

# Evaluating the Prey Base for Lynx: Snowshoe Hare Distribution and Abundance in Glacier National Park



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## FINAL REPORT

### BACKGROUND AND MOTIVATING QUESTIONS

In 2000, the Canada lynx (*Lynx canadensis*) was awarded protection under the ESA as a Threatened species throughout its range in the lower 48 US states. Glacier National Park (Glacier NP) contains a population of lynx, and is one of the few US Parks known to do so. Because of its location within the Northern Rockies ecosystem, regional efforts to protect lynx will require effective protection of lynx in Glacier NP. In addition to serving as a potential reservoir and corridor for lynx populations beyond the Park, Glacier NP is an ecosystem untouched by logging and still sculpted by wildfires. As such, it can provide insight into how lynx dynamics are influenced by historically important natural disturbance processes, compared to the managed logging and prescribed burns that have replaced wildfires in many US forests. Currently, data are insufficient to identify important habitat or develop a management plan for Canada lynx in Glacier NP. Personnel have been monitoring the Park's lynx population through informal track surveys for the past 15+ years, with limited results. Sightings of lynx have been infrequent in the Park. However, lynx have occasionally been captured in wolverine traps around Many Glacier, on the Park's east side. In 2000, the National Lynx Survey also identified at least 4 unique lynx individuals in the northeast section of Glacier NP and at least 2 unique individuals in its southeast corner. These data, though sparse, have suggested that lynx in the Park primarily occur east of the Continental Divide and in the 1988 Red Bench burn area in the Park's northwest corner (Fig. 1).

Throughout their range, lynx prevalence coincides with densities of snowshoe hares (*Lepus americanus*), their primary prey (Koehler 1990; Parker et al. 1983; Ruggiero et al. 2000; Squires and Ruggiero 2007). The fundamental link between snowshoe hare densities and Canada lynx abundance, survival, and productivity was recognized by the US Fish and Wildlife Service with its inclusion of snowshoe hares as an essential component of critical habitat for Canada lynx. Thus, to understand lynx distribution and dynamics requires knowledge of hare distribution and dynamics.

In addition to their role as primary prey of Canada lynx, snowshoe hares are also important as a strongly interacting species in boreal forests (Ruesink et al. 2002). In addition, hares have become a sentinel for evaluating climate change effects, due to the potential mismatch between their seasonal coat color change and a reduction in snow cover (Mills et al. In Prep; Huang 2009).

From 2005 to 2007, we conducted an intensive field survey of snowshoe hares in Glacier NP. We had three primary objectives. The first was to identify the distribution and abundance of snowshoe hares in the Park, and what factors may influence where they occur. In particular, we were interested in understanding whether infrequent reporting of lynx on Glacier NP's west side may be due to low densities of snowshoe hares there. Forests on the west side are primarily mixed conifer stands. Regenerating stands from the 1988 Red Bench fire occur in a mosaic with mature multistory stands. Forests on the east side are patchier, with multistory conifer stands interspersed among shrub fields, aspen stands, fescue grasslands, and subalpine meadows. Our research investigated whether snowshoe hare densities are higher in the east

than in the west, and addressed related questions of how landscape patterns affect snowshoe hare abundance and distribution in Glacier NP.

Our second objective was to assess how wildfires and post-fire regeneration affect hares. Large-scale wildfires occur regularly on Glacier NP's west side, with an average 2,000 hectares burned each year since 1988. In 2003, the largest fire year for Glacier NP since 1910, approximately 13% of the Park's more than 410,000 hectares burned in wildfires. Understanding how snowshoe hares respond to post-fire regenerating habitats would allow the Park to assess likely impacts of this and future fires on snowshoe hares and lynx. Our research focused on hare use of regeneration from the 1988 Red Bench Fire, another major fire that had burned over 11,000 hectares of primarily lodgepole pine (*Pinus contorta*) forest in the Park's northwest corner. Our third objective was to develop a cost-effective non-invasive genetic approach to abundance estimation that could be of benefit to national parks and other areas surveying snowshoe hares and other moderately abundant species. The field and laboratory work for this component of the study continued into 2011, with additional funding provided by Animal Welfare Institute. We present the results of this method development and cost-benefit analysis as Appendix I to this report.

Although little was known about snowshoe hares in Glacier NP when this study began, many studies have examined snowshoe hare habitat use in other parts of the species' range, especially in relation to forestry practices. From these studies, we know that snowshoe hares use a variety of habitat types, with understory cover being one of the most important elements to them (Hodges 2000a, 2000b). Researchers have found that stands with shrubs, stands that are densely stocked, and stands at ages where branches have more lateral cover are more heavily used by hares (Black 1965; Dolbeer and Clark 1975; Koehler 1990; Litvaitis et al. 1985; Monthey 1986; Walker et al. 2011; Wolfe et al. 1982). Overstory cover is sometimes correlated with hare habitat use patterns, but typically in cases where it is also significantly correlated with understory cover (Orr and Dodds 1982; Parker et al. 1983; Richmond and Chien 1976; Rogowitz 1988). The species composition in a stand appears to be less correlated with hare habitat use than is understory structure (Ferron and Ouellet 1992, Griffin and Mills 2007). Stand age per se does not appear to be critical, again because of the importance of stand structure.

