

RESEARCH ARTICLE

IMPACTS OF FIRE ON SNOWSHOE HARES IN GLACIER NATIONAL PARK, MONTANA, USA

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ABSTRACT

Forest fires fundamentally shape the habitats available for wildlife. Current predictions for fire under a warming climate suggest larger and more severe fires may occur, thus challenging scientists and managers to understand and predict impacts of fire on focal species, especially species of management concern. Snowshoe hares (*Lepus americanus* Erxleben) are a common and important prey animal in boreal forests and are the primary prey for the US federally threatened Canada lynx (*Lynx canadensis* Kerr), so understanding hare dynamics in post-fire landscapes is critical for managing lynx. We collected habitat and fecal pellet data from 114 sites across three natural burn treatments (mature forest, 1988 Red Bench burn, and 1994 Adair and Howling burns) to evaluate impacts of fire and fire-habitat interactions on snowshoe hare in Glacier National Park, Mon-

RESUMEN

Los incendios forestales modelan de forma fundamental los hábitats disponibles para la fauna silvestre. Las predicciones actuales de incendios debidas al calentamiento global, sugieren que podrían ocurrir fuegos más extensos y severos, desafiando así a científicos y gestores a entender y predecir los impactos del fuego en especies focales, especialmente a aquellas sometidas al manejo. Las liebres americanas (*Lepus americanus* Erxleben) son animales de presa comunes e importantes en los bosques boreales, y son la presa principal del lince canadiense (*Lynx canadensis* Kerr), especie considerada como amenazada en los EEUU. Por ese motivo, entender la dinámica de la liebre en paisajes post-fuego es crítica para el manejo del lince. Para ello recolectamos datos de hábitats y pellets fecales de 114 sitios a través de tres tratamientos de incendios naturales (en el bosque maduro, en el incendio del *Red Bench* de 1988, y en los incendios de *Adair* y *Howling*), para evaluar los impactos del fuego y las interacciones hábitat-fuego en la liebre americana en el Parque Nacional *Glacier*, en Montana,

tana, USA. We found that hare numbers were low throughout the park, with hares absent at 17% of surveyed sites and occurring at densities above 0.5 hares ha⁻¹ (a commonly suggested threshold for supporting Canada lynx) at only 7% of sites. Hare densities were variable but 10 to 20 times higher in regenerating lodgepole pine (*Pinus contorta* Douglas ex Loudon) stands of 1988 Red Bench burn compared to lodgepole stands in other burn treatments. In stands dominated by other tree species, we found little difference in hare densities across burn treatments. Regardless of burn history or dominant canopy type, percent canopy cover was positively associated with hare relative abundance. Hare densities also increased with percent understory cover up to 80% cover, beyond which they began to decline. The regular occurrence of wildfires in Glacier National Park, with 2003 being a particularly large fire year (the largest since 1910), suggest that hare and lynx distribution and abundance within the park may shift substantially in the coming decades as these animals respond to changing spatiotemporal patterns of regenerating forest.

EEUU. Encontramos que el número de liebres era bajo a través del parque, con liebres ausentes en el 17% de los lugares relevados, y con densidades por encima de 0,5 liebres ha⁻¹ (umbral comúnmente sugerido para mantener el lince canadiense), en solo el 7% de los sitios. La densidad de liebres fue variable pero 10 a 20 veces más alta en rodales con regeneración de pino contorta (*Pinus contorta* Douglas ex Loudon) en el incendio del *Red Bench* de 1988, comparado con rodales de pino contorta en los otros tratamientos de quemados. En rodales dominados por otras especies arbóreas, encontramos poca diferencia en la densidad de liebres en los distintos tratamientos de quemados. Sin tener en cuenta la historia del fuego o el tipo de dosel dominante, el porcentaje de cobertura del dosel fue asociado positivamente con la abundancia relativa de liebres. La densidad de liebres también aumentó en el estrato inferior del dosel con porcentajes de cobertura de hasta el 80%, a partir del cual empezaban a declinar. La ocurrencia regular de incendios naturales en el Parque Nacional *Glacier*, con un año particular de grandes incendios en 2003 (los más grandes desde 1910), sugieren que la distribución y la abundancia de la liebre y el lince dentro del parque podrían cambiar sustancialmente en las próximas décadas, en la medida en que estos animales respondan a los cambios en los patrones espacio-temporales del bosque en regeneración.

Keywords: fire effects, Glacier National Park, habitat use, *Lepus americanus*, lodgepole pine, *Pinus contorta*, post-fire regeneration, Red Bench Fire, snowshoe hare

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INTRODUCTION

Wildfires are a dominant disturbance in coniferous forests across Canada and the United States (Baker 2009, Marlon *et al.* 2012, Archibald *et al.* 2013). Fires in Western forests

are projected to increase in frequency, intensity, and size with climate change (Rogers *et al.* 2011, Westerling *et al.* 2011, Attiwill and Binkley 2013), thus fundamentally altering the distribution of seral stages and tree densities on Western landscapes for centuries to come.

Forest mammals often respond strongly to post-fire habitats (Fisher and Wilkinson 2005, Fontaine and Kennedy 2012), but for many species, post-fire responses through time remain poorly characterized, as do the attributes of regenerating post-burn landscapes that enable use or persistence (Spies *et al.* 2012).

