Snowshoe Hares in Yellowstone

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ALL PHOTOS COURTESY KAREN E. HODGES

This snowshoe hare is starting to turn from its brown summer coat to its white winter coat.

WHEN PEOPLE THINK of "Yellowstone wildlife," the most immediate images that spring to mind are likely bison, elk, wolves, and bears. But Yellowstone National Park also acts as a haven for scores of other species, some of which are more elusive and rarer than these bigger animals. For example, Canada lynx (*Lynx canadensis*) occur in Yellowstone, but with very low numbers (see article by Murphy et al. in this issue of *Yellowstone Science*). Canada lynx were listed as threatened under the Endangered Species Act in 2000, and researchers across the country began more intensive work on them as the listing was developed. Because historic records showed that lynx occurred in Yellowstone, park biologists wondered how many lynx the park could support. Lynx are specialist predators on snowshoe hares (*Lepus americanus*), and it is clear from previous research that insufficient hare densities mean no lynx. We therefore initiated snowshoe hare studies in Yellowstone, in part to assess what the prey base was for lynx.

In undertaking this research, we were basically asking one of the fundamental questions in ecology: what determines the distribution and abundance of a species? Prey species, like snowshoe hares, can respond to physiological limits (e.g., climate variables), food abundance, presence of competitors, and predator abundance. In Yellowstone, we knew snowshoe hares occurred; people saw them periodically, and the presence of lynx was another sure indicator. But we knew nothing about what habitats snowshoe hares used in the park, how abundant they became in the best habitats available, or what factors were shaping where they occurred. We knew from previous research, by ourselves and others, that snowshoe hares respond strongly to understory structure; they like dense cover close to the ground or snow surface. Dense understory is even better when accompanied by reasonably thick overstory cover. Given the dramatic fire history of Yellowstone, we speculated that some of the stands regenerating after the 1988 burns would be good for hares: the dense, regenerating trees could provide

excellent understory cover, and in some places the trees were getting tall enough to impair hunting raptors.

Our goals with this research were therefore simple: we wanted to identify where snowshoe hares were in Yellowstone, how large their populations were, and whether areas regenerating after the 1988 fires provided good habitat for them. In 2004, we were provided with another opportunity to address the impacts of fire on snowshoe hares. The large East Fire in 2003 burned three study areas that we knew had contained hares during our previous surveys. We re-sampled these areas in 2004 to find out whether snowshoe hares persisted there immediately after the fires.

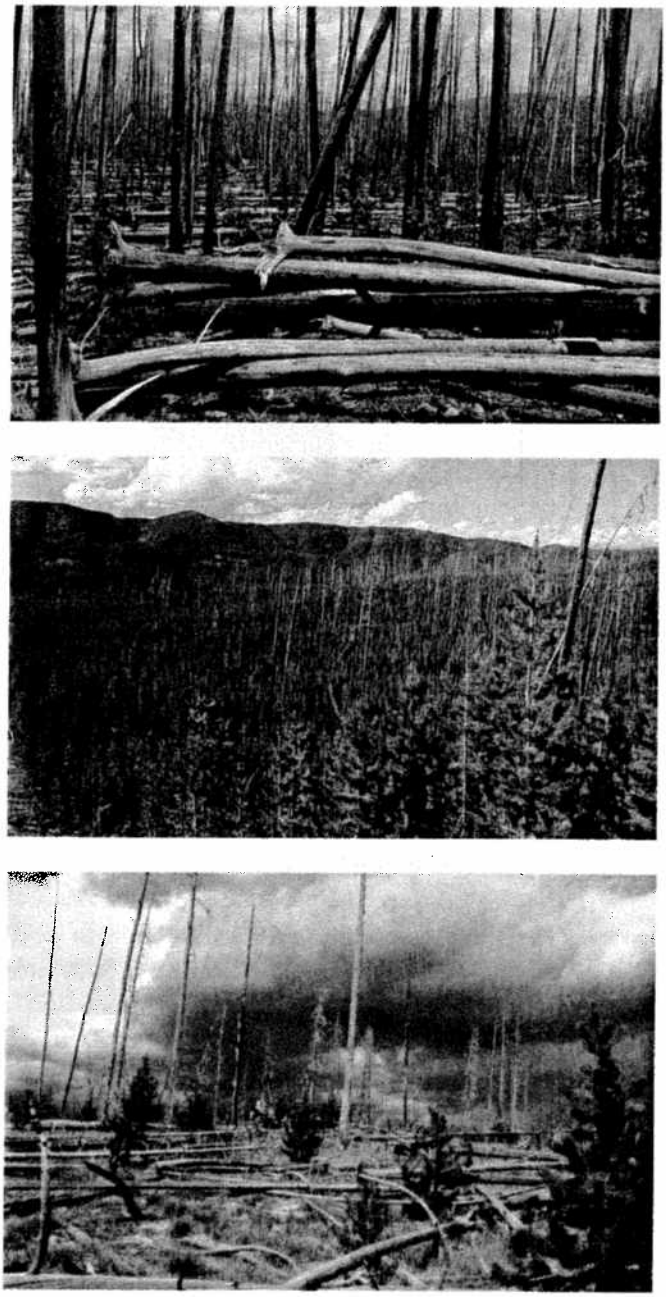
Our results clearly show that snowshoe hares are uncommon in Yellowstone.

