THE IMPORTANCE OF WILDFIRE AND MOUNTAIN PINE BEETLE INFESTATIONS AS BLACK-BACKED WOODPECKER HABITAT

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Introduction

Black-backed woodpeckers (*Picoides arcticus*) are uncommon residents of northern coniferous forests. These woodpeckers are a disturbance dependent species that rely on recently killed trees for nesting and foraging. Black-backed woodpeckers are most strongly associated with early post-fire forest (Bock and Lynch 1970, Hutto 1995, Murphy and Lehnhausen 1998, Hobson and Schieck 1999, Nappi et al. 2003, Hanson and North 2008, Nappi and Drapeau 2009). Despite this burn-centric association, beetle infestations also play an important and increasingly recognized role in creating habitat for black-backed woodpeckers (Goggans et al. 1989, Bonnot et al. 2008, 2009). Finally, black-backed woodpeckers are known occur in unburned, late successional forests (Setterington et al. 2000, Mohren 2002, Tremblay et al. 2009), particularly when disturbed forests are unavailable (Hoyt and Hannon 2002). This strong association with disturbed forests makes the black-backed woodpecker an important indicator of the positive and regenerative role that wildfire and pine beetle epidemics can play in western forests.

Despite the importance of burned forests and beetle infestations for black-backed woodpeckers, these disturbances reduce or eliminate timber resources in affected areas. Considerable effort is thus put into preventing the occurrence of such disturbances or mitigating the impact of these disturbances once they occur. Salvage logging, which is the partial or total harvest of standing dead trees in forest stands affected by wildfire or beetle infestations, is often used to mitigate these economic losses. If any economic value is to be salvaged from disturbed timber stands, harvest must occur shortly following the disturbance, which also coincides with the peak value of resources for black-backed woodpeckers (Murphy and Lehnhausen 1998).

Because of their dependence on burned forests and beetle infestations and potential habitat loss due to salvage logging, black-backed woodpeckers have attracted the attention of various state and federal resource conservation agencies throughout their range (Dixon and Saab 2000). Additionally, in the Black Hills of South Dakota, black-backed woodpeckers are an isolated population with little or no connectivity between other populations (Pierson et al. 2010). The combination of these factors has led the black-backed woodpecker to be considered a Sensitive Species by Region 2 of the United States Forest Service and a Species of Greatest Conservation Concern by the state of South Dakota (South Dakota Department of Game, Fish, and Parks 2006).

Management actions that promote both economic development and habitat conservation for this sensitive species require knowledge of how black-backed woodpeckers respond to wildfire and mountain pine beetle (MPB) infestations. Further, knowledge of the relative role each disturbance may play in maintaining black-backed woodpecker populations will enable an evaluation of trade-offs among alternative management objectives. We evaluated the relative role of wildfire and mountain pine beetle infestations in maintaining black-backed woodpecker populations by studying home range size, foraging behavior, resource selection, and survival. Studying home range size provides mangers with an estimate of the minimum area required for black-backed woodpeckers occupying burned forest or mountain pine beetle infestations. By studying foraging behavior and resource selection within their home range, we can gain additional insight into how those home ranges should be structured. Understanding foraging behavior in these areas provides insight into which vegetation characteristics may provide the greatest food resources for black-backed woodpeckers. An analysis of foraging behavior is complemented by understand how forest resources are used in comparison with what resources are available within a woodpecker's home range. Finally, a comparison of survival rates of adults and juveniles in burned forest and mountain pine beetle infestations will allow us to understand the population-level consequences of occupying these two habitats. We believe an integrated study of home range, resource selection, and demography will provide managers a solid foundation for conserving this sensitive species in burned forests and MPB infestations in the Black Hills of South Dakota.