Such questions become even more pressing for species of conservation concern and the species on which they depend. For example, Canada lynx (*Lynx canadensis* Kerr) is listed as federally threatened in the contiguous United States (USFWS 2000). In the north Cascade Range of Washington, USA, over half of the suitable lynx habitat identified in 2001 has subsequently burned in wildfires (Koehler *et al.* 2008). Similarly, in 1988, large stand-replacing fires in Yellowstone National Park, Wyoming, USA, converted mature forest stands that probably supported lynx into early seral stands that could not support lynx (Murphy *et al.* 2006). Throughout their range, lynx presence coincides with densities of snowshoe hares (*Lepus americanus* Erxleben), their primary prey (Ruggiero *et al.* 2000). Because Canada lynx specialize on hares, the US Fish and Wildlife Service included snowshoe hare habitat as an essential component of critical habitat for Canada lynx (USFWS 2008, 2013). Thus, to understand lynx distribution and dynamics requires knowledge of hare distribution and dynamics.

The impact of fire on snowshoe hares is not yet well characterized, as only a few studies have examined such questions and they used a range of forest types. In black spruce (*Picea mariana* Mill.) forest in Alaska, USA, snowshoe hare tracks were more abundant in a ~25 yr old burn than in a 6 yr old burn or in forests that were 100 yr to 115 yr old (Paragi *et al.* 1997). In aspen (*Populus tremuloides* Michx) forests in the Yukon, hare relative abundance was higher in young stands (<20 yr) than in stands 21 yr to 120 yr old (Strong and Jung 2012). In the southeastern Yukon, dense lodgepole pine (*Pinus contorta* Douglas

ex Loudon) stands regenerating ~30 yr post fire supported higher hare numbers than did mature pine or white spruce (*Picea glauca* [Moench] Voss) stands (Mowat and Slough 2003). In Quebec, Canada, forests of black spruce and balsam fir (*Abies balsamea* L.), hares responded similarly to post-fire and post-harvest sites, with peaks in density in stands 40 yr to 50 yr old and in stands >180 yr old (Hodson *et al.* 2011). In Yellowstone National Park, Wyoming, USA, from 2002 to 2007, three of the five highest hare density sites occurred in lodgepole pine stands regenerating from Yellowstone's 1988 fires (Hodges *et al.* 2009). Despite this use of some dense regenerating stands, 53% of the regenerating stands surveyed had no hares, in contrast to mature stands where hares were absent in 33% of stands (Hodges *et al.* 2009).

These post-fire patterns cohere with what is known about hare habitat use more generally. Snowshoe hares use a variety of habitat types, with understory cover *per se* being one of the most important elements (Hodges 2000a, 2000b). Stands with shrubs, stands that are densely stocked, and stands at ages in which branches have more lateral cover are more heavily used by hares (Dolbeer and Clark 1975, Wolfe *et al.* 1982, Monthey 1986, Koehler 1990, Lewis *et al.* 2011). Overstory cover is sometimes correlated with hare habitat use patterns, but typically in cases in which it is also significantly correlated with understory cover (Richmond and Chien 1976, Orr and Dodds 1982, Parker *et al.* 1983, 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* is seldom critical except insofar as it predicts stand structure (Berg *et al.* 2012).

Particularly in hares' southern range, where habitats are patchy and fragmented, landscape patterns may also be important for persistence of snowshoe hare populations (Wirsing *et al.* 2002, Griffin and Mills 2003,

2009, Thornton *et al.* 2013). Habitat interspersions may provide hares access to habitats with different protective cover and food availabilities (Koehler and Brittell 1990). 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 (Lewis *et al.* 2011, Thornton *et al.* 2013). Fire is critical in this landscape context because, if much of a landscape has recently burned, hare populations may be isolated in remaining forest stands. Several authors have suggested that fire contributes to the cycling of snowshoe hare populations by transiently providing dense stands of regenerating forest rich in food and cover for hares (Howell 1923, Grange 1965, Fox 1978, Ferron and St-Laurent 2008), but it is unclear what spatial patterns of fire are relevant for cycles that occur across much of the boreal forest.

In this paper, we examine the distribution and relative abundance of snowshoe hares in Glacier National Park (Glacier NP), Montana, USA, where fires are common and tend to cluster in time because of regional climatic drivers (Morgan *et al.* 2008). Like Yellowstone National Park, both 1988 and 2003 were large fire years in Glacier NP; in 2003, the largest fire year for Glacier NP since 1910, approximately 13% (55 000 ha) of the park's more than 410 000 ha burned in wildfires. Over the past century, memorable fire years have occurred at an average frequency of 15.5 years. The majority of wildfires are stand-replacing fires on the park's west side. Fires on the east side of the park are both rarer (due to forest type and spatial configuration) and more actively managed to avoid fires burning into nearby human communities. Our research focused on hare use of the 1988 Red Bench Fire, which burned over 13 000 ha of primarily lodgepole pine forest in the park's northwest corner, and on the 1994 Adair and Howling fires, which burned 340 ha along the park's western edge (an additional 3000 ha that

burned in these fires were re-burned in 2001 and 2003, so were excluded from our study).

Glacier NP supports a population of lynx, so part of our objective was to examine where hares were in relation to the park's records of opportunistic lynx sightings (Glacier NP, West Glacier, Montana, USA, unpublished data). In particular, we were interested in understanding whether infrequent reporting of lynx on Glacier NP's west side reflected lower densities of snowshoe hares there. Our primary objectives were to compare snowshoe hare densities among three burn treatments (mature forest, 1988 Red Bench burn, and 1994 Adair and Howling burns), examine finer-scale habitat attributes (e.g., dominant canopy cover, sapling density) within these burn treatments, and quantify the relative importance of different variables in predicting habitat use by snowshoe hares in Glacier National Park.