Particularly in their southern range, where habitats are patchy and fragmented, landscape-level factors and metapopulation dynamics may be important for persistence of snowshoe hare populations (Griffin and Mills 2003, 2009; Wirsing et al. 2002). Habitat interspersions may be valuable to hares by providing them access to habitats with different protective abilities and food availabilities (Koehler and Brittell 1990; Krenz 1988; Thomas et al. 1997). In Minnesota, hare habitat use was more correlated with habitat interspersions than with stand type, and hares used the edges more than centers of the heavily used stand types (Conroy et al. 1979). Habitat patchiness can also create source-sink dynamics, dampening landscape-scale population growth (Griffin and Mills 2009), and landscape structure around a patch can influence local dynamics (Walker et al. 2011).

Although there are few field studies of hares' use of burned stands, several authors have suggested that fire contributes to the cycling of hare populations, by transiently providing dense stands of regenerating forest rich in food and cover for hares (Ferron and St-Laurent 2007; Fox 1978; Grange 1965; Howell 1923). Our recent work on snowshoe hares in Yellowstone National Park (Hodges et al. 2009) found three of our five highest hare density

sites occurred in lodgepole pine stands regenerating from Yellowstone's 1988 fires. Hare densities in regenerating stands were positively correlated with sapling density and understory cover.

Much of our understanding of hare-habitat relationships comes from studies of forests managed at least in part for timber production. We investigated whether hares would be more abundant in the more patchy forests of Glacier NP's east side, compared to the more closed canopy forests west of the Continental Divide. Also, we tested for effects of understory structure and amount of forest edge habitat in the unharvested landscape of Glacier NP. Finally, we tested whether hares would have higher densities in the regenerating forest from the 1988 Red Bench Fire.

## **METHODS**

### *Site Selection*

We surveyed three types of study sites: Random Unburned, Targeted Unburned, and Red Bench Fire sites. All study sites met these criteria: 1) at least 85% forest cover, 2) did not occur in areas burned since 2001, 3) at least 500 m from the nearest road, 4) did not overlay Park hiking trails, and 5) at least 300 m from the nearest study site. We set a minimum threshold of 85% forest cover because snowshoe hares are obligate forest species infrequently found in large open areas (Hodges 2000a, 2000b). For the same reason, we did not survey recent burns. Remaining criteria were set to minimize potential impacts of anthropogenic disturbances, and to maximize independence of sites.

For Random Unburned sites, we used a tessellated random sampling approach to ensure unbiased selection of sites, but fairly even coverage of the full extent of the Park. We used an existing geographic information system (GIS) layer that gridded the Park into 46 large sampling blocks corresponding to USGS Digital Orthophoto Quadrangle maps. Each year of the study (2005–2007), we used Hawth's Analysis Tools ([www.spatialecology.com/htools/tooldesc.php](http://www.spatialecology.com/htools/tooldesc.php)) to randomly allocate 3 points to each of the 46 sampling blocks. Using GIS, we superimposed a 20-ha study site (500 m X 400 m) centered on each of these points. We then excluded all sites that did not meet the five site criteria listed above. With this method, the number of sites per sampling block was correlated with forest cover, producing a relatively even distribution of sites across Glacier NP's forested habitats, which comprise 55% of the Park.

Targeted Unburned sites were identified by Park officials as areas likely to support snowshoe hares, based on previous sightings. We ground surveyed these areas and selected sites with high densities of snowshoe hare pellets. These sites were used to pilot test a protocol for non-invasive genetic abundance estimation of snowshoe hares (Appendix I), and to provide additional data for characterizing high hare density habitats in Glacier NP.

Red Bench Fire sites were randomly selected points within the area delineated by GIS as the 1988 Red Bench Fire. To ensure a sufficiently large sample size for characterizing hare use of regeneration, we sampled these sites at a higher density than Random Unburned sites.

We attempted to survey as many pre-selected sites as possible each year, and to cover the Park widely. However, for logistical and safety reasons, we excluded sites that required potentially dangerous river crossings as well as sites that required more than a two days' hike to access and could not be combined with nearby sites in a multiple day backcountry survey trip. Within a field season, we could only complete a subset of pre-selected sites. We prioritized sites that

could be more easily accessed as well as sites that filled spatial sampling gaps. Except for sites that were live-trapped, each site was surveyed a single time.

When we arrived at a site, we conducted a ground reconnaissance to verify the site met all criteria (in particular, 85% forest cover could not be accurately determined from GIS at the scale of our study site). When necessary, we used a predefined field protocol to objectively shift sites (by <500m) that did not meet criteria.

