 0.35 pellets/0.155-m<sup>2</sup> plot  $\pm$  0.33 and 0.25  $\pm$  0.12 pellets/0.155-m<sup>2</sup> plot, respectively), they were not statistically significantly different than other stand types (ANOVA, excluding the 1 aspen stand:

$F = 0.63$ ,  $d.f. = 5, 59$ ,  $P = 0.68$ ). Across all stand types, only 64% of stands had pellets at all and the average pellet density was  $0.16 \pm 0.04$  pellets/0.155-m<sup>2</sup> plot, which is very low; using a common equation relating pellet counts to snowshoe hare densities (density =  $1.567 \times \exp[-1.203 + 0.889 \times \ln(\text{pellets}/0.155\text{-m}^2 \text{ plot})]$ —Krebs et al. 2001), this value indicates 0.09 hares/ha. Pellet counts of  $<0.6$  pellets/0.155-m<sup>2</sup> plot uniformly indicate hare densities from mark-recapture estimates of  $<0.3$  hares/ha (Mills et al. 2005). Our 5 stands with the highest pellet densities averaged from 0.63 pellets to 1.91 pellets, or, using the above equation, 0.31–0.84 hares/ha. Three of these 5 sites were LP0, and the other 2 were a Douglas-fir and an LP2. The 4 mature forest types (LP2, LP3, spruce-fir, and Douglas-fir) had pellets present on  $>67\%$  of sites; in contrast, LP0, willow, and aspen sites had pellets on  $<50\%$  of sites. There were no obvious spatial patterns in pellet density across the park, nor was distance between sites correlated with pellet counts on sites (Mantel test,  $Z = 0.032$ ,  $P = 0.31$ ).

The range of annual variation in pellet counts within each site was small (Fig. 4); across 38 sites sampled 2–6 years, only 9 had variation of  $>0.5$  pellet in the mean pellet count (coefficients of variation [CVs] for these 9 sites averaged 0.82, and CVs across the 29 sites with nonzero pellet densities averaged 0.93); only 2 sites varied by  $>1$  pellet. To put this variation in perspective, the equation linking pellets to hare density (Krebs et al. 2001) shows the addition of  $\sim 0.25$  hares/ha for a 0.5-pellet increase at these densities. Six sites for which we have 5–6 years of data showed increases from 2006 to 2007, with 3 of these increases  $>0.5$  pellet. Except for this potential increase in abundance, fluctuations in the time series were minor and sites did not vary in the same way through time.

The pellet data collected independently by Yellowstone National Park staff were consistent with these patterns. Average pellet density was  $0.14 \pm 0.06$  pellets/0.155-m<sup>2</sup> plot, with a high of 0.84 pellets/0.155-m<sup>2</sup> plot; the rest were  $<0.24$  pellets/0.155-m<sup>2</sup> plot, and 11 (73.3%) of 15 sites had pellets. Pellet densities in the LP2, LP3, spruce-fir, and Douglas-fir stands they sampled fell within the values we found for these stand types. Park staff also sampled in 4 stands of whitebark pine (*Pinus albicaulis*; average  $0.15 \pm 0.05$  pellets), but did not sample LP0, willow, or aspen types.

The forest types we examined differed from each other for most habitat attributes (Table 1). Not surprisingly, mature cover types had higher basal areas of overstory trees, higher canopy closure, and fewer saplings than the regenerating lodgepole, willow-riparian, and aspen stands. We ran separate logistic regressions of pellet presence or absence against each of 9 structural and 2 compositional variables (Table 2). Neither of the compositional variables (percent lodgepole in overstory and percent lodgepole saplings) was statistically significant in relation to pellet presence. Six of the structural variables were statistically significant: canopy closure, basal area of overstory trees, sapling density, and 3 of the cover estimates (0.5–1 m, 1–1.5 m, and 1.5–2 m). Each variable successfully classified whether pellets were present or absent