We also wanted to address some of the temporal dynamics of snowshoe hares in Yellowstone. In the northern forests of Canada and Alaska, snowshoe hares have stunning population cycles every 10 years, with peak abundances dramatically higher than low abundances. Researchers still are not certain whether snowshoe hares cycle in southern portions of their range, like the Rocky Mountains and Yellowstone. So far, we have three years of data on snowshoe hares in Yellowstone—too short to answer the cycle question definitively, but a good start along the way.

We approached our questions with a mixture of field techniques. We used some live-trapping with mark/re-capture estimation, one of the best methods for estimating densities of small mammals. We also used pellet counts—that is, surveying a forest stand by counting all snowshoe hare pellets on 50 to 100 small rectangular patches of forest floor. Our other work in Yukon Territory and Montana, as well as work by other research groups, has shown that pellet counts provide a pretty good indicator of snowshoe hare relative abundance in different forest types. These pellet surveys are fast and easy compared to trapping, enabling us to sample many more stands than we could with trapping alone. During the three years we have surveyed so far, we sampled some locations in each year to get an idea of how snowshoe hare populations change with time, and sampled many areas once only, to see how hares are distributed.

We chose to survey a variety of stand types across the entire park. Because biologists have been studying snowshoe hare habitat use for a century, we were able to immediately target the most likely sites. Areas with well-developed understories (e.g., saplings, shrubs) typically have the most hares, and mature forests with well-developed canopies also usually support snowshoe hares. Good bison habitat was out of the picture for hares: open forests and meadows are simply not used by this forest-dwelling herbivore, so we did not need to sample there. We used Yellowstone's GIS maps of habitat types to select lodgepole pine stands of differing stages, ranging from the stands regenerating after the 1988 burns to mature stands with lodgepole understories. We also targeted forest stands containing Engelmann spruce and subalpine fir, because there was some speculation in the literature that hares would prefer these more boreal trees to the lodgepoles.

Our results clearly show that snowshoe hares are uncommon in Yellowstone. The highest densities we recorded were less than one hare per hectare; densities above 0.5 hares per hectare were rare in the park. There was no evidence of snowshoe hares in the majority of the stands we surveyed. In our



All of these areas burned in the 1988 fires. Fire severity and regeneration patterns are very different. The center picture is of a site with one of the highest snowshoe hare densities seen in Yellowstone.

Snowshoe hares are more likely to use stands with boreal characteristics.

first year, we trapped in 13 large stands, and caught snowshoe hares in only four of them—for a total of 13 animals. In contrast, when we did similar trapping in northwest Montana in the same year, we caught over 250 individuals, and had some stands with hare densities of two to three hares per hectare. The snowshoe hare pellet surveys confirmed this picture of Yellowstone. Over half of the more than 60 stands surveyed had no pellets or only one pellet present. Only six stands had enough pellets to indicate a reasonable resident hare population. Even on these best plots, the pellet counts were quite low, reflecting small numbers of hares. Yellowstone simply is not good snowshoe hare country.

