Population Distribution of Snowshoe Hares in Yellowstone National Park

2002-2005

Dr. Karen E. Hodges*
Dr. L. Scott Mills

Wildlife Biology Program
University of Montana
Missoula, MT 59812

*Current address: Biology and Physical Geography, University of British Columbia Okanagan, 3333 University Way, Kelowna B.C. V1V 1V7, Canada

Background and motivating questions

Snowshoe hares (*Lepus americanus*) are an important prey species for a number of forest mesocarnivores, such as wolverine, marten, fisher, and especially the federally threatened Canada lynx (*Lynx canadensis*). Despite a wide range across most boreal and montane forests in North America, the distribution, relative abundance, and population dynamics of snowshoe hares in the southern areas of their range are less known than for northern populations (Hodges 2000a,b). In boreal forests, snowshoe hares exhibit spectacular population cycles, which impact many other species (Krebs et al. 2001). In the Greater Yellowstone Ecosystem, the same complement of boreal species occurs, but at lower densities and with more patchy distributions, but it is not known if snowshoe hares cycle in this region. Lynx occur in Yellowstone, but at low densities (Murphy et al. 2006).

Yellowstone's forests vary enormously, with underlying rock and forest fire history best predicting forest cover (Turner et al. 1999). Stands regenerating after fires often support the understory structure favored by hares (Hodges 2000b). Many forested areas (e.g., lodgepole pine cover types) of the park that burned in 1988 are now in a seral condition that is known to support hares in other regions, leading to the question of whether there is now an abundance of high quality hare habitat there. Another major habitat expected to be good for hares in this region is mature spruce-fir forest. These stands often have an understory developing below the canopy provided by mature trees. There is little of this stand type remaining in Yellowstone, particularly following the 2001 and 2003 fire seasons.

Our primary interest in this system was to understand how the patchiness in forest cover affected snowshoe hare relative abundance and distribution among patches. Elsewhere, snowshoe hares respond both to the cover type of a stand and to the cover of the neighboring patches (Hodges 2000b, Walker et al. in review). Across many landscape types, hares typically reach their highest abundances in stands with dense understories (Hodges 2000b), and it seems that the proportion of moderate to high-quality habitat in a given landscape affects the over-all abundance of hares. Thus landscapes with a majority of poorer stand types are expected to have low numbers of hares, and the hares that do occur are likely to be in the few better-quality patches. In contrast, landscapes with a majority of moderate to high quality stand types are predicted to support higher hare densities over-all, and the variance among patch types may be low because hares are able to use more stand types. Because no systematic work on snowshoe hares in Yellowstone had previously been conducted, our primary motivating objectives were to:

1) characterize the distribution and relative abundance of snowshoe hares in a variety of stand types;
2) characterize the effects of different post-fire regeneration patterns on snowshoe hare relative abundance; and
3) determine whether there was clearly noticeable multi-annual variation in hare numbers.

Objective 3 is a necessary preliminary to addressing the question of whether hares cycle in Yellowstone. The classic snowshoe hare cycle in boreal forests is 8-11 years (Hodges 2000a), so a 4 year study cannot document a cycle, but can detect whether significant changes in abundance occur, as in a cyclic population. We also had a fourth minor objective: to conduct a genetic analysis of snowshoe hares to document genetic connectivity between different areas of the Park. This objective is linked to our work on hares in other regions, and enables us to contrast genetic structuring among landscapes that support different abundances and distributions of hares. Our sampling design in Yellowstone was based on the first three objectives.

Research approach

We began our work on snowshoe hares in Yellowstone National Park in 2002. This report focuses on the period 2002-2005 (i.e. the period with funding from the RM-CESU), although we are continuing this work with other funding sources. All of our work was conducted in July and August of each year.

We worked with Dr. Kerry Murphy and other Park biologists to identify forest stand types that were likely to contain snowshoe hares and that were more than minor forest components within Yellowstone National Park. We dismissed cover types that were rare or that were deemed unlikely to support snowshoe hares because they were too open or were non-forested. The seven types we chose were: spruce-fir, three seral stages of lodgepole pine (*Pinus contorta*; LP0, LP2, LP3), Douglas Fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and willow-riparian (*Salix spp)*. Spruce-fir stands are characterized by both overstory and understory primarily composed of Engelmann spruce (*Picea englemannii*) and subalpine fir (*Abies lasiocarpa*). LP0 lodgepole stands are regenerating post-disturbance, usually within 0-40 years post-fire. In our case, we chose LP0 stands that had burned in the 1988 fires. LP2 stands typically are closed canopy lodgepole stands, with the canopy largely intact; understory trees may be lodgepole or other species. LP3 stands have canopies that are a mix of lodgepole, spruce, and fir, and these stands often have well-developed understories. The three remaining cover types (Douglas fir, aspen, willow-riparian) are dominated by the species named. Willow-riparian occurred along streams or rivers, and often did not contain trees.