Methods

Study Sites. This study was divided among several study sites representing habitat created by wildfire, prescribed fire, or mountain pine beetle infestations. Sampling began in April 2008 and continued year-round through August 2011. One wildfire study site was located at the Box Elder fire (44°9'N, 103°24'W), which burned 319 acres in 2007. Sampling occurred at the Box Elder field site between the spring of 2008 and the spring of 2010. Another wildfire study site was located at the Four Mile fire (43°41'N, 103°26'W), which burned 2,359 acres in Custer State Park in 2007. Sampling occurred at this site for the duration of the study. A third burned forest study site was located at the Ricco fire (44°13'N, 103°25'W), which burned 3,959 acres in 2005. Sampling occurred at the Ricco field site only during the 2008 breeding season. We also included three study sites in habitat created by prescribed fire. One prescribed fire study site was located in the Bullock prescribed fire (44°0'N, 103°30'W), which burned approximately 1,200 acres in October of 2008. Sampling at the Bullock prescribed fire started in the winter of 2010 and lasted through the 2011 breeding season. The second prescribed fire study site was located in the Bitter prescribed fire (43°58'N, 103°26'W), which burned approximately 750 acres in October 2010. Sampling at the Bitter prescribed fire occurred only in the 2011 breeding season. The third prescribed fire study site was located in the Headquarter West prescribed fire in Wind

Cave National Park (43°34’N, 103°30’W), which burned approximately 630 acres in September 2009. Sampling at the Headquarters West fire started in the autumn of 2010 and lasted through the 2011 breeding season. Finally, we included a multitude of study sites in habitat created by mountain pine beetles. While study sites were in numerous discrete patches of MPB infestations, they occurred in two main areas. One beetle infested study site was located in the Norbeck area (43°50’N, 103°30’W) of the Black Hills National Forest. This site has been infested with beetles since at least 2003. As of 2009, more than 4,000 acres had been affected (Allen and Long 2008, USDA Forest Service 2009b). Sampling occurred in Norbeck only during the 2008 breeding season. The other beetle infested study site was located west of Hill City, between Bear Mountain and Deerfield Lake (43°55’N, 103°42’W). This infestation affected at least 8,000 acres by 2009. Sampling occurred in this study site for the duration of the study.

Radio-telemetry. Black-backed woodpecker home range size, resource selection, and demography were estimated by fitting VHF radio-transmitters to individual birds. Adult woodpeckers were captured and fitted with VHF transmitters using hoop nets and netguns. Hoop nets were an efficient capture method during the breeding season, but were only effective when woodpeckers were actively attending cavities. Alternatively, the netgun allowed capture away from nest cavities and outside the breeding season (Lehman et al. 2011).

Adult black-backed woodpeckers were initially targeted for capture by searching potential study sites for signs of woodpeckers. Once captured, all adults were weighed and a small (3.0 – 3.3 g) transmitter was attached (Rappole and Tipton 1991). Adult black-backed woodpeckers captured during the course of this study weighed an average of 75g, so transmitters weighed < 5% of an average adult bird’s mass (Gaunt and Oring 1997). Additionally, all birds were given a unique combination of colored leg bands, including a uniquely numbered USFWS aluminum leg band. As VHF radio-transmitters died, we attempted to recapture previously marked individuals and replace transmitters. However, previously marked birds were sometimes difficult to capture perhaps because of increased wariness, movements out of the study areas, and premature transmitter failures. We thus recaptured marked birds that we could and supplemented these with unmarked birds that were captured opportunistically.

We captured black-backed woodpecker nestlings at the nest cavity and attached VHF radio-transmitters. We accessed the nest by using a 3-inch hole-saw, which we used to drill into the side of the cavity (Ibarzabal and Tremblay 2006). Nestlings were captured approximately 3 days prior to fledging. Once captured, nestlings were weighted and a 2.2 g transmitter was attached (Rappole and Tipton 1991). Nestlings weighed an average of 57g and transmitters weighed <5% of an average nestling's mass (Gaunt and Oring 1997). As with adults, all nestlings were given a uniquely numbered USFWS aluminum leg band and a unique combination of colored leg bands.