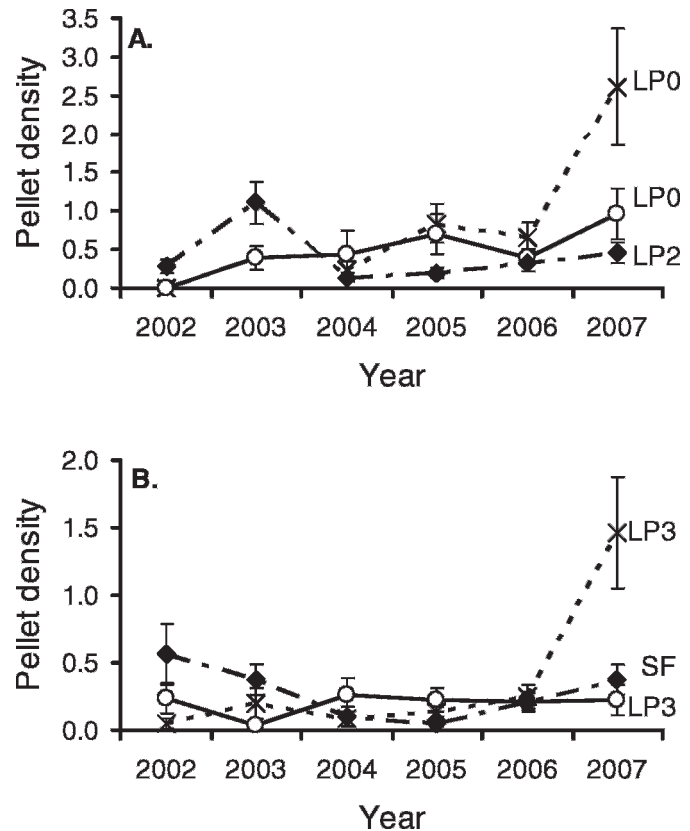


FIG. 4.—Variation in snowshoe hare (*Lepus americanus*) pellet counts for sites sampled from 2002 to 2007. Values are means with SEs. A) Two LP0 (regenerating lodgepole) stands and 1 LP2 (mature lodgepole) stand. B) Two LP3 (mixed lodgepole) stands and 1 SF (spruce-fir) stand.

in  $\sim 70\%$  of cases. Our best-fit multivariable model (fit by stepwise removal of variables and assessment of residual deviance) included only canopy closure and cover from 1 to 1.5 m, correctly classifying 78.3% of cases. For sites with pellets, linear regression indicated only 1 significant habitat variable: the percentage of saplings  $<1.5$  m tall was negatively correlated with pellet density ( $R^2 = 0.140$ ,  $n = 39$ ,  $P = 0.02$ ). Cover from 1.5 to 2 m was nearly significant ( $R^2 = 0.093$ ,  $n = 39$ ,  $P = 0.06$ ).

For the sites surveyed before and after the East Fire, overstory and understory cover dropped precipitously (Table 3) because the majority of canopy trees, saplings, and downed wood burned. In 2002 and 2003, pellet densities before the fire averaged  $0.08 \pm 0.08$  pellets/0.155-m<sup>2</sup> plot and  $0.09 \pm 0.04$  pellets/0.155-m<sup>2</sup> plot for the LP3 and spruce-fir sites, respectively (hare densities of  $\sim 0.05$ /ha). The Douglas-fir site had a pellet density of  $1.01 \pm 0.27$  pellets/0.155-m<sup>2</sup> plot in 2003 (hare density of  $\sim 0.47$ /ha). We sampled each site twice in the 4 years since the fire, and found no pellets.

For sites that burned in 1988, sites where we found pellets had  $>3$  times as many saplings (15,597/ha versus 4,695/ha) as those where no pellets were found, resulting in 1.8–2.7 times as much cover for 3 of 4 height classes (all  $P < 0.025$ ; Table 3). Regenerating stands with  $<4,000$  saplings/ha never had hare pellets, whereas 9 of 10 stands with  $\geq 4,000$  saplings/

**TABLE 1.**—Attributes of vegetation on sites surveyed for snowshoe hares (*Lepus americanus*) in Yellowstone National Park, Wyoming. LP0, LP2, and LP3 are regenerating, mature, and mixed lodgepole stands, respectively. The sample size is given in parentheses for each stand; in some cases more stands were sampled for pellets than for vegetation because our vegetation sampling protocols were finalized after pellet surveys began. The values for the ANOVAs exclude the lone aspen site (*df.* = 5, 59). Values are means across sites  $\pm$  1 SE.