### *Fecal Pellet Counts and Habitat Measurements*

A detailed field protocol is provided in Appendix II. We conducted field work May to August in 2005, 2006 and 2007. Each 20-ha study site was divided into an 8 X 10 grid, with 80 sampling points and 50-m spacing between points. We averaged fecal pellet counts across 80 sampling points per site to index hare abundance (Hodges and Mills 2008; Krebs et al. 2001; Krebs et al. 1987; Mills et al. 2005). At every sampling point, a 0.155 m<sup>2</sup> rectangular transect was laid due north from a random start. All pellets that fell at least one-half within the transect area were counted.

Along three internal grid rows of each site (2<sup>nd</sup>, 4<sup>th</sup>, and 7<sup>th</sup> rows), we conducted vegetation surveys at 50-m spacing, for a total of 30 vegetation sampling points. Vegetation surveys focused on overstory and understory habitat variables well-established as correlates with hare densities. For overstory habitat, we recorded the dominant canopy species as the species for which the canopy covered the largest percentage of our fish-eye view at each point. We estimated canopy closure as % view obstructed (viewed through a vertical PVC tube) at the sampling point and at 6 m east and 6 m west of the sampling point. For understory habitat, we measured understory cover, sapling density, and an index of downed logs. We used a 0.532-m<sup>2</sup> cover board, vertically divided into four blocks, to measure understory cover. A person standing at the sampling point estimated % view obstructed at 0.5-m increments above the ground, while the cover board was held at 6 m east and also at 6 m west of the sampling point. Sapling density was calculated as the number of live saplings with trunk centerline within a 2-m radius of the sampling point. Saplings, defined as trees with <5 cm diameter-at-breast-height, were recorded to species and categorized into three height categories: 0.5 – 1.5 m, 1.5 – 3 m, and >3 m. Our index of downed logs was the number of downed logs >5 cm diameter encountered along a 12 m east-west transect centered on the sampling point.

Characteristics of the surrounding landscape may influence snowshoe hare density within a study site (Shick 2003; Thomas et al. 1997; Walker et al. 2011). As a rough index of landscape heterogeneity around hare study plots, we used Glacier NP's 2007 GIS vegetation coverage to calculate linear distance of edge habitat (defined as the boundary between NVC2\_L1X forest and all other habitats) within a 600 m and a 1000 m radius circle centered on each study site (Hop et al. 2007).

### *Statistical Analyses*

Average pellet count for each site was converted to hare density, using a standard regression equation modified for single-survey (i.e., uncleared) pellet transects (Hodges and Mills 2008; Hodges et al. 2009). Because pellet counts are a relatively coarse index of hare abundance, especially at densities below 0.3 hares/ha (Mills et al. 2005), we used pellet counts to categorize sites as low (< 0.3 hares/ha) or moderate ( $\geq$  0.3 hares/ha) hare density. In this

context, the  $<0.3$  hares/ha threshold is used to describe areas where hares are functionally absent, persisting well below a threshold likely to support lynx (e.g., 0.5 hares/ha; Ruggiero et al. 2000). Likewise, our designation of “moderate” density as  $\geq 0.3$  hares/ha is a relative term about where lynx might be supported in conjunction with alternate prey. For comparison purposes to show that  $\geq 0.3$  is a moderate density for this part of the hare’s range, we considered our density estimates based on capture-mark-recapture of 33 sites within 200 km of GNP that we have sampled for up to 12 years between 1998 and 2010 (for a total of  $N = 198$  site-years of density estimates) (Mills et al. 2005; Mills and Hodges, unpublished data). For these 198 site-years across a variety of climate conditions, land uses, structure types, and landscape contexts, hare densities ranged from 0.03 to 3.38 hares/ha, with mean = 0.69 (SE = 0.043) and median = 0.53.

With the GIS data available when this study commenced, it was difficult to identify forest stands by dominant canopy species during the initial GIS-based site selection process. Therefore, we used GIS simply to identify forested habitats, and subsequently used field-collected data to classify sites into broad categories of dominant canopy species for analyses:

- 1) Subalpine fir-Engelmann spruce (ABLA\_PIEN, *Abies lasiocarpa*-*Picea engelmannii*)—Sites predominantly comprising one or a mixture of both species.
- 2) Lodgepole pine (PICO, *Pinus contorta*)—Lodgepole pine was the dominant canopy species at 70% or more of sampling points in the site.
- 3) Lodgepole pine saplings (PICOsap) —Regenerating lodgepole pine forests with few canopy trees. All PICOsap sites were burned in the 1988 Red Bench Fire, but not all Red Bench Fire sites fell in this category because some regenerating stands had achieved mixed canopies or the canopies were dominated by a species other than lodgepole.
- 4) Mixed canopy (MIXED) —Sites were MIXED if no single species was recorded as the dominant canopy species at 70% (or more) of sampling points in the site.
- 5) Other single-species stands (OTHERS) —Sites dominated by a single canopy species other than lodgepole pine, subalpine fir, or Engelmann spruce. Primarily, these stands were dominated by either Douglas fir (*Pseudotsuga menziesii*) or western hemlock (*Tsuga heterophylla*).