METHODS

We collected data from three types of burn treatment: mature forest (not burned at least since 1967, the first year for which we had comprehensive fire spatial data), a 1988 burn (i.e. Red Bench Fire), and 1994 burns (i.e., Adair and Howling fires). We excluded all sites that had burned in 2001 or later as being too young in the regeneration cycle at the time of this study (2005 to 2007; site walk-throughs of some recent burns confirmed minimal tree cover and no hare sign). Study sites had to: 1) have at least 85% forest cover, 2) be at least 500 m from the nearest road, 3) not overlay park hiking trails, and 4) be at least 300 m apart from each other (in actuality the closest mature forest sites were 572 m apart and the closest burn sites were 723 m apart). We set a minimum threshold of 85% forest cover because snowshoe hares are obligate forest species (Hodges 2000a, 2000b). The remaining criteria minimized potential impacts of anthropogenic disturbances and maximized site independence. We also excluded sites that required

dangerous river crossings or that required more than a two-day trip to access and could not be combined with nearby sites in a multiple-day survey trip.

For mature forest sites, we used a tessellated random sampling approach to ensure unbiased selection of sites with fairly even coverage of the 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 to 2007), we used Hawth's Analysis Tools (www.spatialecology.com/htools/tooldesc.php) to randomly allocate three points to each of the 46 sampling blocks. Using GIS, we superimposed a 20 ha study site (500 m × 400 m) centered on each of these points. We then excluded all sites that did not meet the 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 two-thirds of the park's land area.

The 1988 burn and 1994 burn sites were randomly selected points within the Red Bench and Adair and Howling fire sites, respectively. To ensure a sufficiently large sample size for characterizing hare use of regenerating stands, we sampled these sites at a higher density than mature forest sites, but maintained the minimum distance threshold of 300 m between sites.

We conducted pellet and vegetation surveys at 114 sites in Glacier NP (Figure 1). Of these, 87 were mature forest sites, 23 were regenerating forest from the 1988 burns, and four were regenerating forest from the 1994 burns. The small sample size for the 1994 burns was due to the small area (340 ha) of regenerating forest remaining from the Adair and Howling fires that was not re-burned in 2001 or 2003.

When we arrived at a site, we conducted a ground reconnaissance to verify that the site

met the criterion of 85% forest cover (this criterion could not be accurately determined from GIS at the scale of our study site), by averaging measurements from a vertical densitometer across 80 sampling points in a systematic 8 m × 10 m grid. When necessary, we used a pre-defined field protocol to objectively shift sites that did not meet criteria. Ultimately, eight sites were shifted because the original coordinates would have had us sampling meadow or marsh with <85% forest cover; we shifted sites by changing which corner the original coordinates represented.

Fecal Pellet Counts and Habitat Measurements

Although evaluation of population responses to stressors are more reliably based on formal estimates of abundance, such as those generated by mark-recapture data, in this case we were interested in spatial replication across >100 sites in Glacier National Park. Therefore, we relied on intensively sampled pellet grids, which correlate sufficiently with estimates of hare relative abundances to understand general patterns of low versus high hare densities (Mills *et al.* 2005, McCann *et al.* 2008, Berg and Gese 2010).

We conducted fieldwork from May to August in 2005, 2006, and 2007. Each 20 ha study site was divided into an 8 × 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 (Krebs *et al.* 1987, Krebs *et al.* 2001, Mills *et al.* 2005, Hodges and Mills 2008). At every sampling point, a 0.155 m² (5.08 cm × 30.5 cm) rectangular transect was laid due north. All pellets that fell at least one half within the transect area were counted.

Along three internal grid rows of each site (second, fourth, and seventh rows), we conducted vegetation surveys at 50 m spacing, for a total of 30 vegetation sampling points. Vegetation surveys focused on overstory and un-