	LP0 (17)	LP2 (13)	LP3 (12)	Spruce–fir (9)	Douglas–fir (3)	Willow (3)	Aspen (1)	<i>F</i>	<i>P</i>
Canopy closure (%)	2.8 $\pm$ 0.9	36.2 $\pm$ 1.7	31.0 $\pm$ 2.1	24.2 $\pm$ 3.5	31.8 $\pm$ 6.3	5.7 $\pm$ 3.0	11.0	44.3	0.000
Basal area of overstory trees	2.5 $\pm$ 1.1	34.0 $\pm$ 3.3	30.4 $\pm$ 1.8	28.7 $\pm$ 4.1	32.3 $\pm$ 4.3	1.2 $\pm$ 1.0	5.5	30.1	0.000
% canopy lodgepole	91.4 $\pm$ 2.0	91.5 $\pm$ 6.1	58.4 $\pm$ 5.6	34.5 $\pm$ 7.6	7.4 $\pm$ 5.0	50.0 $\pm$ 50.0	2.1	14.4	0.000
Saplings per ha	10,425 $\pm$ 2,626	5,491 $\pm$ 637	4,615 $\pm$ 398	3,183 $\pm$ 398	1,114 $\pm$ 955	0	398	3.2	0.013
% saplings lodgepole	97.1 $\pm$ 1.4	64.4 $\pm$ 8.4	22.7 $\pm$ 7.6	20.1 $\pm$ 7.9	0.6 $\pm$ 0.6	–	14.3	33.0	0.000
% saplings <1.5 m tall	50.9 $\pm$ 5.8	73.2 $\pm$ 3.0	65.8 $\pm$ 5.3	72.3 $\pm$ 2.8	68.6 $\pm$ 4.2	–	71.4	3.9	0.008
Logs (per 6 m)	4.0 $\pm$ 0.4	2.0 $\pm$ 0.2	2.6 $\pm$ 0.4	2.1 $\pm$ 0.3	0.9 $\pm$ 0.4	0.03 $\pm$ 0.02	0.8	9.8	0.000
Cover (%) 0–0.5 m	59.7 $\pm$ 3.8	40.5 $\pm$ 3.3	53.3 $\pm$ 4.4	63.7 $\pm$ 6.9	38.4 $\pm$ 4.9	69.0 $\pm$ 4.9	38.9	4.5	0.002
Cover (%) 0.5–1.0 m	36.9 $\pm$ 4.8	20.1 $\pm$ 3.0	28.7 $\pm$ 3.1	36.0 $\pm$ 7.7	18.4 $\pm$ 2.6	44.4 $\pm$ 13.1	5.3	2.5	0.044
Cover (%) 1.0–1.5 m	27.6 $\pm$ 4.7	16.2 $\pm$ 2.4	22.5 $\pm$ 2.1	25.7 $\pm$ 6.3	10.6 $\pm$ 1.4	30.4 $\pm$ 14.6	1.2	1.5	0.218
Cover (%) 1.5–2.0 m	21.2 $\pm$ 4.0	13.7 $\pm$ 2.0	20.5 $\pm$ 2.2	21.1 $\pm$ 4.7	7.0 $\pm$ 1.2	26.0 $\pm$ 12.6	0.7	1.4	0.251

ha had hare pellets. There were no significant differences ( $P > 0.05$ ) between sites with and without pellets for canopy closure, basal area of canopy trees, downed logs, or cover from 0 to 0.5 m above ground.