To explore hare habitat use, we conducted univariate comparisons of habitat variables versus hare density category (moderate or low). We used Fisher’s Exact Test to determine if moderate versus low hare density sites differ by dominant canopy category, site type (Random Unburned, Targeted Unburned), or by location east versus west of the Continental Divide. The Wilcoxon Rank Sum Test was used to determine if moderate versus low hare density sites differ in habitat characteristics measured as continuous variables: % canopy, downed logs, understory cover, and forest edge habitat (600 m and 1000 m radius).

We also combined habitat variables in a logistic multiple regression with hare density category as the response variable. Based on results of univariate analyses, which suggested PICOsap was the only dominant canopy category that influenced hare density, we included dominant canopy as a single variable coded as 1 if the site was PICOsap and 0 if the site was not PICOsap. We compared information criteria (Akaike’s Information Criterion and Bayesian Information Criterion) and two cross-validation approaches (delete-d and K-fold) for selecting the best model, as implemented in the R statistical package, *bestglm* (McLeod and Xu 2010). Bayesian

Information Criterion (BIC; Schwarz 1978) applies a higher penalty to parameters, so often selects more parsimonious models than Akaike's Information Criterion (AIC; Akaike 1974). Cross-validation methods identify the best model for each of  $p = 0$  (intercept only) to the maximum number of model parameters, then use cross-validation to select the predictive model with the smallest deviance. Delete-d uses a much larger validation set than typically used in K-fold cross-validation, and (unlike K-fold) its predictive ability appropriately converges to 1 as the number of observations increases (Shao 1993). For delete-d cross-validation, our data were analyzed with a training set of 31 sites and a validation set of 89 sites, as recommended for a sample size of  $N = 120$  sites (Shao 1997). Results were based on 1000 replications. For K-fold cross-validation, our data were analyzed with a training set of 90 sites ( $K = 4$ ) and a validation set of 30 sites. One study site was excluded from logistic regression and model selection analysis because sapling density data were not available.

## RESULTS

We conducted pellet counts and vegetation surveys at 121 sites in Glacier NP. Of these, 20 were regenerating lodgepole pine forest from the Red Bench Fire, 92 were Random Unburned sites, and 9 were Targeted Unburned sites. Almost one-third ( $N = 42$ ) of the 121 sites were MIXED canopy sites, with no single canopy species dominating. Almost a quarter ( $N = 28$ ) were dominated by lodgepole pine. We distinguished between mature lodgepole pine forests (PICO,  $N = 16$ ) and regenerating forests primarily comprising saplings  $<10$  m tall (PICOsap,  $N = 12$ ) because habitat characteristics were very different for these categories. Over a quarter ( $N = 28$ ) of sites were mature subalpine fir-Engelmann spruce forests. The remaining 13 sites were categorized as OTHER—these sites were dominated by Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), or other less represented species. PICOsap was our only category of regenerating forest; all other categories were mature forest with extensive canopy cover. Our PICOsap sites occurred only in the Red Bench Fire area in the northwestern corner of the Park. Other dominant canopy categories were well distributed throughout the Park (Fig. 2).

Hare densities were low in much of the Park. We found no snowshoe hare pellets on 14% of study sites. Only 18% ( $N = 22$  of 121) of sites had estimated hare densities greater than 0.3 hares/ha. Less than 7% ( $N = 8$  of 121) of sites had hare densities exceeding 0.5 hares/ha, a commonly cited minimum threshold for an area to sustain a lynx population (Ruggiero et al. 2000). Five of the 8 sites that exceeded 0.5 hares/ha occurred in regenerating lodgepole forests of the Red Bench Fire; the other 3 sites were Random Unburned sites east of the Continental Divide (Fig. 3).

Among Random Unburned sites, the proportion of moderate density sites ( $\geq 0.3$  hares/ha) was greater east of the Continental Divide (20% of 35 sites) than west of the Continental Divide (7% of 57 sites; Fisher's Exact Test,  $N = 92$ ,  $p = 0.10$ ). All Red Bench Fire sites occurred west of the Continental Divide, and had a relatively high proportion (35% of 20 sites) of moderate hare density sites. When Random Unburned and Red Bench Fire sites were combined in analysis, we found no significant difference in hare density category east or west of the Continental Divide (Fisher's Exact Test,  $N = 112$ ,  $p = 0.58$ ).

The proportion of moderate hare density sites was significantly greater for Red Bench Fire sites than for Random Unburned sites (35% compared to 12%, Fig. 4; Fisher's Exact Test,  $N = 112$ ,  $p =$

0.018). Not surprisingly, Targeted Unburned sites were also more likely than Random Unburned sites to support moderate hare densities (Fisher's Exact Test,  $N = 101$ ,  $p = 0.026$ ).