So where do we find snowshoe hares in Yellowstone? We divided our sites according to whether they had fewer or more than five pellets present per survey. This pellet count value is quite low, corresponding to hare densities of roughly one every ten hectares. Below this number, we suspected that hares may have been traveling through a habitat but were not resident. Hares can produce 400 to 700 pellets per day, so when we sampled a 20-hectare area and found fewer than five pellets, it means hares basically aren't using the stand. In Figure 1, we show that the more boreal habitat types of spruce-fir and LP3 (a mixed canopy of lodgepole, spruce, and fir) were the most likely to have snowshoe hare pellets present. In contrast, only a quarter of the lodgepole-dominated young stands that were either regenerating after the 1988 fires (LP0) or that had a lodgepole canopy and understory (LP2) had reasonable evidence of snowshoe hares. Snowshoe hares are more likely to use stands with boreal characteristics.

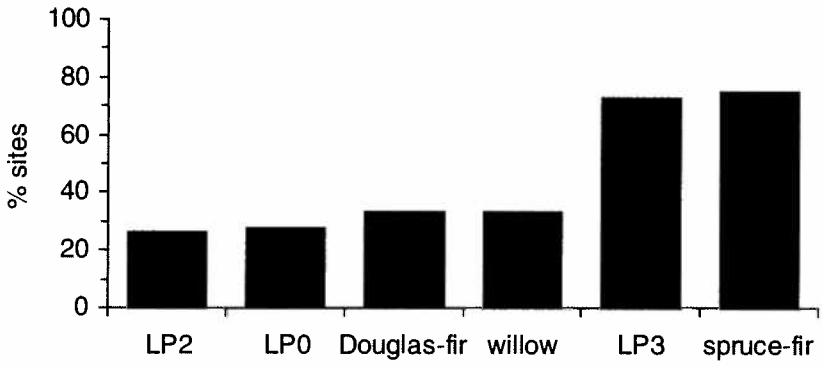
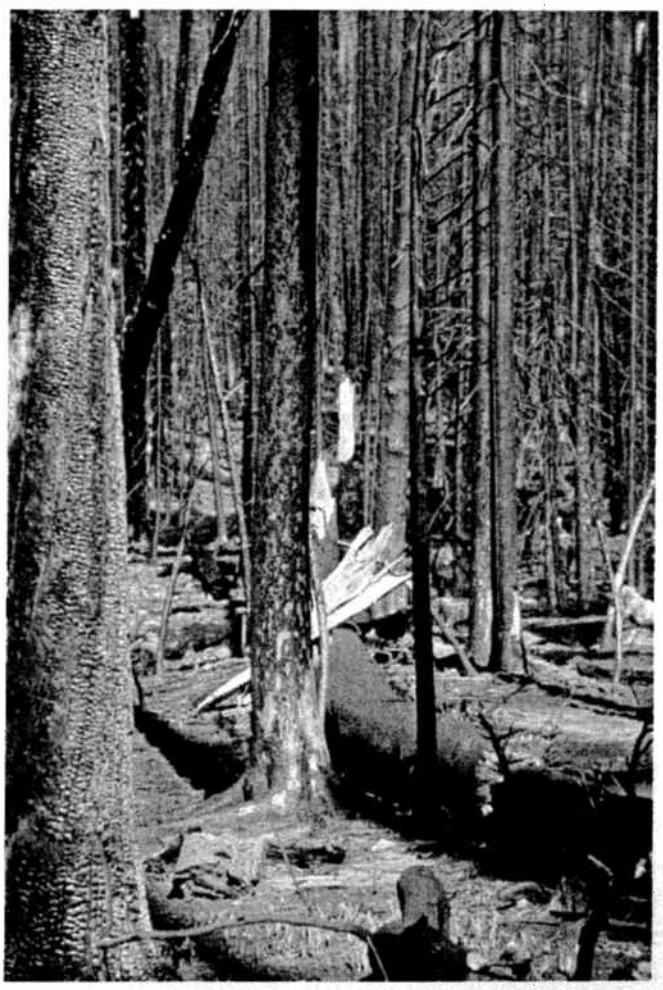


Figure 1. The percentage of each habitat type with more than five snowshoe hare pellets per survey (i.e., >0.06 pellets/plot). LP is lodgepole. LP0 sites are stands regenerating after the 1988 fires. LP2 stands have a canopy of lodgepole with some understory trees. LP3 has a mixed canopy of lodgepole, spruce, and fir. "Willow" refers to three riparian areas we sampled, one of which had some pellets; the other two did not.



The photos above and right show a mature stand before and after the 2003 East Fire.