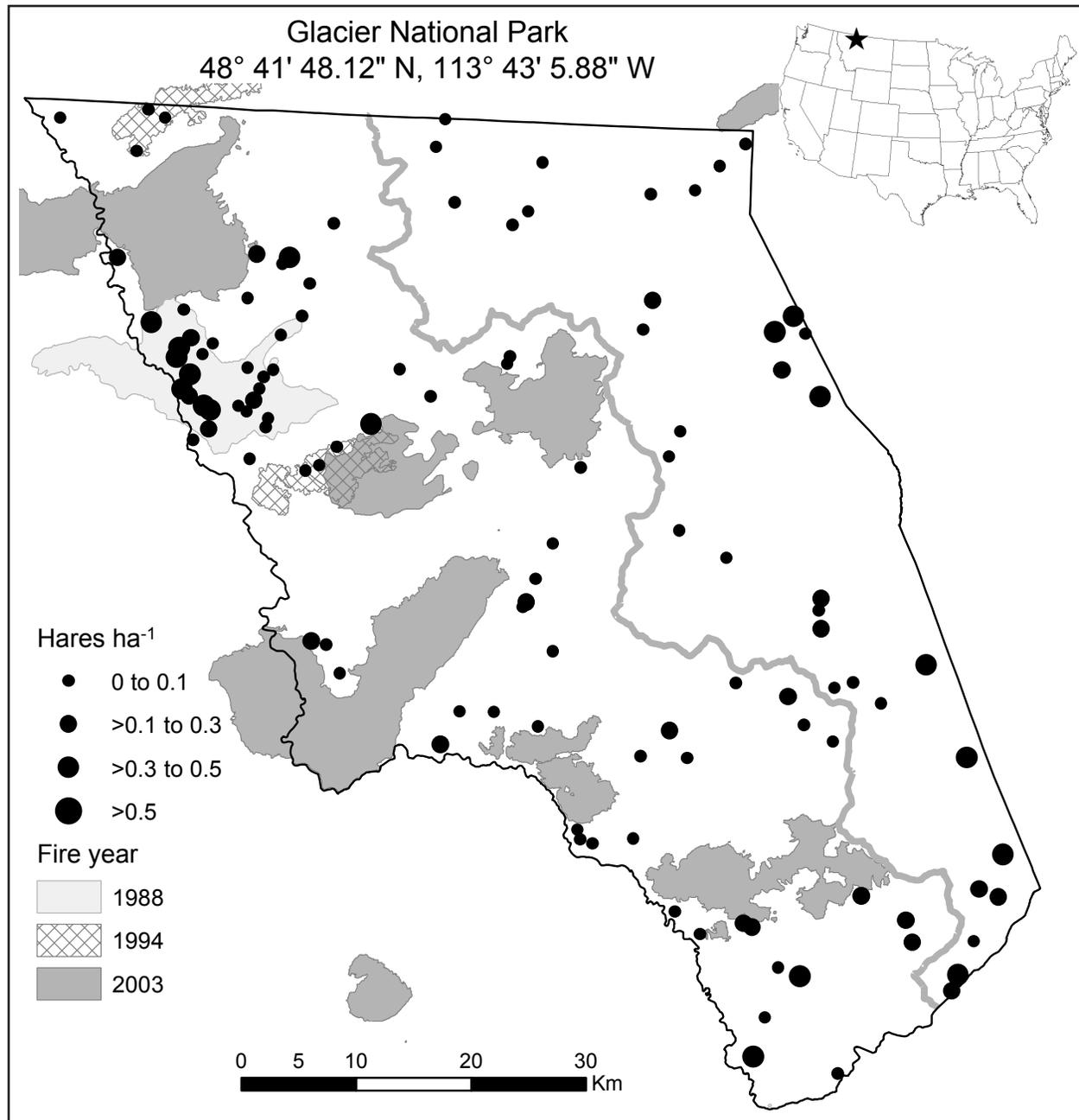


Figure 1. Distribution of study sites and relative snowshoe hare abundances in relation to natural fires in Glacier National Park, Montana, USA. The solid outline is the park border, and the shaded line within the park is the Continental Divide, which we used to separate the park into east and west in multivariate analyses. Areas burned in 2003 were excluded from this study because sites could not have regenerated sufficiently to support hares by the time of this study (2005 to 2007).

derstory habitat variables that contribute to structure or food supply and often correlate with hare densities. For overstory habitat, we recorded the dominant canopy species as the species for which the canopy covered the larg-

est percentage of our fish-eye view across the 30 vegetation sampling points. 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 four broad categories of dominant canopy species for analyses:

- 1) Spruce-fir. These sites were dominated by Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) or subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) at $\geq 70\%$ of sampling points.
- 2) Lodgepole pine. Lodgepole pine was the dominant canopy species at $\geq 70\%$ of sampling points.
- 3) Mixed canopy. These were sites for which no single species was recorded as the dominant canopy species at $\geq 70\%$ of sampling points.
- 4) Other canopy. These sites were 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* [Mirb.] Franco) or western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) at $\geq 70\%$ of sampling points.

In addition to classifying sites by dominant canopy, we estimated canopy closure as percent view obstructed (viewed through a vertical 13 cm long PVC tube with 5 cm diameter) averaged across the 30 vegetation sampling points and at 6 m east and 6 m west of each sampling point. For understory habitat, we measured understory cover, sapling density, and an index of downed logs. We used a 0.532 m² cover board, vertically divided into four blocks, to measure understory cover. A person at the sampling point estimated percent view obstructed at 0.5 m increments above the ground (viewed at eye level for each height band), while the cover board was held at 6 m east and also at 6 m west of the sampling point. The three categories of understory cover above 0.5 m were highly correlated ($r >$

0.78), so we included only understory 0 m to 0.5 m and understory 0.5 m to 1.0 m in analyses. Sapling density was calculated as the number of live saplings with trunk centerline within a 2 m radius of the sampling point. Saplings were defined as trees with < 5 cm diameter at breast height. Results are presented as average number of saplings ha⁻¹. Our index of downed logs was the average number of downed logs > 5 cm diameter encountered per transect. Two 6 m transects were laid at each sampling point, one extending east and the other west from the central point.

Statistical Analyses

We compared snowshoe hare densities among burn treatments (mature forest, 1988 burn, 1994 burns), with a negative binomial GLM model of total pellet counts (per site) as a function of burn treatment. To understand habitat differences among burn treatments, we compared average values of habitat parameters across category levels. We applied a negative binomial GLM model for habitat response variables that were count data (i.e., saplings and logs), and used ANOVA when response variables were continuous data. Data were transformed as appropriate to satisfy ANOVA assumptions. We used Tukey's HSD tests to determine pairwise sources of significant variation.

For two burn treatments (mature forest and 1988 burn), we had sample sizes sufficient to conduct a multivariate analysis of habitat use by snowshoe hares in Glacier National Park. Akaike's information criterion corrected for small sample sizes (AICc), and Akaike weights (w_i ; Burnham and Anderson 2002) were applied in this analysis. We used a negative binomial GLM to model total pellet count as a function of all continuous habitat variables (excluding the two correlated understory parameters, 1 m to 1.5 m and 1.5 m to 2 m aboveground) measured in this study. The included variables had been *a priori* identified from

other research as having biologically meaningful relationships with hare density. Based on graphical assessment of the data and residual plots, percent understory at 0 m to 0.5 m was included in the model as a quadratic, rather than a linear, function.