Of these seven types, we chose four for the most effort (live-trapping some sites, and more replication for pellet surveys). Two of these types (spruce-fir, LP3) were chosen because they were likely lynx habitat, and another two types (1988 burn, LP2) were chosen because they were dominant stand types in Yellowstone and were likely to contain snowshoe hares. The remaining three types were rarer in the Park and were less likely to contain hares, so we sampled fewer of these sites. The majority of our sites were 20 hectares, as this size is larger than the typical home range of snowshoe hares (Hodges 2000a), yet is small enough to be logistically feasible. A few sites were 10 ha, when we could not locate a suitable 20 ha patch of the target habitat type within the particular area of the Park we wished to sample. We attempted to sample across the Park insofar as it was feasible; we selected sites randomly from the set of sites that were logistically available within each area. In 2003, three of our study sites near the East Entrance road burned in the East fire; we have conducted some pellet counts on these sites since then, to see how hares responded to this loss of live forest cover.

We did our most extensive work in 2002, with the dual goals of conducting a fairly broad survey to give us a base of knowledge about the types of habitats hares were using in Yellowstone and whether particular parts of the Park supported higher hare numbers. A secondary goal was to establish sites for repeated annual live-trapping and fecal pellet surveys (Krebs et al. 2001, Mills et al. 2005). In subsequent years, our sampling took three forms: repeat trapping of some sites to establish a time series of population estimates; sampling of new sites with fecal pellet surveys to broaden the number and kind of sites surveyed; and repeat sampling of some sites with pellet surveys to provide another set of sites with time series data. The number of sites sampled in each way is summarized in Table 1.

Table 1. Our sampling for snowshoe hares in Yellowstone National Park. The sites selected for repeated sampling, either via trapping or via pellet counts, had hares or pellets present in the first year the site was sampled.

	2002	2003	2004	2005
sites trapped	13	4	3	3
new sites surveyed for fecal pellets	41	8	33	0
sites with a repeat survey for pellets	--	29	16	14

Snowshoe hare trapping

In 2002, we trapped 13 sites in four habitat types: spruce-fir, 1988 burn, LP2, and LP3. In 2003-2005, we retrapped 3-4 of these original sites, based on previous capture of animals or pellet counts that were comparatively high. For each trapped site, we established an 8 x 10 array of Tomahawk live-traps, with 50 m between traps. We baited traps with alfalfa and apple, setting traps in the evening and checking them early the next morning. Each site was trapped for a minimum of 3 nights and a maximum of 5 nights. Each captured snowshoe hare was weighed, eartagged with a Monel #3 tag, and sexed. We recorded the length of the right hind foot, and took a 3 mm tissue punch from the ear for genetic analysis. Handling took 2-5 minutes per animal, and hares were released at the point of capture. All trapping and handling was done with Institutional Animal Care and Use Committee approval from the University of Montana (2001-2004) and Animal Care Committee approval from Okanagan University College (2005).

Pellet counts

Pellet counts can provide a fairly fast way of surveying areas for relative hare abundance (Krebs et al. 1987, 2001, Mills et al. 2005). We surveyed a number of sites in Yellowstone for snowshoe hares by using 50 to 80 2”x10’ plots per site and counting all fecal pellets observed in each plot. The small stands (10 ha) were sampled with 50 pellet plots; the 20 ha stands were sampled with 80 plots. We surveyed the sites on which we trapped by locating transects near each trap location (50 m between transects, in an 8 x 10 array). For the sites that we did not trap, we used GIS to randomly position pellet plots within the boundaries of the site; in the field we used GPS to locate the starting point, then used a compass and measuring tape to move to other points to sample.