We obtained a slightly different view of what makes the best Yellowstone habitats for snowshoe hares when we considered the stands where we trapped snowshoe hares or where we observed the highest pellet counts. We caught the most hares on an LP0 site near Madison Junction and on an LP2 site near the South Entrance—a pattern that held true for all three years of trapping. For pellets, our top six sites—which were substantially better than all the rest—were a Douglas-fir site, two post-1988 regenerating stands, two LP2 stands, and one LP3 stand. These sites were scattered throughout the park, from the Gallatin Mountains to the East Entrance, meaning there is not a cluster of good sites in the park. Pellet counts on these sites ranged from 0.47 pellets per plot to 1.44 pellets per plot, which corresponds roughly to hare densities of one hare per four hectares to one hare per 1.5 hectares. We think these stands support the highest hare densities we have seen in Yellowstone because they have some of the best mix of understory and overstory cover; we are currently analyzing our data on vegetation structure in more detail. Curiously, no spruce-fir stands made it into our top list of sites, even though three quarters of the spruce-fir stands we sampled had more than our cutoff of five pellets.

So far, there are no clear temporal patterns for the sites we sampled in all three years. Some sites stayed constant from year to year, while others showed slight year-to-year variation in the pellet counts. Our trapping data have also not shown any clear patterns through time. These data do not yet allow us to distinguish whether hares cycle in Yellowstone or not, because even in populations that cycle dramatically, there can be two-to-four year periods with little change in numbers.

Our results from the sites that burned in the 2003 East Fire are clear. We surveyed three stands (Douglas-fir, spruce-fir, and an LP3) in 2002 and prior to the fire in 2003. All three had high pellet numbers before the fire; indeed, the Douglas-fir stand showed our third-highest pellet count in Yellowstone. The 2003 fire burned all of these stands completely, leaving no green vegetation. In 2004, unsurprisingly, none of these sites had any sign of snowshoe hares.

Our work in Yellowstone has confirmed the general pattern of snowshoe hare habitat studies from elsewhere, in that dense stands are much more likely to support hares than open stands. We were surprised to find that snowshoe hare densities were so very low. Even the best stands we have found in Yellowstone support far fewer hares than can occur further north in the Rockies (i.e., our Montana sites) or in the truly boreal forests of Canada and Alaska.

We think snowshoe hares in Yellowstone are probably quite mobile, for two reasons. First, we found some snowshoe hare pellets in almost all of the locations that had reasonable understory cover, which suggests that snowshoe hares are able to colonize these sites even if they are surrounded by very poor habitat types. Second, about a quarter of our sites had one to four pellets present, suggesting a snowshoe hare had been there, but likely did not stay for long. Snowshoe hares in Yellowstone may therefore be behaviorally different than hares that live in better habitats.

Our data about snowshoe hares' response to fire indicates quite clearly that fire initially destroys habitat, and that the regeneration pattern is the key ingredient for whether snowshoe hares will use a burned area or not. A substantial proportion of the stands burned in 1988 have regenerated with low tree densities. These stands are essentially useless for snowshoe hares and, we suspect, will remain useless until a canopy has formed with a second story underneath. For now, the trees are simply too thin on the ground. In contrast, regenerating stands where saplings form fairly continuous cover (e.g., branches are touching and trees are reasonably tall) are currently supporting some of the highest hare densities we have observed in Yellowstone. These stands are certainly good now, but we are not sure how long they will remain of high quality. As the trees increasingly compete with each other, loss of lower branches and the deaths of some saplings may make these stands less and less appealing to snowshoe hares. This process will take years or decades, however, and hares may well start to find other good habitats as these decline.

What do these patterns mean for lynx? The most obvious implication is that Yellowstone is unlikely to support large lynx populations. Even the snowshoe hare hotspots had very few individual hares in them, so any lynx present in the park probably have to travel widely to find prey consistently. Still, a wide range of places had hare pellets within them, so a traveling lynx might encounter a snowshoe hare that was also traveling to find better habitat. We suspect that lynx in Yellowstone may make more use of alternative prey (e.g., squirrels, grouse, maybe even carrion) than do lynx in areas with many more hares.

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Between them, they have researched snowshoe hares for over 15 years, and worked on the population dynamics and habitat use of small mammals for over 35 years. They have been studying snowshoe hares in Yellowstone since 2002.