In addition to the five continuous variables, three categorical variables (burn treatment, dominant canopy, and east-west) and a single interaction term (burn treatment:dominant canopy) were included in the global model. The variable east-west has two levels, indicating that a site is east or west of the Continental Divide that divides Glacier NP into Atlantic and Pacific watersheds. Forests differ across the Continental Divide (Robinson 1972)—a contrast arising from differences in moisture, landscape heterogeneity, and other unmeasured factors that may subtly influence snowshoe hare abundance but were not the focus of our study.

Considering all possible combinations of the predictor variables, we summed the Akaike weights of predictor variables across all models to rank variables by their relative importance (Arnold 2010). Variables with summed weights >0.75 were deemed to be relatively important predictors of pellet density in our study system. Model-averaged coefficients for these useful predictors were combined in a “best” model to create prediction plots (with 95% confidence intervals) across the observed range of each predictor variable by fixing values of other predictors at their median values or, in the case of categorical data, at their proportional distribution in the data. These prediction plots were used to assess the biological significance of individual predictor variables for snowshoe hares.

All analyses were implemented in R Version 3.2.0 (R Development Core Team 2015). For all analyses, model fit was assessed with likelihood ratio chi-square tests and examination of residual plots. We used the Vuong test to compare the fit of different model distributions to the data. To report results in the con-

text of hare densities relevant for lynx management, we also converted pellet densities to (approximate) hare density, using a standard regression equation modified for uncleared pellet transects (Hodges and Mills 2008; Hodges *et al.* 2009).

RESULTS

Snowshoe hare densities were low in much of Glacier National Park (Figure 1). We found no snowshoe hare pellets on 17% ($n = 19$) of study sites. Only 7% ($n = 8$) of sites had estimated hare densities exceeding 0.5 hares ha^{-1} , a commonly cited minimum threshold for an area to sustain a lynx population (Ruggiero *et al.* 2000, Simons-Legaard *et al.* 2013). Five of the sites that exceeded this hare density threshold were regenerating lodgepole forests of the 1988 burn in northwest Glacier NP; the other three were mature forest sites east of the Continental Divide. With fewer than 0.05 hares ha^{-1} , the four stands regenerating after the 1994 burns were essentially not hare habitat, regardless of dominant canopy species.

Distribution of Dominant Canopy Species across Glacier National Park

Our survey provided insights on the relative abundance of different canopy types across the park and in relation to the 1988 and 1994 burns. Mixed canopy sites and spruce-fir dominant canopies each comprised about one third of the sites we surveyed ($n = 42$ and $n = 35$, respectively). Almost a quarter of sites ($n = 24$) were dominated by lodgepole pine. The remaining 13 sites were categorized as “other,” as they were dominated by Douglas-fir, western hemlock, or other less common species. Lodgepole pine-dominated habitats made up 50% of the 1988 burns, a considerably higher proportion than for mature forest sites. For mature forest sites, the dominant canopy categories were well distributed throughout the park.

Hare Abundance and Habitat Differences among Burn Treatments

In univariate analyses, pellet densities differed significantly among the three burn treatments ($\chi_2^2 = 18.27$, $P < 0.001$), with highest densities in 1988 burn sites and lowest in 1994 burn sites (Figure 2). *Post hoc* analyses indi-

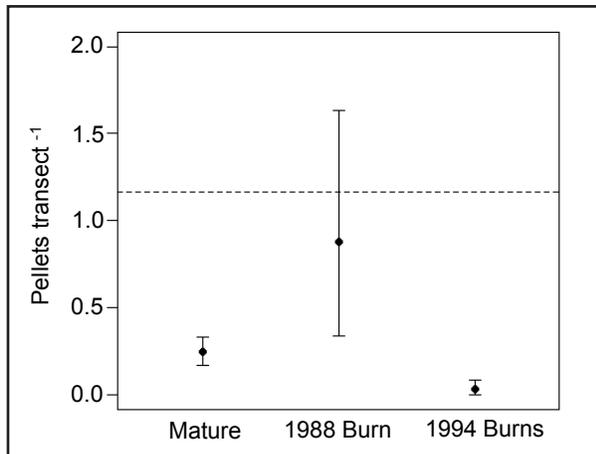


Figure 2. Pellet densities (pellets transect⁻¹) in relation to burns. The dashed horizontal line represents the regression-based pellet density equivalent to the threshold of 0.5 hares ha⁻¹ believed necessary to sustain lynx populations.

cated that differences were significant for all pairwise comparisons.

Given the differences in pellet densities among burn treatments, we used univariate analyses to understand how these categories differed in vegetation characteristics. Regenerating sites from the 1988 and 1994 burns differed significantly from mature forests in many habitat attributes. In particular, burn sites had higher densities of saplings and downed logs, and lower canopy cover than mature forest sites (Table 1). Understory cover 0 m to 0.5 m also differed among burn treatments, being higher in burns than mature forest, but the Tukey HSD test did not identify significant pairwise comparisons.

Relative Importance of Different Variables in Predicting Habitat Use by Snowshoe Hares

Multivariate analyses with multi-model inference confirmed the relative importance of understory cover (0.5 m to 1.0 m), canopy cover, and three categorical variables (dominant canopy, east-west, burn treatment) in predicting pellet densities in Glacier National Park (Table 2). The interaction between burn

Table 1. Habitat characteristics of forested sites in Glacier National Park, Montana, USA, classified by burn treatment. Values are means and 95% bootstrapped confidence intervals. We also show the percentage of each burn treatment that did not support snowshoe hares; overall, 19 of 114 sites (16.7%) had no pellets. We fit negative binomial models for saplings and downed logs and ANOVA (transformed if necessary) for the cover variables. Superscript letters indicate groups identified by *post-hoc* Tukey tests.