Vegetation surveys

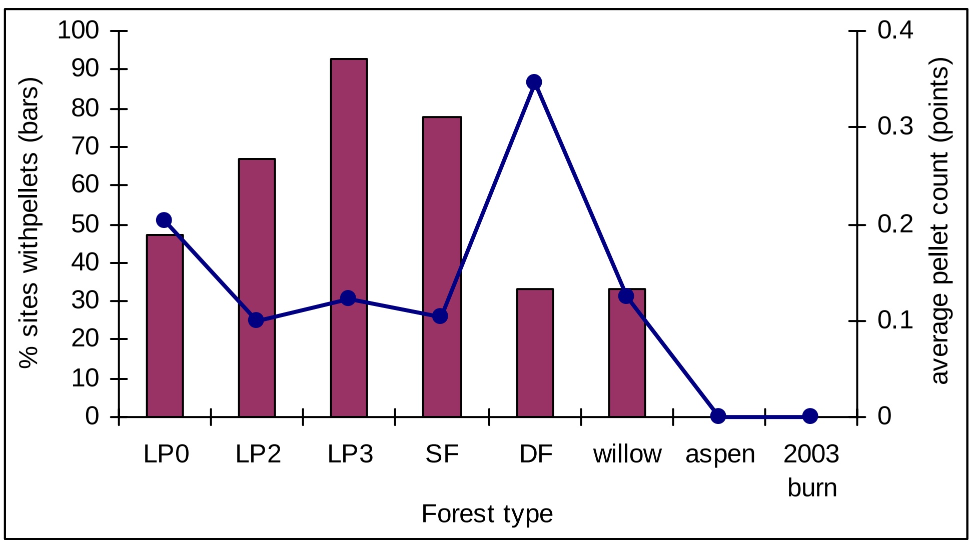
To characterize our study sites in more detail than afforded by the existing GIS data layers, we measured overstory and understory cover. At 20-30 locations per stand, the density of overstory trees was estimated with variable radius sampling. We identified the canopy tree species and measured the diameter at breast height; trees had to be >8 cm dbh to be included. The density of saplings (trees >0.5 m tall and <8 cm dbh) was estimated by counting the number of saplings within a 2 m radius. Coarse woody debris was described by counting the number of downed trees that intersected a transect. Horizontal cover was estimated by using a 0.5 x 2 m cover board divided into blocks 0.25 m square and estimating the percent covered in 0.5 m height increments. We will not discuss these data further in this report, but we are developing a manuscript that will address how these variables affected the relative abundance of snowshoe hares in the different stand types.

Major results

Snowshoe hares were not present in many of the stands we surveyed. In our 2002 trapping efforts on 13 sites, only 4 sites had hares, and these sites had low numbers. We captured a total of 13 animals, and the largest population estimate was 7 hares (95% CI, 2.5-11.5). In subsequent years of trapping 3 of these sites (the 4th site burned in the 2003 East fire), we obtained population estimates of 0-11 hares per trapping site. We could not detect any temporal trend in hare abundance on these sites, in part because it difficult to obtain good estimates of small population numbers, and in part because the estimates within each site varied little; the confidence limits overlap from year to year. The three sites are in different habitat types: LP0, LP2, and spruce-fir; the fourth site that had hares in 2002 was also a spruce-fir site.

Our pellet surveys showed a similar pattern: many of our sites had no pellets, and the sites with pellets usually had pellet counts indicative of small numbers of hares (Figure 1). Out of 69 sites we surveyed in at least one year, 25 had no pellets (36.2%). Only 4 sites had above 0.6 pellets per pellet plot; this value corresponds to an estimate of fewer than 0.3 hares per hectare (Krebs et al. 2005), which is quite low. Snowshoe hares in cyclic populations can easily reach densities of 4-6 hares/ha (Hodges 2000a). The four sites with the most pellets were 2 LP0 stands, one LP2 stand, and one Douglas fir stand; this latter stand burned in the 2003 East fire. In general, stands with mature canopies of lodgepole (LP2 and LP3) or spruce-fir were most likely to have at least some pellets present (67-93% of stands).

Figure 1. Surveys of snowshoe hare fecal pellets in Yellowstone National Park. We surveyed 69 sites from 2002-2005; bars show the percentage of sites that had pellets, while points show the average number of pellets per plot across each stand type. DF=Douglas fir; 2003 burn = stands we had surveyed in 2002 or 2003, that then burned in 2003.



Snowshoe hares showed a variety of responses to regenerating forests after fires. We had three sites that we surveyed before and after the 2003 East fire. In all cases, the stands supported hares before the fire, but we found no pellets in the years after the fire. The stands regenerating after the 1988 fires show an enormous range of densities of lodgepole pine saplings (Turner et al. 1999), and hares also varied in their densities. Over half of the regenerating sites we surveyed had no pellets. On the regenerating sites where we did find pellets, the average density was the highest of any stand type, at 0.43 pellets/plot, or roughly three times as high as the LP2, LP3, and spruce-fir stands that had pellets.