## DISCUSSION

Snowshoe hares are rare and apparently acyclic in Yellowstone. Many sites supported no hares, and sites with hares had low numbers. Given that individual hares drop an average of 579 pellets/day in winter (Hodges 1999) and that many pellets persist without degrading for years (Krebs et al. 1987; Prugh and Krebs 2004), the low numbers of pellets we observed suggest that many sites in Yellowstone do not support breeding populations of hares, although the occasional hare might disperse across a site. Snowshoe hares in Yellowstone primarily occupy areas with substantive understory cover. Hare abundances were not spatially correlated within Yellowstone; we found no evidence that stands closer together were more similar in relative abundance than were stands that were far apart. In contrast, the physical structure of a stand, particularly in the understory, predicted hare presence and abundance. Our surveys confirm earlier snow-track surveys (Murphy et al. 2006) that also found little sign of snowshoe

hares and limited habitat, particularly in the central and southwestern portions of the park.

Snowshoe hares within Yellowstone National Park occur in a patchy distribution, with hares absent from many stands. The majority of stands with substantial understory cover did have hares, which suggests that hares are able to locate suitable habitat within the park. Similarly low-density, patchy patterns of distribution also occur in Targhee National Forest (Idaho), an area west of Yellowstone also dominated by regenerating lodgepole pine forests (McKelvey and McDaniel 2001). It is possible that Yellowstone hares exhibit metapopulation dynamics, with a source–sink dynamic across patches, as has been documented in western Montana (Griffin and Mills 2003).

Our time-series data did not show the substantial variation that typifies cyclic populations of hares elsewhere, although we caution that we have only 6 years of records. Cyclical lows typically last only 2–4 years (Boonstra et al. 1998), so our low and relatively stable numbers likely reflect acyclicity rather than inadequate duration of sampling. Our 6 longest pellet time series all increased from 2006 to 2007, but the sustained low numbers and asynchronous variation for 5 years before 2007 suggest that snowshoe hare populations are acyclic in Yellowstone.

**TABLE 2.**—Logistic regressions relating vegetation attributes to presence of snowshoe hare (*Lepus americanus*) pellets in Yellowstone National Park, Wyoming. Our best-fit multiple logistic regression included only canopy closure ( $P = 0.002$ ) and cover from 1.0 to 1.5 m ( $P = 0.001$ ) and correctly classified 78.3% of cases.

	$\beta_0$	Estimate	Wald's $\chi^2$	<i>P</i>	% classified correctly
Canopy closure (%)	0.479	–0.053	6.938	0.008	68.3
Basal area of overstory trees	0.215	–0.043	5.467	0.019	70.5
% canopy lodgepole	–0.154	–0.010	1.134	0.287	–
Sapling density	0.210	–0.143	3.940	0.047	73.8
% saplings lodgepole	–1.335	–0.011	2.013	0.156	–
% saplings <1.5 m tall	–0.281	–0.007	0.245	0.620	–
Logs (per 6 m)	–0.273	–0.123	0.480	0.488	–
Cover (%) 0–0.5 m	0.420	–0.019	1.540	0.215	–
Cover (%) 0.5–1.0 m	1.070	–0.063	6.487	0.011	72.1
Cover (%) 1.0–1.5 m	1.917	–0.142	10.17	0.001	73.8
Cover (%) 1.5–2.0 m	1.641	–0.153	11.36	0.001	73.8

**TABLE 3.**—Attributes of burned sites surveyed for snowshoe hares (*Lepus americanus*) in Yellowstone National Park, Wyoming. Three sites (Douglas-fir, LP3, and spruce-fir) were sampled before they burned in the 2003 East Fire (“preburn”), allowing us to detect short-term impacts postfire. We also compare 8 sites that burned in 1988 that had no fecal pellets with 9 sites that did have pellets. Values are means across sites  $\pm$  1 SE.