The frequency of moderate hare density sites differed significantly among dominant canopy categories (Kruskal-Wallis Rank Sum Test,  $\chi^2 = 17.2$ ,  $p = 0.0015$ ), with PICOsap stands supporting a higher percentage of moderate hare densities than any other stand type (Fig. 5). PICOsap was the only dominant canopy category with moderate hare densities at more than half of sites surveyed. With PICOsap excluded, we found no significant differences in the frequency of moderate hare densities among dominant canopy categories (Kruskal-Wallis Rank Sum Test,  $\chi^2 = 3.4$ ,  $p = 0.33$ ).

All PICOsap sites were regenerating lodgepole forests from the Red Bench Fire, but the Red Bench Fire also included sites categorized as MIXED and OTHERS (Fig. 6). Among Red Bench Fire sites, only those categorized as PICOsap had moderate hare densities (Fig. 7). Subalpine fir-Engelmann spruce (ABLA\_PIEN) sites made up more than one-third of the Unburned (Random and Targeted) sites surveyed. For Unburned sites, the distribution of dominant canopy categories did not clearly differ between moderate and low hare density sites (Fig. 8).

We used univariate analyses to examine differences in vegetation characteristics among dominant canopy categories, with particular focus on how PICOsap differed from other categories. The three categories of understory cover above 0.5 were highly correlated ( $r > 0.78$ ), so were collapsed into a single variable (understory cover 0.5 – 2 m) for all analyses. We also combined all sapling data (species and size classifications) into a single measure of average sapling density per site. The regenerating lodgepole pine forests that characterized PICOsap had lower % canopy, more downed logs, higher sapling density, higher understory cover at 0.5 - 2 m above ground, and more edge habitat than other dominant canopy categories (Table 1). Most striking was the difference in sapling density—which was, on average, more than an order of magnitude greater in PICOsap than in other dominant canopy categories.

We explored differences in vegetation characteristics between moderate and low hare density sites, separately for Red Bench Fire and Unburned sites. Based on univariate analyses of Red Bench Fire sites, we found significantly higher sapling density and forest edge in moderate- compared to low-hare density sites (Fig. 9, Table 2, Wilcoxon Rank Sum Test,  $p = 0.0005 - 0.046$ ). Among Unburned (Random and Targeted) sites, understory cover at 0 – 0.5 m above ground was significantly lower in moderate- compared to low-hare density sites (Fig. 10, Table 3, Wilcoxon Rank Sum Test  $p = 0.005$ ). Sapling density tended to be higher in moderate hare density sites ( $p = 0.083$ ).

Multivariate analyses confirmed the overriding importance of Red Bench Fire regenerating lodgepole forests in predicting moderate hare density sites in Glacier NP. Whether or not a site was categorized as PICOsap was the one habitat variable that was identified by all multivariate methods as an important predictor of hare density category (Table 4). It was the only variable included in the best-fit models based on cross-validation. BIC model selection identified two additional variables—understory cover 0 – 0.5 m and East-West category—as important predictors. Sites with low understory cover 0 – 0.5 m and sites east of the Continental Divide were more likely to have moderate hare densities. AIC model selection included these three variables as well as % canopy and sapling density in the best-fit model, but the only statistically significant variables were those shared with the BIC model.

## DISCUSSION

Snowshoe hares occur at low densities and are patchily distributed in Glacier National Park, with highest densities found in regenerating lodgepole forests of the 1988 Red Bench Fire. Red Bench Fire sites were three times more likely to support densities  $\geq 0.3$  hares/ha than were randomly selected unburned sites. Given the well-known association between snowshoe hares and early- to mid-stage lodgepole pine regeneration (recently reviewed in Ellsworth and Reynolds 2006) we expect regenerating forests of the Red Bench Fire to continue supporting moderate hare densities and lynx over the next decade. Indeed, during our 3-year study, our field crew reported two lynx sightings, both in Red Bench Fire study sites.

Overall, hare densities in the Park were higher east of the Continental Divide. This pattern was not significant in univariate analyses, but the (east-west) location of a site was included in best-fit AIC and BIC models for predicting hare density. However, as regenerating forests from Glacier NP's west side 2003 fires (which burned forty times more area than the Red Bench Fire) mature to stages favorable for hares and lynx over the next several decades, Glacier NP may observe a shift in distribution of its hare and lynx populations to take advantage of transiently favorable food and cover conditions west of the Continental Divide.

Within Glacier NP's unburned forested habitats, moderate hare densities occurred most frequently in mature conifer forests along the eastern and southern boundaries of the Park—particularly in the areas of Many Glacier, Two Medicine, and Railroad Creek. The regions of moderate hare density identified by our random sampling of the Park corresponded well with areas of lynx occurrences and also matched areas Park biologists had independently identified as snowshoe hare hotspots.

In univariate analyses, hare densities in the Park were positively associated with sapling densities. This association was statistically significant in Red Bench Burn sites and nearly significant in Unburned (both Random and Targeted) sites. In some analyses we also found a significant negative association between hare densities and understory cover at 0 – 0.5 m (the height at which a hare would travel) and a positive association between hare densities and forest edge within a 600 m and 1000 m site radius. However, high sapling density and classification as a Red Bench Fire site were the two variables that most consistently predicted moderate hare densities.