Radio-marked birds were relocated using two different schedules. Some birds were randomly selected as 'home-range / resource selection' birds. These individuals were relocated at least 2-3 times per week in order to gather enough telemetry locations to estimate home range size and evaluate resource selection. Those birds that were not selected as home-range / resource selection birds were relocated approximately every other week to evaluate survival probabilities.

Home Range. We estimated home-range size using kernel density techniques (Worton 1989). Whenever woodpeckers were located, we recorded spatial coordinates using a hand-held GPS unit (NAD83, UTM Zone 13N) and flagged the tree for future vegetation sampling (see *resource selection* below). Seaman et al. (1999) recommend a minimum of 30 points when estimating home range boundaries using kernel density techniques, so we only included woodpeckers in the home range analysis if we obtained at least 30 telemetry locations. We estimated home ranges using the 'ks' package in Program R (R Development Core Team 2012) and we used the 'plug-in' method for calculating the bandwidth parameter (Millspaugh et al. 2006). Home range size estimates are based on 99% home range contours.

Resource Selection. We evaluated resource selection for all birds with at least 30 telemetry locations by comparing used and available resources within a woodpecker's home range. After obtaining at least 30 telemetry locations, we defined the area available to the woodpecker based on the 99% home range contour. Each telemetry location was paired with randomly generated points that fell within 99% home range contours. At all used and available trees, we recorded diameter at breast height (DBH), whether the tree was alive, and tree condition; tree condition was classified based on burn severity or age of MPB infestations. We classified burn severity as low (scorching restricted to below breast height), moderate (scorching above breast height but some canopy left unburned), high (canopy completely scorched), or unburned. We classified MPB infested trees as 'green hits' (infestations with green or yellow needles that were <1 year old), 'red hits' (infestations with red needles that were 1-3 years old) or 'gray hits' (beetle-killed trees that have lost all of their needles, generally >3 years old). In addition to comparing characteristics of used and available trees, we also compared the characteristics of the surrounding forest. We characterized vegetation immediately surrounding the used or available tree using a 10 basal area factor prism (variable-radius plots) to identify trees to include in measurements. These data were used to calculate basal area, tree density per acre, and proportion of dead trees.

We estimated resource selection using modified case-control models (Lancaster and Imbens 1996, Keating and Cherry 2004, Rota et al. *in review*). Modified case-control models allow estimation of the absolute probability of use, conditioned on habitat covariates, from use-availability data. We calculate the probability that resource unit *i* is used as:

$$logit(\psi_i) = \beta_0 + \ln\left(\frac{n_1}{\pi n_a} + 1\right) + \beta_1 x_{i1} + \cdots + \beta_j x_{ij}$$

where β_0 is the intercept parameter, $\beta_1 \ldots \beta_j$ are the *j* regression coefficients describing the strength and selection of resource selection, $x_{i1} \ldots x_{ij}$ are the resource variables for site *i*, n_1 and n_2 are the number of used and available sites in the study, respectively, and π is the unconditional (mean) probability any particular resource is used. We fit modified case-control models using Bayesian methods in WinBUGS (Spiegelhalter et al. 2003) via the R2WinBUGS package (Sturtz et al. 2005) in program R.

Foraging Behavior. We evaluated foraging behavior in all adult radio-marked black-backed woodpeckers starting in October of 2008. We thus were unable to observe foraging behavior the first breeding season post-fire in the Ricco, 4-Mile, and Box Elder field sites. We evaluated foraging behavior by conducting 10-minute focal observations when woodpeckers were located. During 10-minute focal observations, observers counted the number of foraging attempts made by woodpeckers on each tree visited. Foraging attempts were defined as exerted efforts to extract prey from a tree through either drilling or flaking bark. Counts of foraging attempts included both observed captures of large and small prey and apparent foraging attempts when the observer was unable to determine if prey were successfully captured. In addition to counting foraging attempts, observers classified trees used for foraging by burn severity or age of MPB infestation (see above) and estimated DBH of the tree.