	Preburn	1–4 years postfire	<i>t</i>	<i>P</i>	1988 burn without pellets	1988 burn with pellets	<i>t</i>	<i>P</i>
Pellet count	0.4 $\pm$ 0.3	0	–1.27	0.272	0	0.5 $\pm$ 0.2	2.38	0.029
Canopy closure (%)	27.1 $\pm$ 4.1	10.4 $\pm$ 3.8	–2.99	0.040	2.3 $\pm$ 0.8	3.4 $\pm$ 1.6	–0.58	0.570
Basal area of overstory trees	36.0 $\pm$ 3.2	0.8 $\pm$ 0.8	–10.72	0.000	1.5 $\pm$ 0.7	3.4 $\pm$ 2.0	–0.85	0.410
% canopy lodgepole	34.1 $\pm$ 20.0	60.0 <sup>a</sup>	–	–	97.5 $\pm$ 2.5	87.5 $\pm$ 12.5	0.62	0.549
Saplings per hectare	3,581 $\pm$ 716	80 $\pm$ 48	–5.02	0.007	4,695 $\pm$ 2,944	15,597 $\pm$ 3,422	–2.39	0.030
% saplings lodgepole	3.7 $\pm$ 2.4	0 <sup>a</sup>	–	–	94.0 $\pm$ 2.5	99.7 $\pm$ 0.2	–2.42	0.029
% saplings <1.5 m tall	70.3 $\pm$ 3.3	80.0 <sup>a</sup>	–	–	47.4 $\pm$ 9.1	54.0 $\pm$ 7.9	–0.55	0.590
Logs (per 6 m)	1.7 $\pm$ 0.2	1.1 $\pm$ 0.4	–1.40	0.235	3.9 $\pm$ 0.4	4.1 $\pm$ 0.6	–0.27	0.787
Cover (%) 0–0.5 m	66.9 $\pm$ 19.3	22.3 $\pm$ 2.3	–2.30	0.083	58.4 $\pm$ 5.4	60.8 $\pm$ 5.5	–0.31	0.759
Cover (%) 0.5–1.0 m	43.0 $\pm$ 14.3	8.5 $\pm$ 1.9	–2.39	0.075	25.7 $\pm$ 5.1	46.9 $\pm$ 6.3	–2.58	0.021
Cover (%) 1.0–1.5 m	26.5 $\pm$ 7.5	5.5 $\pm$ 1.9	–2.72	0.053	16.3 $\pm$ 4.2	37.6 $\pm$ 6.5	–2.69	0.017
Cover (%) 1.5–2.0 m	23.1 $\pm$ 7.5	4.4 $\pm$ 1.8	–2.42	0.073	11.1 $\pm$ 3.3	30.2 $\pm$ 5.4	–2.92	0.010

<sup>a</sup> Only 1 of the 3 burned sites had any saplings or overstory trees, so we did not calculate *t* or *P* for these variables.

One particularly noteworthy aspect of our results links hare presence, and relative abundance, to mature forest stands. Mature cover types (LP2, LP3, spruce-fir, and Douglas-fir) were much more likely to have hare sign than were the immature or open cover types (many LP0, willow, and aspen). This pattern contrasts with other studies that suggest that regenerating lodgepole stands provide particularly good habitat for snowshoe hares (Hodges 2000b; Koehler 1990; Mowat and Slough 2003) and are counter to results from the adjoining and heavily harvested Targhee National Forest immediately to the west of Yellowstone, where there was little sign of hares in the few mature forests that were sampled (McKelvey and McDaniel 2001). In Yellowstone, we suspect that the pattern we observed stems from the characteristic openness of many young lodgepole pine stands, which promotes exposure and accumulation of snow. Winter food and cover in these open cover types would likely be lower than in mature stands, whereas snow depths would be greater. Hares lose more mass overwinter in high-snow years (Hodges et al. 2006), and predation is generally more severe in more open habitats (Griffin and Mills 2009; Hodges 2000b).

Consistent with the interpretation that the openness of young stands in Yellowstone compromised their value for hares, we also found that the only regenerating stands that supported hares were those with higher sapling densities and more understory cover. Our surveys began 14 years after the 1988 fires, and patterns in hare distribution in these regenerating stands map fairly clearly on to the density of regenerating saplings. There was a clear threshold in sapling density below which hares did not occur. Stands with <4,000 saplings/ha never supported hares. Finally, snowshoe hares showed a clear negative response immediately after stand-replacing fires: forested sites that had hares in 2002 or 2003 showed no hares after the 2003 East Fire. Such a pattern is consistent with observed short-term effects of precommercial thinning on snowshoe hares (Griffin and Mills 2007).