The strong association of snowshoe hares with regenerating lodgepole pine in Glacier NP is consistent with findings from many other studies (Koehler et al. 1979; Malloy 2000; Miller 2005; Sullivan 1984; McKelvey and McDaniel 2001). More surprising was the lack of strong positive association between hare densities and understory cover, as is often reported (reviewed in Hodges 2000a, 2000b). In this study, the lack of a strong positive association between hare densities and understory cover, as measured by horizontal coverboards, may be due in part to changes in shrub and other deciduous foliage density during the course of each field season (May – August). These seasonal changes meant a study site could yield different understory cover measurements depending on which month of the growing season it was surveyed. In comparison, sapling density (which was significantly associated with hare density in this study) was a potentially more stable metric of year-round understory cover, as well as an important measure of winter food availability.

Overall, the range of hare densities recorded in Glacier National Park are within the range of other parts of the hare's southern range (e.g., 0 to 2.7 hares/ha for US Rocky Mountains;

Ellsworth and Reynolds 2006), but somewhat lower than other areas we have studied in the Northern Rockies region. In this study, we find in GNP that only 18% (22/121) of sites had hare densities  $>0.3$  hares/ha, and less than 7% (8/121) had densities  $>0.5$  hares/ha; notably, 9 of the 121 sampled sites were subjectively chosen to represent the best hare habitat in the Park (based on observations by Park biologists). By contrast, we find in our other study area in Montana and Washington that at least 50% of sites tend to have hare densities exceeding 0.3 hares/ha (e.g., medians 0.3 or greater). From 1998 to present, at multiple sites in 3 regions within 300 km of Glacier National Park, we have estimated abundance using either live trapping or pellet plots converted to density as in this study. If we average across multiple years of sampling at each site to calculate a site mean, including site/year combinations with 0 hares, we find summer densities of:

- Okanogan National Forest (north-central Washington), 2003 and 2004: median = 0.67; N = 76 sites; pellet sampling (Walker et al. 2011).
- Seeley Lake Ranger District, Montana, 1998–2010; median = 0.28 hares/ha; N = 25 sites; live trapping (Mills et al. 2005; Mills unpublished data).
- Tally Lake Ranger District, Montana, 2001–2009; median = 0.9 hares/ha; N = 8 sites, live trapping (Mills and Hodges, unpublished data).

In short, Glacier National Park's relative hare density appears well below the densities in complexes of sites we have sampled in WA and MT within 200km of GNP. On the other hand, Glacier hare densities are well above what we found in Yellowstone National Park (Hodges et al. 2009), an area of poor hare habitat, where 38% of sampled stands had no pellets at all (nearly 3 times the rate of zeros as in this GNP study).

The high variability in hare densities at Red Bench Fire sites primarily reflects differences in forest regeneration rates, which vary at a fine scale due to topographic relief, soil moisture, and other habitat factors (Baumgartner et al. 1984; Koch 1996). In a study concurrent with our Glacier work, we found a similar patchiness in hare distribution among lodgepole pine forests burned in Yellowstone National Park's 1988 fires (Hodges et al. 2009). At a landscape scale, differences in forest regeneration rates can translate to differences in optimal post-disturbance age for supporting hares and lynx. Studies in the western US have found highest hare densities correlated with regenerating forests ranging from 20 to 67 years old (Koehler et al. 1979; Zimmer 2004; Miller 2005). Regardless of when the optimum sapling densities and understory conditions are reached, snowshoe hares' association with regenerating lodgepole pine forests is transient. As lodgepole pine forests mature, the trees self-prune their lower branches, creating a more open understory. Thus, the distribution of snowshoe hares in Glacier NP will change over time, particularly with the changing mosaic of post-fire succession on the Park's west side. Notably, a history of fire suppression throughout the west may be expected to reduce the availability of young post-fire stands. To the extent that GNP maintains fire return intervals more characteristic of background levels, then post-fire stands, and the higher densities of hares they support, will serve as yet another example of an important ecological process maintained within the Park.

Finally, we reiterate that Appendix I contains a draft manuscript in preparation describing our work to compare the performance of non-invasive genotyping of hare pellets to traditional trap-based capture-mark-recapture sampling as methods of estimating abundance. This project was funded in part by this project, and some of the sampling was conducted in Glacier NP. We

found that abundance estimates based on non-invasive genetic sampling were comparable to traditional live capture studies; more importantly for Park management, when we incorporated logistics and costs, we found that non-invasive genetic sampling was more efficient than live-trapping for all but the highest density hare sites, especially as distance from roads increased (see especially Fig. 10, Appendix I). Thus, we provide both a methodology and a rationale for increasing the use of non-invasive genetic sampling for estimating hare abundance, especially at backcountry sites.