We analyzed counts of foraging attempts using a negative binomial generalized linear mixed modeling approach. We used a negative binomial model to account for overdispersion in count data relative to a theoretical Poisson model. Additionally, we used a mixed modeling approach to account for repeated foraging observations on the same woodpeckers and to account for random variation in foraging counts between observers. We fit negative binomial models using the glmmADMB package in program R.

Survival. We estimated habitat-specific survival rates for all individually-marked woodpeckers using Kaplan-Meier known-fate models (Pollock et al. 1989). Kaplan-Meier known-fate models estimate the probability of surviving from the beginning of the study to an arbitrary time point *t*. For adults, we estimated the probability of a woodpecker surviving from the beginning to the end of the study. Assuming constant survival probabilities throughout the study, we used this estimate to calculate annual survival probabilities. We used non-parametric bootstrapping procedures to estimate 95% confidence intervals of annual survival probabilities.

To estimate juvenile survival probabilities, we aggregated juvenile capture, mortality, and censoring dates without regard to year. We aggregated juvenile survival data because there were intermittent periods where no juveniles were 'at risk' of death, which leads to complications with Kaplan-Meier estimates. For juveniles, we thus estimated the probability of surviving from fledging to the beginning of the next breeding season. We again used non-parametric bootstrapping procedures to estimate 95% confidence intervals of annual juvenile survival probabilities.

Results

Home Range. We collected 30 or more telemetry locations on 36 woodpeckers occupying burned forest and 26 woodpeckers occupying MPB infestations. The mean home range size of woodpeckers occupying burned forest was 521 acres (range = [49, 3099]). The mean home range size of woodpeckers occupying MPB infestations was 896 acres (range = [167, 2876], Figure 1).

Resource Selection. We conducted analyses of resource selection using 132 used and 222 available locations from 13 woodpeckers in burned forest and 70 used and 70 available locations from 2 woodpeckers in MPB infested forest. Black-backed woodpeckers in both disturbance types showed strong selection for trees killed either by wildfire or mountain pine beetle infestations relative to live trees (mean regression coefficient for fire-killed trees = 2.46, 95% credible interval = [0.58, 5.81], mean regression coefficient for beetle-killed trees = 2.90, 95% credible interval = [0.66, 5.94], Figures 2, 3). In burned forests, black-backed woodpeckers exhibited strong selection for trees surrounded by a high proportion of dead trees (mean regression coefficient = 3.08, 95% credible interval = [0.44, 6.73]). Selection was strongest in areas where 100% of trees measured by variable-radius plots were dead. Woodpeckers also exhibited selection for trees burned at both low and moderate to high severity, although selection was strongest for trees burned at moderate to high severity (mean regression coefficient = 2.99, 95% credible interval = [1.26, 5.59]) relative to low severity (regression coefficient = 1.24, 95% credible interval = [0.17, 2.61]). In MPB infested forests, woodpeckers exhibited weak selection for trees surrounded by a high basal area (mean regression coefficient = 1.24, 95% credible interval = [-0.87, 4.20]), high tree density (mean regression coefficient = 1.02, 95% credible interval = [-0.61, 2.95]), and a high proportion of green hits (regression coefficient = 0.83, 95% credible interval = [-2.02, 4.18]), though 95% credible intervals overlapped 0 for all regression coefficients. Selection was strongest in areas with basal area > 117 ft^2, tree density > 368 trees per acre, and 100% of trees measured in variable-radius plots classified as green hits. Woodpeckers also exhibited weak selection for trees with larger DBH (mean regression coefficient =0.61, 95% credible interval = [-0.27, 1.57]), though 95% credible intervals also overlapped 0. Selection was strongest for trees > 9.5 inches DBH.