Implications of this research

In terms of our motivating questions, these results indicate that Yellowstone currently does not contain abundant habitats that support high numbers of snowshoe hares. Rather, hares are scattered across the Park in pockets of suitable habitat, but even in these sites they do not occur at high densities. Although we specifically selected sites we thought were likely to have hares, based on an extensive literature and our knowledge from working in other areas, about ⅓ of our surveyed sites had no evidence of hares at all, and another half or more showed extremely low densities. By far the majority of our surveyed sites had fecal pellet counts so low that these sites probably did not even support a single hare during the entire year, but instead had hares that were occasionally present. Some of the best sites for hares are indeed stands that are regenerating post-fire, but many burned stands are regenerating thin tree cover that does not support hares. Although we have observed some variability in hare numbers from year to year, the numbers of hares are so low that we cannot confidently tell yet whether the dynamics resemble part of a population cycle, are simply variable, or are reflecting measurement error.

We are currently working on manuscripts for submission to peer-reviewed journals from our work to date, and we are continuing our snowshoe hare surveys within Yellowstone. The patterns we are observing here are particularly intriguing in comparison to the disparate patterns that we and other scientists are observing elsewhere in their range (Hodges and Mills, unpublished data).

The results from this work are pertinent to Yellowstone's natural resource mandates in several ways. Canada lynx, a federally threatened species, are specialist predators on snowshoe hares. Because Yellowstone contains Canada lynx (Murphy et al. 2006), work describing the distribution of their primary prey is important for habitat mapping and endangered species consultation efforts. Furthermore, the YNP Resource Management Plan has identified two specific goals that pertain to snowshoe hares and lynx:

(1) to complete systematic park-wide surveys to document the distribution of T&E species and mid-sizes carnivores and conduct necessary research (YELL-N-012 and YELL-N-033);

(2) to develop inventory and monitoring systems to track trends in small mammal populations and determine their abundance and distribution in selected habitats (YELL N-029).

Understanding the forest structures that support snowshoe hare populations will therefore contribute to effective management of lynx, through habitat mapping and consultation between the Park and the U.S. Fish and Wildlife Service required under the Endangered Species Act.

References

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, editors L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires. 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, editors L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires. University Press of Colorado, Boulder.

Krebs, C.J., Boonstra, R., Nams, V., O'Donoghue, M., Hodges, K.E., and Boutin, S. 2001. Estimation of snowshoe hare population density from pellet plots--a further evaluation. Canadian Journal of Zoology 79: 1-4.
Krebs, C.J., Gilbert, B.S., Boutin, S., and Boonstra, R. 1987. Estimation of snowshoe hare population density from turd transects. Canadian Journal of Zoology 65: 565-567.
Mills, L.S, P.G. Griffin, K.E. Hodges, K. McKelvey, L. Ruggiero, C. Henderson, and T. Ulizio. 2005. Pellet count indices compared to mark-recapture estimates for evaluating snowshoe hare density. Journal of Wildlife Management 69:1053-1062.
Murphy, K.M., Potter, T.M., Halfpenny, J.C., Gunther, K.A., Jones, M.T., Lundberg, P.A., and Berg, N.D. 2006. Distribution of Canada lynx in Yellowstone National Park. Northwest Science 80:199-206.
Turner, M.G., Romme, W.H., and Gardner, R.H. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. International Journal of Wildland Fire 9: 21-36.
Walker, C.J., K.E. Hodges, L.S. Mills, and G.M. Koehler. In review. Multi-scale factors influencing snowshoe hare densities in fragmented forests. Submitted to Journal of Wildlife Management.

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Appendix 1: Sites live-trapped for snowshoe hares in Yellowstone National Park. Site names are based on nearby named geographic features.

site	UTM easting	UTM northing
Spruce-Fir		
Cub Creek	564141	4927398
Frank Island*	550873	4918320
Spirea Creek	526055	4890131
1988 Burn		
Cygnet Lake	533573	4950311
Firehole	511394	4941449
Ice Lake	528715	4951823
Kepler	515332	4921871
LP2		
Gull Point	545640	4929809
Mesa	515055	4942203
S. Moose Falls	526351	4888176
LP3		
Cub Creek II	562767	4927844
Lone Star	515589	4920325
Sand Point	545059	4925703

Appendix 2: Sites in Yellowstone National Park where we counted snowshoe hare pellets as an index of abundance. Sites are grouped by stand type.