In conclusion, snowshoe hares appear to exist in low density, patchy, and acyclic populations within Yellowstone

National Park. Numerous explanations have been posited to explain purported north-south gradients in hare cyclicality, including high predation pressure mediated by “refuge” habitats (Wolff 1980, 1981) and various models of prey or predator dispersal. Although our study was not designed to examine hypotheses about cyclicality, it appears that Yellowstone provides hares with few, low-quality habitats that are patchily distributed. Hares may be proficient at locating and using the best of these sites, but many areas, including lodgepole pine stands with low sapling densities, do not support hares at all.

In contrast with forests elsewhere in the western United States, most Yellowstone stands may not offer adequate cover or food. Our results differ from studies that found high relative abundances of hares in regenerating lodgepole stands in British Columbia (Sullivan et al. 2006), the Yukon (Mowat and Slough 2003), and Washington (Koehler 1990). Although lodgepole pine is eaten by hares (Wirsing and Murray 2002), most diet studies indicate that snowshoe hares eat mixed rather than monotypic diets (Hodges 2000a, 2000b; Hodges and Sinclair 2003; Wirsing and Murray 2002); we wonder if hares are nutritionally stressed overwinter in Yellowstone in the more extensive monotypic lodgepole stands, which are more extensive relative to the landscapes of these other study areas.

Our results also have implications for understanding Canada lynx and other species that might prey upon or compete with snowshoe hares. Hare numbers are known to affect populations of lynx, other predators, and alternative prey in boreal forests (Krebs et al. 2001), but interactions among hares, their predators, and other prey have been less studied in southern parts of the hare range. Snowshoe hares are the major winter prey of lynx in northwestern Montana (Squires and Ruggiero 2007). Although lynx have been observed in the park throughout the last century, a recent survey was able to confirm only 3 individuals in the park (Murphy et al. 2006). It has been estimated that areas must have at least 0.5 hares/ha (Ruggiero et al. 2000) or 1.1 hares/ha (Steury and Murray 2004) to sustain a lynx population. In Yellowstone, only 4% of



our study sites exceeded the 0.5-hares/ha threshold and none exceeded 1.1 hares/ha. Nonetheless, lynx recurrently use Yellowstone, with some evidence of reproduction (Murphy et al. 2006). As yet it is unclear whether these estimated thresholds in hare densities can be applied to Yellowstone, whether Yellowstone lynx rely more on alternative prey than those in other parts of their range, or whether some other factor, such as ingress from northern or southern populations (Schwartz et al. 2002), is necessary to explain how lynx persist in this system.

#### ACKNOWLEDGMENTS

T. Potter and S. Miller helped with site selection and geographic information system mapping. We thank our field crew leaders J. Fuller, E. Barr, D. Ravenel, K. Nittinger, and J. Newby and our many field assistants. This research was funded by Yellowstone National Park, the Greater Yellowstone Coordinating Committee, the Rocky Mountain Cooperative Ecosystem Studies Unit, Okanagan University College, the Natural Sciences and Engineering Research Council (Canada), and the United States National Science Foundation (DEB-9876054 and DEB-0105123).