Foraging Behavior. Our analysis of black-backed woodpecker foraging behavior was based counts of foraging attempts from 3980 trees collected from 78 marked adults. Black-backed woodpeckers exhibited greater foraging rates on disturbance-killed trees relative to undisturbed trees (Figure 4). Overall foraging rates on disturbance-killed trees were similar, though the highest foraging rates were on green hit trees in MPB infestations (mean count of foraging attempts per tree visited = 1.24, 95% CI = [0.96, 1.61]) and red hit trees (mean count of foraging attempts per tree visited = 1.17, 95% CI = [0.89, 1.53]) and the lowest foraging rates on disturbance-killed trees were on trees burned at low severity (mean count of foraging attempts per tree visited = 0.87, 95% CI = [0.68, 1.11] and trees burned at moderate severity (mean count of foraging attempts per tree visited = 0.90, 95% CI = [0.71, 1.13]). Foraging rates were similar in the summer, autumn, and winter months (mean count of foraging attempts in summer = 1.24, 95% CI = [0.89, 1.72], autumn = 1.38, 95% CI = 1.12, 1.71], winter = 1.34, 95% CI = [1.05, 1.71]), though foraging rates were lower in the spring months (mean count of foraging attempts in spring = 0.93, 95% CI = [0.76, 1.13]). Black-backed woodpeckers demonstrated a quadratic response in foraging rates to tree diameter, with the greatest foraging rates occurring on 17 inch DBH trees.

Counts of successful extraction of large and small prey differed between burned trees and MPB infested trees (Figure 5). In general, black-backed woodpeckers obtained more small prey items in mountain pine beetle infested trees and obtained more large prey items in burned trees. Woodpeckers captured the most small prey items in green hits (mean count of small prey items per tree visited = 0.25, 95% CI = [0.15, 0.43]) and captured the fewest small prey items in trees burned at low severity (mean count of small prey items per tree visited = 0.12, 95% CI = [0.08, 0.19]). Woodpeckers captured the most large prey items in trees burned at low severity (mean count of large prey items per tree visited = 0.06, 95% CI = [0.03, 0.12]) and captured the fewest large prey items in green hits (mean count of large prey items per tree visited = 0.02, 95% CI = [0.01, 0.05]). We may have observed the greatest foraging success for large prey items in trees burned at low severity because we did not observe foraging behavior the first breeding season post-fire in Ricco, 4-Mile, or Box Elder.

Survival. Estimated annual black-backed woodpecker survival differed by age and habitat (Figure 6). Annual adult survival probabilities were slightly greater in burned forest (annual survival probability = 0.70, 95% CI = [0.56, 0.81], *n* = 81) than mountain pine beetle infested forests (annual survival probability = 0.63, 95% CI = [0.44, 0.90], *n* = 55), though confidence intervals overlapped broadly. Juvenile survival was consistently lower than adult survival and showed similar differences between disturbance types. Annual juvenile survival probabilities were greater in burned forest (annual survival probability = 0.46, 95% CI = [0.24, 0.69], *n* = 48) than mountain pine beetle infested forests (annual survival probability = 0.27, 95% CI = [0.00, 0.60], *n* = 24), though confidence intervals again overlapped broadly.

Discussion

Our study highlights important differences between the value of burned forest and mountain pine beetle infestations as black-backed woodpecker habitat. Numerous studies have demonstrated that black-backed woodpeckers use both burned forest (Bock and Lynch 1970, Murphy and Lehnhausen 1998, Hobson and Schieck 1999, Nappi et al. 2003, Hanson and North 2008, Nappi and Drapeau 2009) and MPB infestations (Goggans et al. 1989, Bonnot et al. 2008, 2009). However, ours is the first to directly compare the relative role these two disturbance types may play in maintaining woodpecker populations. Our comparison of home range, resource selection, and demography between these two habitats suggest that burned forests may provide more valuable habitat for black-backed woodpeckers than mountain pine beetle infestations.