Parameter	Mature (n = 87)	1988 burn (n = 23)	1994 burns (n = 4)	χ^2 or F	P
Sapling density (n ha ⁻¹)	1358 (1130 to 1606) ^a	28770 (12476 to 55247) ^b	6976 (4914 to 8362) ^c	153.00	<0.001
Downed logs (n (6m ⁻¹))	0.24 (0.21 to 0.27) ^a	0.56 (0.45 to 0.67) ^b	0.62 (0.33 to 0.95) ^b	39.99	<0.001
Canopy cover (%)	40.6 (37.6 to 43.5) ^a	25.2 (21.5 to 28.8) ^b	27.3 (20.0 to 34.8) ^b	13.93	<0.001
Understory cover 0 m to 0.5 m (%)	85.9 (84.0 to 87.7)	89.6 (86.9 to 91.9)	94.5 (93.0 to 96.0)	3.46	0.035
Understory cover 0.5 m to 1 m (%)	51.6 (48.3 to 54.9)	51.2 (45.7 to 57.0)	45.3 (40.5 to 51.5)	0.328	0.721
Sites with no hare pellets (%)	13.8	21.7	50.0		

Table 2. The sum of Akaike weights ($\sum w_i$) of parameters across all models, number of models the parameter is included in out of 320 candidate models, model averaged parameter estimates, and unconditional 95% confidence intervals from an all-subsets negative binomial regression analysis to assess snowshoe hare relative abundance in 114 forest sites in Glacier National Park, Montana, USA. For categorical variables, parameter estimates and unconditional 95% confidence intervals are provided for each category level, relative to the reference category. For percent understory cover 0 m to 0.5 m aboveground, the estimates and 95% confidence intervals are provided for the linear component of the function, followed by the squared component.

Parameter	$\sum w_i$	Models (<i>n</i>)	Estimate	Lower 95 %	Upper 95 %
Dominant canopy tree species					
Mixed	1.00	192			
Others			1.57	0.56	4.35
Spruce-fir			1.13	0.53	2.39
Lodgepole			3.33	0.87	12.69
Understory cover 0 m to 0.5 m (%)	1.00	160	2.46; 0.99	1.51; 0.99	4.00; 1.00
Canopy cover (%)	0.97	160	1.04	1.02	1.07
East-west					
West	0.97	160			
East			2.81	1.40	5.63
Burn treatment					
Mature	0.91	192			
1988 burns			1.46	0.30	7
Dominant canopy:burn treatment					
Mixed:random	0.75	64			
Others:1988 burns			1.04	0.22	4.93
Spruce-fir:1988 burns			0.53	0.04	7.47
Lodgepole:1988 burns			7.33	0.56	96.47
Logs (average <i>n</i> transect ⁻¹)	0.61	160	0.41	0.07	2.56
Saplings (<i>n</i> ha ⁻¹)	0.52	160	1.00	0.99	1.02
Understory cover 0.5 m to 1.0 m (%)	0.35	160	1.01	0.99	1.03

treatment and dominant canopy was also identified as important. These six parameters were combined in a “best” model for predicting hare abundance because each of their summed Akaike weights across all candidate models exceeded 0.75.

Predictions of pellet densities were strongly influenced by a burn treatment:dominant canopy interaction (Figure 3). With other variables held at their typical values, mean pellet

density ($\bar{x} = 3.52$ pellets per transect, 95% CI = 1.54 to 8.025) for lodgepole stands in the 1988 burn was predicted to be almost 20 times greater than other dominant canopy types in the 1988 burn, and more than 10 times greater than any (including lodgepole) dominant canopy type in mature forests. Canopy cover had the next largest effect, with mean pellet densities increasing from 0.06 (95% CI = 0.03 to 0.04) at 10% canopy closure to 0.57 (95% CI