#### LITERATURE CITED

- AVERY, T. E., AND H. E. BURKHART. 1994. Forest measurements. 4th ed. McGraw-Hill, Inc., New York.
- BOONSTRA, R., C. J. KREBS, AND N. C. STENSETH. 1998. Population cycles in small mammals: the problem of explaining the low phase. *Ecology* 79:1479–1488.
- CHAPMAN, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. *University of California Publications on Statistics* 1:131–160.
- DAVIS, S. A., L. K. AKISON, L. N. FARROWAY, G. R. SINGLETON, AND K. E. LESLIE. 2003. Abundance estimators and truth: accounting for individual heterogeneity in wild house mice. *Journal of Wildlife Management* 67:634–645.
- DESPAIN, D. G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart, Boulder, Colorado.
- FERRON, J., AND M.-H. ST-LAURENT. 2008. Forest-fire regime: the missing link to understand snowshoe hare population fluctuations? Pp. 141–152 in *Lagomorph biology: evolution, ecology, and conservation* (P. C. Alves, N. Ferrand, and K. Hackländer, eds.). Springer-Verlag, Berlin, Germany.
- FISHER, J. T., AND L. WILKINSON. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* 35:51–81.
- FOX, J. F. 1978. Forest fires and the snowshoe hare—Canada lynx cycle. *Oecologia* 31:349–374.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GRIFFIN, P. C., AND L. S. MILLS. 2003. Snowshoe hares in a dynamic managed landscape. Pp. 439–449 in *Species conservation and management: case studies* (H. R. Akcakaya et al., eds.). Oxford University Press, Oxford, United Kingdom.
- GRIFFIN, P. C., AND L. S. MILLS. 2007. Precommercial thinning reduces snowshoe hare abundance in the short term. *Journal of Wildlife Management* 71:559–564.
- GRIFFIN, P. C., AND L. S. MILLS. 2009. Sinks without borders: snowshoe hare dynamics in a complex landscape. *Oikos*.
- HANSEN, A. J., J. J. ROTELLA, M. P. V. KRASKA, AND D. BROWN. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. *Landscape Ecology* 15:505–522.
- HODGES, K. E. 1999. Proximate factors affecting snowshoe hare movements during a cyclic population low phase. *Ecoscience* 6:487–496.
- HODGES, K. E. 2000a. The ecology of snowshoe hares in northern boreal forests. Pp. 117–162 in *Ecology and conservation of lynx in the United States* (L. F. Ruggiero, et al., eds.). University Press of Colorado, Boulder.
- HODGES, K. E. 2000b. Ecology of snowshoe hares in southern boreal and montane forests. Pp. 163–206 in *Ecology and conservation of lynx in the United States* (L. F. Ruggiero, et al., eds.). University Press of Colorado, Boulder.
- HODGES, K. E., R. BOONSTRA, AND C. J. KREBS. 2006. Overwinter mass loss of snowshoe hares in the Yukon: starvation, stress, adaptation or artifact? *Journal of Animal Ecology* 75:1–13.
- HODGES, K. E., AND L. S. MILLS. 2008. Designing fecal pellet surveys for snowshoe hares. *Forest Ecology and Management* 256:1918–1926.
- HODGES, K. E., AND A. R. E. SINCLAIR. 2003. Does predation risk cause snowshoe hares to modify their diets? *Canadian Journal of Zoology* 81:1973–1985.
- KASHIAN, D. M., D. B. TINKER, M. G. TURNER, AND F. L. SCARPACE. 2004. Spatial heterogeneity of lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park, Wyoming, USA. *Canadian Journal of Forest Research* 34:2263–2276.
- KEITH, L. B. 1990. Dynamics of snowshoe hare populations. Pp. 119–195 in *Current mammalogy* (H. H. Genoways, ed.). Plenum, New York.
- KOEHLER, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. *Canadian Journal of Zoology* 68: 845–851.
- KREBS, C. J., R. BOONSTRA, V. NAMS, M. O'DONOGHUE, K. E. HODGES, AND S. BOUTIN. 2001. Estimating snowshoe hare population density from pellet plots: a further evaluation. *Canadian Journal of Zoology* 79:1–4.
- KREBS, C. J., B. S. GILBERT, S. BOUTIN, AND R. BOONSTRA. 1987. Estimation of snowshoe hare population-density from turd transects. *Canadian Journal of Zoology* 65:565–567.
- MALLOY, J. C. 2000. Snowshoe hare, *Lepus americanus*, fecal pellet fluctuations in western Montana. *Canadian Field-Naturalist* 114:409–412.
- MANNING, T. W., D. EDGE, AND J. O. WOLFF. 1995. Evaluating population-size estimators: an empirical approach. *Journal of Mammalogy* 76:1149–1158.
- McKELVEY, K. S., AND G. W. McDANIEL. 2001. An analysis of snowshoe hare (*Lepus americanus*) numbers in Island Park based on pellet sampling and capture/recapture trapping. Rocky Mountain Research Station, Internal Report.
- MICROSOFT INC. 2005. Microsoft Office professional edition. Microsoft Corporation, Redmond, Washington.
- MILLS, L. S., P. C. GRIFFIN, K. E. HODGES, K. McKELVEY, L. RUGGIERO, AND T. ULIZIO. 2005. Pellet count indices compared to mark-recapture estimates for evaluating snowshoe hare density. *Journal of Wildlife Management* 69:1053–1062.
- MOWAT, G., AND B. SLOUGH. 2003. Habitat preference of Canada lynx through a cycle in snowshoe hare abundance. *Canadian Journal of Zoology* 81:1736–1745.