Several lines of evidence from our study suggest recently burned forests may provide the most valuable habitat for black-backed woodpeckers. Home range size was generally smaller in burned forests relative to MPB infestations. Additionally, black-backed woodpeckers were more likely to encounter large prey items when foraging in burned forests relative to mountain pine beetle infestations. The large prey items were most likely wood-boring beetle larvae, which rapidly colonize burned forests after fire (Murphy and Lehnhausen 1998, Saint-Germain et al. 2004). These wood-boring beetles thus provide a major food source for black-backed woodpeckers occupying recently burned forest (Dixon and Saab 2000). In contrast, MPB larvae are the main prey item of black-backed woodpeckers occupying beetle infestations. These larvae are much smaller than wood-boring beetle larvae but are extremely abundant in green hits. Though we observed black-backed woodpeckers foraging for wood boring beetle larvae on trees infested with MPBs for >1 year and Bonnot et al (2009) noted selection for nest sites in MPB infestations with increased abundance of woodborer egg niches, woodpeckers mostly foraged in currently infested “green hit” trees. The abundant, larger prey base in recently burned forests could thus lead to the smaller average home range size in burned forests observed in this study.

In addition to a potentially larger prey base in recently burned forests, adult and juvenile survival was greatest in burned forests. Increased survival in recently burned forest was probably independent of differences in prey availability between habitats since most observed mortality of black-backed woodpeckers were predation events. Although burned forests and mountain pine beetle infestations both contain high volumes of standing dead trees, they are structurally very different. Recently burned forest often has little or no vegetation remaining in either the canopy or ground, while recent MPB infestations often contain high canopy cover in addition to ground vegetation. Thus, MPB infestations may attract a different suite of predator species than burned forests or hunting efficiency of predators (e.g., increased cover) may improve in MPB infestations.

Although food resources and survival rates of black-backed woodpeckers may be greater in recently burned forests, mountain pine beetle infestations still provide valuable woodpecker habitat. Burned forests provide black-backed woodpecker habitat for the first few years following disturbance (Murphy and Lehnhausen 1998). Consequently, given the infrequent occurrence of large wild fires, MPB infestations may become more valuable as forest burns age or when there is little available burned forest. MPBs occur naturally in ponderosa pine forest, particularly in stands >100 ft^2/acre basal area (Schmid and Mata 2005) As our burned study sites aged, we consistently found black-backed woodpeckers traveling outside burned forests and foraging on nearby MPB infestations. Indeed, the largest home range recorded was of a woodpecker nesting in a 3 year-old burn and foraging on small beetle infestations around the perimeter of the burn. Ensuring both habitats are available across the landscape will likely be important in maintaining black-backed woodpecker populations.

Management Implications. We believe an ideal management strategy for maintaining regional black-backed woodpecker populations would include maintaining a mosaic of recently burned or MPB infested forest. The range of patch sizes should reflect the home-range sizes we observed (50 – 3000 acres). Managers have several options for maintaining such a mosaic of disturbed forest for black-backed woodpeckers. Using prescribed fire is one promising option for creating a mosiac of recently burned forest patches. Several of our study sites were located in prescribed burns, demonstrating that black-backed woodpeckers will readily use such habitat.

Prescribed burns in the Black Hills often fall within the recommended size for disturbed patches. For example, the Bullock prescribed fire in the Black Hills National Forest burned approximately 1,200 acres, while the American Elk prescribed fire in Wind Cave National Park burned approximately 3,400 acres. Another option is to allow naturally occurring disturbances to create a mosiac of disturbed patches. For example, wildland fires that do not threaten life or property can be closely monitored but not immediately extinguished. Additionally, managers can exempt isolated mountain pine beetle infestations < 1,000 acres in size from 'sanitation' logging and thinning. When large-scale wildfire or mountain pine beetle infestations occur, managers might consider exempting patches from salvage or 'sanitation' logging. We recommend exempting all forest burns < 1,000 acres and ½ the area of forest burns > 1,000 acres from salvage logging.