## **OTHER DELIVERABLES**

In addition to this report and the Appendices already discussed in this report (Appendix I: draft manuscript on non-invasive genotyping to estimate hare abundance; Appendix II: Glacier Project Field Manual), we also include three other products. Appendix III describes modifications made to the project from start to finish. Appendix IV mentions key outreach and education outcomes of the project. Appendix V includes the Raw GIS and data files (to be transmitted to Park personnel separately due to their size).

## **LITERATURE CITED**

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FIGURE 1. LYNX OCCURRENCES IN GLACIER NATIONAL PARK, 2001 – 2005.

FIGURE 2. DISTRIBUTION OF SNOWSHOE HARE STUDY SITES AND DOMINANT CANOPY CATEGORIES.

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*Cheng et al. DRAFT MANUSCRIPT – please do not circulate*

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## APPENDIX III. PROJECT MODIFICATIONS

Our original proposal included some elements that were subsequently modified or removed, with Park approval, for cost-efficiency or logistical reasons. We had proposed to radio collar 30-45 snowshoe hares, to estimate survival rates and causes of death, and to obtain coarse movement information. In our first field season we found that hare densities are low and patchily distributed in much of Glacier NP, and radio collaring sufficient hares for survival and movement estimates would be a time-intensive activity with relatively little return in information gained and would prevent a sufficient sampling of hare abundances across the park. Therefore, we removed this component of the study and instead put additional effort (including finding supplemental funding from other sources) into developing and testing our non-invasive genetic approach for abundance estimation (see Appendix I). Consequently, the genetic approach has proven to be especially suitable for monitoring hares in Glacier NP, because its cost-effectiveness as an alternative to live-trapping is greatest at low hare densities and with difficult-to-access field sites.

In 2006, we live-trapped snowshoe hares at seven study sites that were chosen for their relatively high densities of hare pellets. We attempted to compare trap-based capture-mark-recapture (CMR) density estimates with density estimates from pellet counts, as initially proposed. Although we had targeted relatively high hare density sites, we were able to recapture sufficient hares at only four of the seven sites, for trap-based density estimation (Table A3.I). Although trap- and pellet-based density estimates seem comparable at these four sites, we have insufficient data for a rigorous comparison of these methods.

TABLE A3.I. COMPARISON OF HARE DENSITIES FROM LIVE-TRAPPING AND PELLET COUNTS. ESTIMATED NUMBER OF SNOWSHOE HARES AT STUDY SITES, BASED ON LIVE-TRAP CMR.

Captures were allocated to two trap sessions for Lincoln-Peterson abundance estimation. In this table, unique individuals = number of unique hares captured,  $n_1$  = number of individuals trapped in first capture session (data combined from first two trap nights at each site),  $n_2$  = number of individuals trapped in second capture session (data combined from remaining trap nights),  $m_2$  = number of individuals trapped in both capture sessions,  $N_{CMR}$  = Lincoln-Peterson estimate of abundance from live-trap data ('NA' means estimate could not be calculated because no hares were recaptured),  $N_{PELLET} = SD$  = Regression-based estimate of abundance from pellet counts.

We had originally proposed to conduct annual surveys to assess temporal changes in hare densities at a subset of study sites. However, at the low hare densities observed in much of the Park (below 0.3 hares/ha), live-trapping and pellets counts have little power to distinguish year-to-year changes in population numbers (Mills et al. 2005), and the biological importance of hares as prey for sustaining lynx populations is also limited (Ruggiero et al. 2000; Steury and Murray 2004). Therefore, we refocused our research efforts to conduct pellet surveys across as many different sites as possible, to identify snowshoe hare hotspots in Glacier NP.

Finally, our original proposal called for indexing lynx abundance via hair snares and genetic analysis, to evaluate the relationship between lynx and snowshoe hare distribution. With the relatively low hare densities in the Park, it seemed unlikely this approach would yield new information on lynx occurrences, unless implemented at a spatial scale and intensity that was beyond the capabilities of this study.

## APPENDIX IV. OUTREACH AND EDUCATION

Two important components of our work in Glacier NP were a public outreach and education program, and training of undergraduate and recent graduate students in wildlife research and field techniques. Over 3 years, we employed 23 undergraduates and recent graduates as field research assistants. We also trained 6 short-term volunteers (1 -2 weeks) on this project: In 2006 and 2007 we conducted 3 evening campfire talks to teach Park visitors about the importance of wildlife research in National Parks and about our research on snowshoe hares in Glacier NP. These talks were well-attended and warmly received by the public and, importantly, provided valuable outreach training for our young crew members who presented the talks. In addition to campfire talks, on invitations from Matt Graves (West District Interpreter) in 2007 and 2008, Ellen Cheng or Scott Mills spent a half-day at Glacier National Park all-interpreter training, giving talks and discussing with interpreters about wildlife issues – including snowshoe hare ecology – relevant to the Park:

MILLS, L. S. *Climate change and winter coats*. Half-day training lectures to all Interpreters/Naturalists at Glacier National Park, June 10, 2008.

CHENG, E. *Population dynamics of Canada lynx and snowshoe hares*. Half-day training lectures to all Interpreters/Naturalists at Glacier National Park, 2007.