- MURPHY, K. M., ET AL. 2006. Distribution of Canada lynx in Yellowstone National Park. *Northwest Science* 80:199–206.
- MURRAY, D. L. 2000. A geographic analysis of snowshoe hare population demography. *Canadian Journal of Zoology* 78:1207–1217.
- NATIONAL PARK SERVICE. 2007. <http://www.nps.gov/yell/parkmgmt/firemanagement.htm>. Accessed September 2008.
- PARAGI, T. F., W. N. JOHNSON, D. D. KATNIK, AND A. J. MAGOUN. 1997. Selection of post-fire seres by lynx and snowshoe hares in the Alaskan taiga. *Northwestern Naturalist* 78:77–86.
- PRUGH, L. R., AND C. J. KREBS. 2004. Snowshoe hare pellet-decay rates and aging in different habitats. *Wildlife Society Bulletin* 32:386–393.
- RUGGIERO, L. F., ET AL. 2000. The scientific basis for lynx conservation: qualified insights. Pp. 443–454 in *Ecology and conservation of lynx in the United States* (L. F. Ruggiero, et al., eds.). University Press of Colorado, Boulder.
- SCHWARTZ, M. K., L. S. MILLS, K. S. MCKELVEY, L. F. RUGGIERO, AND F. W. ALLENDORF. 2002. DNA reveals high dispersal synchronizing the population dynamics of Canada lynx. *Nature* 415:520–522.
- SEBER, G. A. F. 1982. *The estimation of animal abundance and related parameters*. 2nd ed. Macmillan, New York.
- SQUIRES, J. R., AND L. F. RUGGIERO. 2007. Winter prey selection of Canada lynx in northwestern Montana. *Journal of Wildlife Management* 71:310–315.
- STEURY, T. D., AND D. L. MURRAY. 2004. Modeling the reintroduction of lynx to the southern portion of its range. *Biological Conservation* 117:127–141.
- SULLIVAN, T. P., D. S. SULLIVAN, P. M. F. LINDGREN, AND D. B. RANSOME. 2006. Influence of repeated fertilization on forest ecosystems: relative habitat use by snowshoe hares (*Lepus americanus*). *Canadian Journal of Forest Research* 36:2080–2089.
- TURNER, M. G., D. B. TINKER, W. H. ROMME, D. M. KASHIAN, AND C. M. LITTON. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* 7:751–775.
- UNITED STATES FISH AND WILDLIFE SERVICE. 2008. Revised critical habitat for the contiguous United States distinct population segment of the Canada Lynx. *Federal Register* 73:10859–10896.
- WIRSING, A. J., AND D. L. MURRAY. 2002. Patterns in consumption of woody plants by snowshoe hares in the northwestern United States. *Ecoscience* 9:440–449.
- WIRSING, A. J., T. D. STEURY, AND D. L. MURRAY. 2002. A demographic analysis of a southern snowshoe hare population in a fragmented habitat: evaluating the refugium model. *Canadian Journal of Zoology* 80:169–177.
- WOLFF, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecological Monographs* 50:111–130.
- WOLFF, J. O. 1981. Refugia, dispersal, predation, and geographic variation in snowshoe hare cycles. Pp. 441–449 in *Proceedings of the world lagomorph conference* (K. Myers and C. D. MacInnes, eds.). University of Guelph, Guelph, Ontario, Canada.
- ZAHRATKA, J. L., AND S. W. BUSKIRK. 2007. Is size of fecal pellets a reliable indicator of species of leporids in the southern Rocky Mountains? *Journal of Wildlife Management* 71:2081–2083.

*Submitted 19 September 2008. Accepted 15 December 2008.*

*Associate Editor was Paul T. Stapp.*