Results from resource selection and foraging analyses suggest that disturbed patches should contain certain structural characteristics. In both burned forests and mountain pine beetle infestations, selection was strongest in areas that experienced 100% tree mortality. In burned forest, this was facilitated by fire that burned at moderate to high severity. In mountain pine beetle infestations, black-backed woodpeckers were attracted to areas with high basal area (>117 ft^2 / acre) and tree density (> 368 trees / acre), which likely facilitated the spread of mountain pine beetles. Additionally, black-backed woodpeckers demonstrated weak selection for trees > 9.5 inches DBH in mountain pine beetle infestations and foraging rates were greatest on 17 inch DBH trees. This is consistent with other studies that examined foraging behavior in black-backed woodpeckers (Nappi et al. 2003) and suggests trees > 9.5 inches DBH should be an important component in disturbed forest patches.

Our study is the first to directly compare the importance of burned forest and MPB infestations as black-backed woodpecker habitat. Our study suggests that black-backed woodpeckers occupying recently burned forests may have smaller spatial requirements, greater food resources, and increased survival relative to MPB infestations. While the ongoing MPB epidemic in the Black Hills ecoregion is clearly benefitting black-backed woodpeckers in the short term, we believe the focus of long-term conservation strategies should focus on ensuring a network of recently burned forest patches while allowing isolated MPB infestations to remain unharvested.

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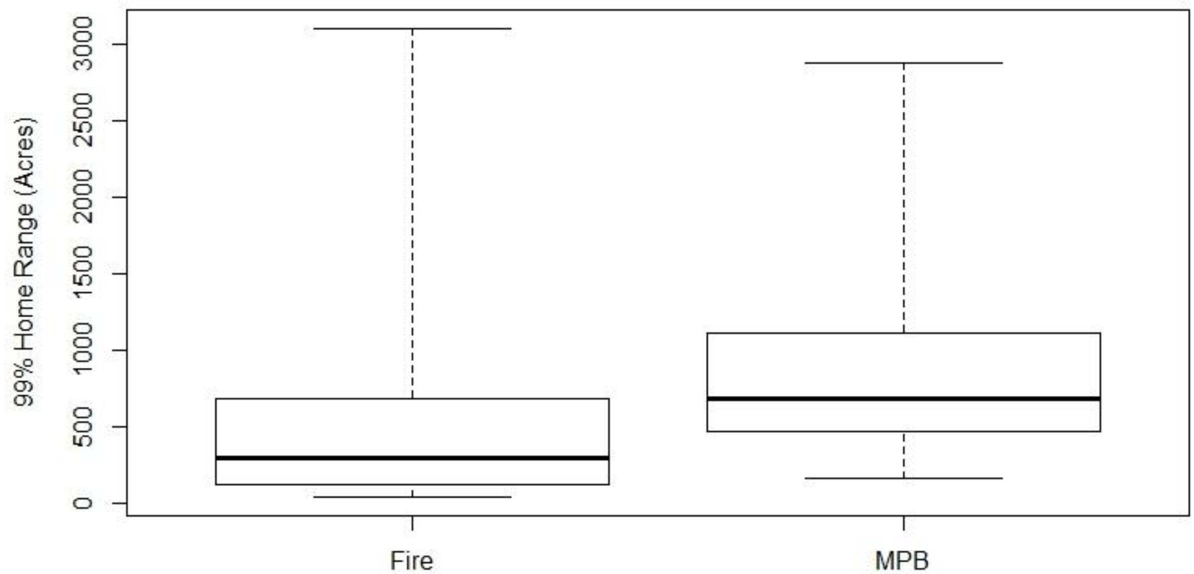

Figure 1 Box and whisker plot of estimated home range size of from 62 black-backed woodpeckers occupying burned forest and mountain pine beetle infestations in the Black Hills of South Dakota. The solid black line represents median home range size, the lower and upper boundaries of the boxes represent the first and third quartiles, and the whiskers represent the minimum and maximum observed home range size.