Results of our work in Glacier NP were also disseminated more broadly through several conference presentations, scientific talks, and one magazine article:

CHENG, E. 2009. Non-invasive genetic sampling: a kinder approach to population estimation. AWI Quarterly, summer issue.

CHENG, E., L.S. MILLS, and K.E. HODGES. March 2008. A comparison of non-invasive genetic and traditional approaches to estimating animal abundance. Donana National Park Research Center (oral; Seville, Spain)

CHENG, E., L.S. MILLS, and K.E. HODGES. March 2008. A comparison of non-invasive genetic and traditional approaches to estimating animal abundance. Northwest Section of The Wildlife Society (oral; Spokane, WA)

CHENG, E., L.S. MILLS, and K.E. HODGES. February 2008. A comparison of non-invasive genetic and traditional approaches to estimating animal abundance. Montana Chapter of The Wildlife Society (oral; Missoula, MT)

CHENG, E., L.S. MILLS, and K.E. HODGES. February 2007. Distribution and abundance of snowshoe hares in Glacier National Park. Montana Chapter of The Wildlife Society (oral; Bozeman, MT)

CHENG, E., L.S. MILLS, and K.E. HODGES. February 2006. Evaluating the prey base for lynx: snowshoe hare abundance, habitat use and population dynamics in Glacier National Park. Montana Chapter of The Wildlife Society (oral; Helena, MT)

We are currently preparing two manuscripts on our research in Glacier NP, for publication in peer-reviewed scientific journals. The first manuscript will report our findings on snowshoe hare distribution and abundance in the Park; the second will detail the cost-benefit analysis of non-invasive versus traditional mark-recapture estimates of abundance (Appendix I of this report).

## APPENDIX V. GIS AND RAW DATA

GIS products and all raw data files from this research have been transmitted to the Park. This Appendix provides a brief description of these products.

## **GIS FILES**

• **GLACIER SSH GIS.mxd (file) & GLACIER SSH GIS.gdb (folder)** — GIS shape files mapping study site locations and the 600 and 1000 m site buffer zones used to analyze landscape-level edge effects on snowshoe hare densities. The attributes table associated with the study sites shape file includes all summary habitat data used in analyses. In addition, the attributes table includes the following information:

- HareDensity = Hare density (# of hares/hectare) estimated from Krebs pellet counts
  - HareCategory = 'Low' for sites with <0.3 hares/ha, 'Moderate' for sites with ≥0.3 hares/ha
  - Analyzed? = 'Y' indicates sites that were included in data analysis. Some sites were surveyed, but not included in final analysis because they did not fulfill site requirements (e.g., minimum 85% forest cover) or because data collection was incomplete.
  - East\_West = 'East' for sites east of the Continental Divide; 'West' for sites west of the Continental Divide
  - SitePhotos = hyperlink to photos of the study site
  - SiteSurvey = hyperlink to a scanned copy of the Site Survey form completed for the study site
  - UTM\_ZONE = 11 or 12, depending on which of Glacier NP's two UTM zones the study site was located in
  - COORDX / COORDY = NAD83 UTM coordinates for study site at the site corner specified in column labeled UTM\_CORNER
  - COORDX\_Z12 / COORDY\_Z12 = For study sites in UTM Zone 11, this column contains the UTM coordinates converted for Zone 12, so all study sites are presented in the same UTM Zone
  - CENTER\_X / CENTER\_Y = The Zone 12 UTM coordinate for the center of each study site
- NOTE: To switch between Site Photos and Site Surveys for the Hyperlink tool, file document properties need to be set to the relevant hyperlink base and the properties for the GLACIER\_FINAL\_GIS need to be set to the relevant attributes table field.*

• **Glacier Site Photos (folder)** — This folder contains digital photographs of study sites, taken from multiple grid points per site. Photos are not available for all sites.

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• **Glacier Site Surveys (folder)** — This folder contains scanned copies of Site Surveys completed for most study sites. Each Site Survey includes directions for accessing the study site, descriptions of vegetation, animal signs, and other features of the study site, and the dates that pellet counts, vegetation surveys, and live-trapping (when applicable) were completed at the site.

## **RAW DATA**

All raw data are provided in a single Excel file (GLACIER SSH RAW DATA 08\_01\_2011). Data columns are explained by 'comments' embedded in the Excel file. Data are split into the following worksheets, by data type:

- **TRAP** — Live-trap data for 2006 (trapping was not conducted in other years)
- **PELLETS** — Krebs pellet count data for 2005 – 2007
- **VEGETATION** — Vegetation data for 2005 – 2007, excluding sapling and relascope data. Some vegetation data were collected only in 2006 & 2007

- **SAPLINGS** — Sapling species and densities data for 2005 – 2007
- **RELASCOPE**— Canopy tree species data collected using relascopes in 2005
- **GENETICS** — Genotypes at 8 highly variable microsatellites, for a subset of live-trapped hares