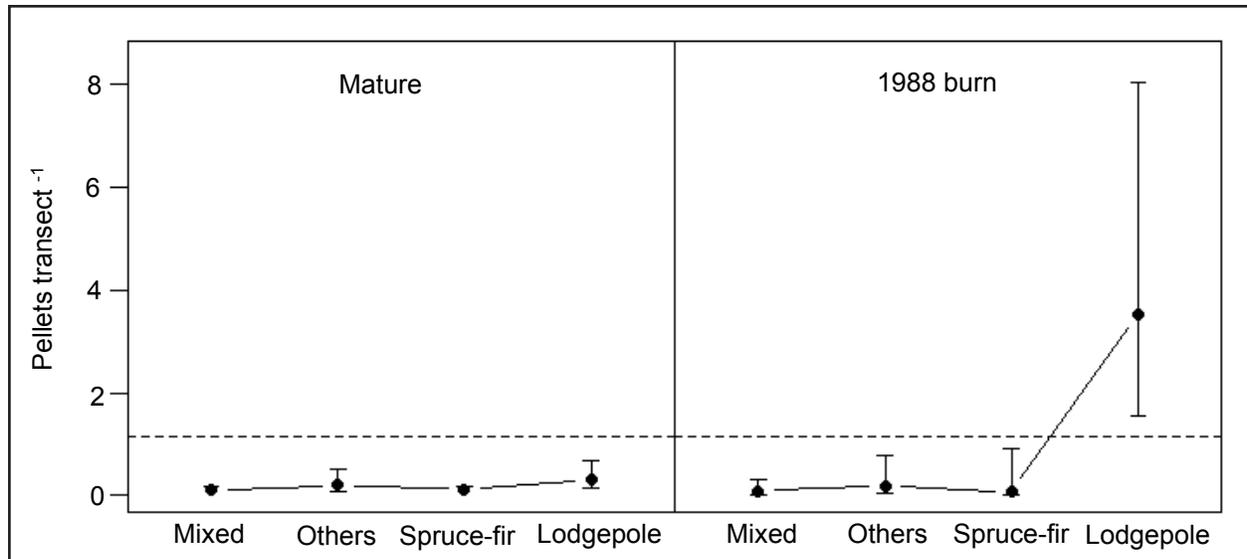


Figure 3. Prediction plots with 95% confidence intervals demonstrating the interaction between burn treatment and dominant canopy type on pellet densities (pellets transect⁻¹). Predicted means and confidence intervals are estimated from the “best” model relating habitat variables to pellet densities, as identified through multivariate analyses with multi-model inference. Other predictor variables in the “best” model are fixed at typical values (medians, or in the case of categorical data, at their proportional distribution in the data). The dashed horizontal line represents the regression-based pellet density equivalent to the threshold of 0.5 hares ha⁻¹ believed necessary to sustain lynx populations.

= 0.26 to 1.24) at 70% canopy closure (Figure 4), when other variables were held at typical values. Pellet density increased slowly with understory cover up to 80% cover, above which pellet densities declined (Figure 5). Everything else being equal, pellet densities in Glacier NP were predicted to be higher east (\bar{x} = 0.35, 95% CI = 0.21 to 0.58) of the Continental Divide than west (\bar{x} = 0.11, 95% CI = 0.08 to 0.16).

DISCUSSION

Snowshoe hares occurred at low densities and were patchily distributed in Glacier National Park. We found an important interaction between burn treatment and dominant canopy type, whereby snowshoe hares were well established and locally more abundant in regenerating lodgepole pine stands of 1988 burn sites (i.e., 17 yr post fire, at the time of this study) compared to other burn treatments (mature forests and 1994 burns) and dominant

canopy types. Areas of higher hare density in the park were associated with areas of frequent lynx reports during the years of this study.

Spatial and Habitat Patterns in Hare Abundance

Overall, the hare densities recorded in Glacier National Park were at the lower end of densities observed in some other parts of the hare’s southern range (e.g., 0 to 2.7 hares ha⁻¹ for US Rocky Mountains; Ellsworth and Reynolds 2006). In Glacier NP, only 7% (8 of 114) of surveyed sites had densities >0.5 hares ha⁻¹. However, Glacier NP hare densities were 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 (more than twice the proportion of zeroes as in this Glacier NP study).

Within Glacier NP’s mature forested habitats, higher hare densities occurred most fre-

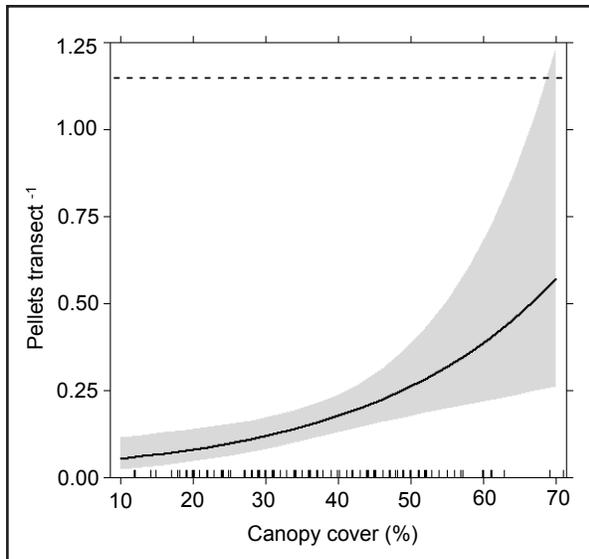


Figure 4. Prediction plots with 95% confidence intervals showing the effect of canopy cover (%) on pellet densities (pellets transect⁻¹). Predicted means and confidence intervals are estimated from the “best” model relating habitat variables to pellet densities, as identified through multivariate analyses with multi-model inference. Other predictor variables in the “best” model are fixed at typical values (medians, or in the case of categorical data, at their proportional distribution in the data), while predictions are made across the range of canopy cover observed in the data. The dashed horizontal line represents the regression-based pellet density equivalent to the threshold of 0.5 hares ha⁻¹ believed necessary to sustain lynx populations.

quently along the eastern and southern boundaries of the park—particularly in the areas of Many Glacier, Two Medicine, and Railroad Creek. The regions of higher hare density identified by our random sampling of mature forest habitats corresponded well with areas of opportunistic lynx sightings recorded by park biologists and visitors.