site	UTM easting	UTM northing
Sites burned in 1988 (LP0)		
Cygnet Lake	533594	4950590
Fairy Creek	505683	4926820
Firehole I	506239	4925494
Heart Lake 1	539447	4905303
Ice Lake	528562	4952053
Kepler	515612	4921901
Lewis Falls 1	528313	4900766
Mallard Creek	514080	4927504
Mallard Lake	515584	4923468
Mary Mtn 1	531529	4940660
Norris	524244	4952198
Old Fountain	497343	4943906
Overlook	499327	4943783
Sewage	533513	4916085
Springs	496439	4967378
Seven Mile	521464	4969930
Swan Lake	520924	4972478
LP 2		
East Ent. Rd	561089	4927815
Firehole II	511670	4941340
Fishing Bridge	548051	4934877
Grayling	494283	4966159
Gull Point	545932	4929875
Heart Lake 2	535040	4907349
Little Thumb	529645	4919312
Mary Mtn 3	529216	4938941
Mesa	515366	4942063
Ochre Springs	545861	4940430
Pumice Point	538746	4923957
S. Moose Falls	526110	4888319
Scaup Lake	518340	4920078
LP 3		
Bacon Rind	494966	4976942
Cub Creek II*	563064	4928052
DeLacy	523350	4921225
IceBox	573703	4979860
Le Hardy	548325	4938437
Lone Star	515328	4920386
Mary Mtn 2	531805	4939795
Pelican Creek	551820	4934315
Sand Point	544607	4925433
Sepulcher	519551	4981739
Sulphur Creek	542692	4956860
West Thumb	531164	4919237

Douglas fir		
East Entrance	576562	4925841
Lake Butte*	557739	4928720
Mammoth	522238	4979990
aspen		
Hoodoos	522778	4977979
willow riparian		
Snake River	528608	4888522
Obsidian	520445	4968154
Specimen Ck.	493402	4983975
Spruce-Fir		
Arnica	537373	4927454
Cub Creek I*	564272	4927583
Divide	496253	4972812
Dunraven	543127	4958057
Frank Island*	550726	4918550
Grand Loop	542865	4924531
Lewis Falls 2	527768	4900681
S.Boundary	530491	4889587
Spirea Creek	526261	4890304

*Sites that burned in the 2003 East Fire. We surveyed all of these sites prior to the fire, and all except Frank Island we have also resurveyed after the fire.

Appendix 3: Publications and presentations drawing from this work.

Completed

Hodges, K.E. 2006. Research in conservation biology: forest mammals, fire and forestry. Undergraduate Biology Course Union Seminar Series, UBC Okanagan, Kelowna BC.

Hodges, K.E. and L.S. Mills. 2005. Snowshoe hares in Yellowstone. Yellowstone Science 13:3-6.

Hodges, K.E. and L.S. Mills. October 2004. Landscape ecology of snowshoe hares. Joint meeting, Lynx Biology Team and Lynx Steering Committee, Winthrop WA.

Hodges, K.E. and L.S. Mills. July 2003. Snowshoe hares in Yellowstone National Park. Interagency Lynx Coordination Meeting, Island Park ID.

Hodges, K.E. and L.S. Mills. Pellet counting protocol for lynx survey team in Yellowstone, developed May 2003.

Hodges, K.E., P. Griffin and L.S. Mills. June 2002. Snowshoe hare habitat use patterns in North America. Lynx Biology Team Meeting, Missoula MT.

Repanshek, K. December 2003. The missing lynx. Wyoming Wildlife 18-25. (Profiles Yellowstone area lynx-snowshoe hare issues).

Instructor, Yellowstone Institute Course on lynx and snowshoe hare ecology, August 2003.

In preparation

Hodges, K.E. and L.S. Mills. Factors affecting snowshoe hare distribution in Yellowstone National Park.

Appendix 4: People trained as part of our research on snowshoe hares in Yellowstone National Park. We value our research not only because of what we learn about species and their environments, but also as opportunities to train people in scientific investigation. We have specifically sought ways to engage undergraduate students and recent graduates with our research endeavors. "Technicians" includes recent graduates as well as people with more experience (e.g. a person between his MSc and PhD degrees and a high school teacher interested in field ecology). "Volunteers" were primarily undergraduate students with no previous field experience, but this category also includes several recent graduates. Our training has also been international, with people from Great Britain and Canada among our field crews.

	2002	**2003**	**2004**	**2005**
undergraduate students	7	2	0	2
technicians	0	0	2	1
volunteers	4	3	0	0
TOTAL	11	5	2	3