Among the continuous habitat parameters measured in this study, only understory cover (0 m to 0.5 m) and percent canopy cover were identified as important predictors of hare density, in line with results from some other studies (Hodges 2000a, 2000b). Predicted effect

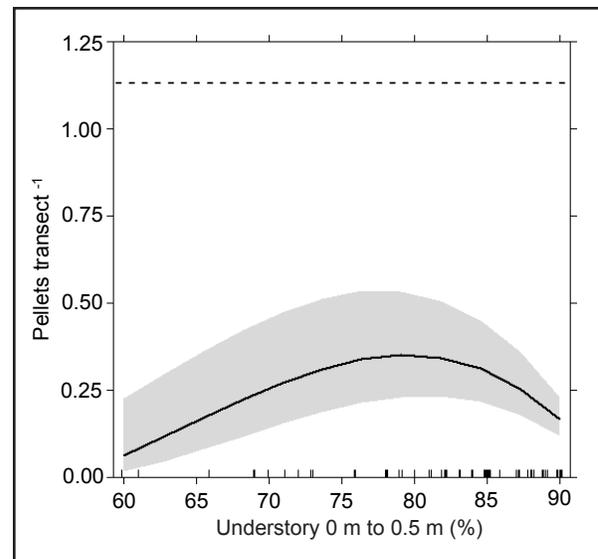


Figure 5. Prediction plots with 95% confidence intervals showing the effect of understory cover at 0 m to 0.5 m aboveground (%) on pellet densities (pellets transect⁻¹). Predicted means and confidence intervals are estimated from the “best” model relating habitat variables to pellet densities, as identified through multivariate analyses with multi-model inference. Other predictor variables in the “best” model are fixed at typical values (medians, or in the case of categorical data, at their proportional distribution in the data), while predictions are made across the range of understory cover observed in the data. The dashed horizontal line represents the regression-based pellet density equivalent to the threshold of 0.5 hares ha⁻¹ believed necessary to sustain lynx populations.

sizes for these variables were relatively small, however. When other model variables were set at typical (median) values, predicted hare densities were well below 0.5 hares ha⁻¹ across the observed range of values for these two variables.

Importantly, we do not know if hares in Glacier NP show the high interannual variation that has been observed in time series of some other southern range snowshoe hare populations (Hodges 2000b). If hares in Glacier NP show high variation in density through time, it is possible that our sampling happened to fall during a period of overall

low densities. We expect that the major patterns in mature forest habitat use that we observed would remain true, but we might well see more habitats used when hares are more generally abundant.

Hares and Post-Fire Forests

Pellet densities in lodgepole stands of 1988 burn sites were far greater than in other canopy types within the 1988 burns, and also exceeded pellet densities in lodgepole forests of other burn treatments (mature forests and 1994 burns) by at least a factor of 10. From our “best” model for habitat correlates of pellet densities, the predicted mean pellet density for lodgepole stands of 1988 burns equates to hare densities nearly three times the 0.5 hares ha⁻¹ threshold believed necessary to support lynx populations. Our field surveys corroborated the importance of Glacier NP’s 1988 post-fire regenerating lodgepole habitats for snowshoe hares. Five of the eight study sites that exceeded the 0.5 hares ha⁻¹ density threshold were lodgepole stands in the 1988 burns, a high proportion since this stand type represented only 10% of our sampling effort. And during our three-year study, our field crew reported two lynx sightings, both in lodgepole stands of Glacier NP’s 1988 burns. The strong association of snowshoe hares with 1988 post-fire regenerating lodgepole pine in Glacier NP is consistent with findings from many other studies (Koehler *et al.* 1979, Sullivan 1984, Malloy 2000, Miller 2005).

Even though a much higher proportion of 1988 burn sites supported threshold hare densities than in mature forest and 1994 burn stands, hare densities were still highly variable (up to 2.4 hares ha⁻¹) at 1988 burn sites. A full 21% of sites burned in 1988 did not support any hares during our surveys, but these sites were all dominated by canopy species other than lodgepole. In addition, variability in hare densities reflected differences in lodgepole regeneration rates, which vary at a fine scale due

to topographic relief, soil moisture, characteristics of the previous stand, fire severity, and other factors (Baumgartner *et al.* 1984, Koch 1996, McKenzie and Tinker 2012). In a study concurrent with our Glacier NP work, we found similar patchiness in hare distribution among lodgepole pine forests burned in Yellowstone National Park’s 1988 fires (Hodges *et al.* 2009).

The age at which stands become useable for hares post fire remains poorly characterized, in part because stands have such different successional trajectories in terms of how long it takes to redevelop high tree densities (Nyland 1998, Turner *et al.* 2004, Pierce and Taylor 2011). Although some stands burned in Glacier NP’s 1988 fire had already created high quality hare habitat supporting the highest densities observed in this study, stands regenerating from Glacier NP’s 1994 burns supported few or no hares. Other studies in the western US have found high hare densities correlated with regenerating (harvested) forests ranging from 20 yr old to 67 yr old (Koehler *et al.* 1979, Zimmer 2004, Miller 2005).

Regardless of when the optimum habitat 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. We expect regenerating forests of the 1988 Red Bench Fire to continue supporting moderate hare densities and lynx over the next few decades at least. As regenerating forests from the park’s 2003 fires (which burned 40 times more area than the 1998 Red Bench Fire) mature to stages favorable for hares and lynx over the next several decades, Glacier NP may observe a further shift in distribution of its hare and lynx populations to take advantage of transiently favorable food and cover conditions.

As forest fire regimes change in the face of global warming, fires are predicted to be more frequent and more severe. Unfortunately, we still know very little about the spatial scales at which regional snowshoe hare dynamics operate. It is possible that there are thresholds in the amount of early seral forest beyond which regional hare densities are very low overall because of insufficient area of high quality regeneration and poor or isolated mature stands to act as reservoirs; Yellowstone National Park might be a current example of this phenomenon.

Alternatively, the predicted future with more young regenerating forest might be quite positive for snowshoe hares, if regenerating forests achieve sufficient tree densities quickly. For lynx, which often den in mature forests, numbers may depend both on hare distribution and sufficient mature habitat for reproduction. For both species, more work on their dynamics in relation to the size of fire, time since fire, and post-fire habitat heterogeneity would help us predict their futures under rapid climate change.

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