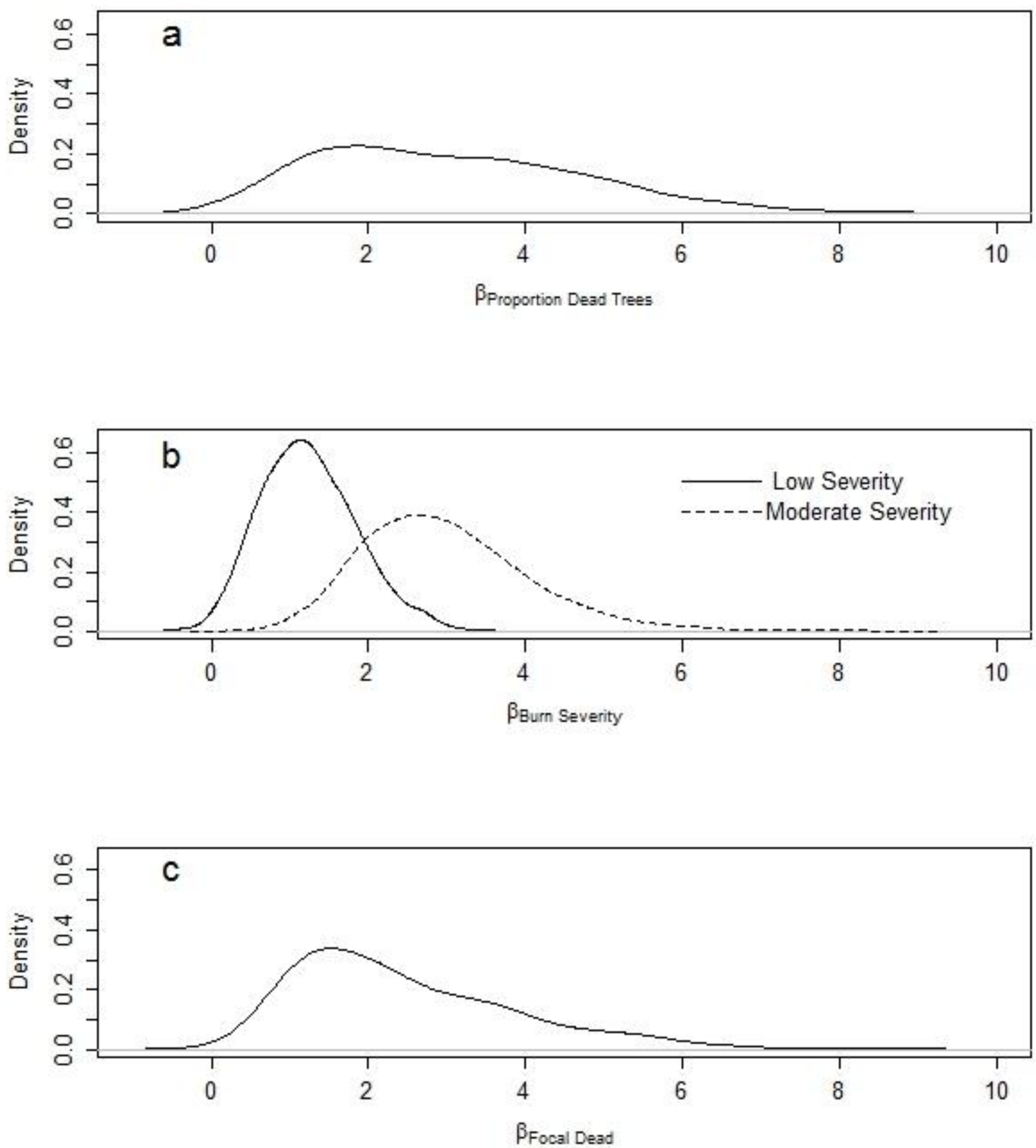

Figure 2 Posterior density estimates for regression coefficients describing Black-backed Woodpecker resource selection a) as a function of the proportion of dead trees surrounding the focal tree, b) as a function of burn severity of the focal tree and c) as a function of whether the focal tree is dead. Greater values of the regression coefficients (β) on the x-axis represent stronger selection. Note that the area under each curve must sum to 1, so tall, narrow curves represent relatively precise posterior density estimates while low wide curves represent relatively imprecise posterior density estimates.

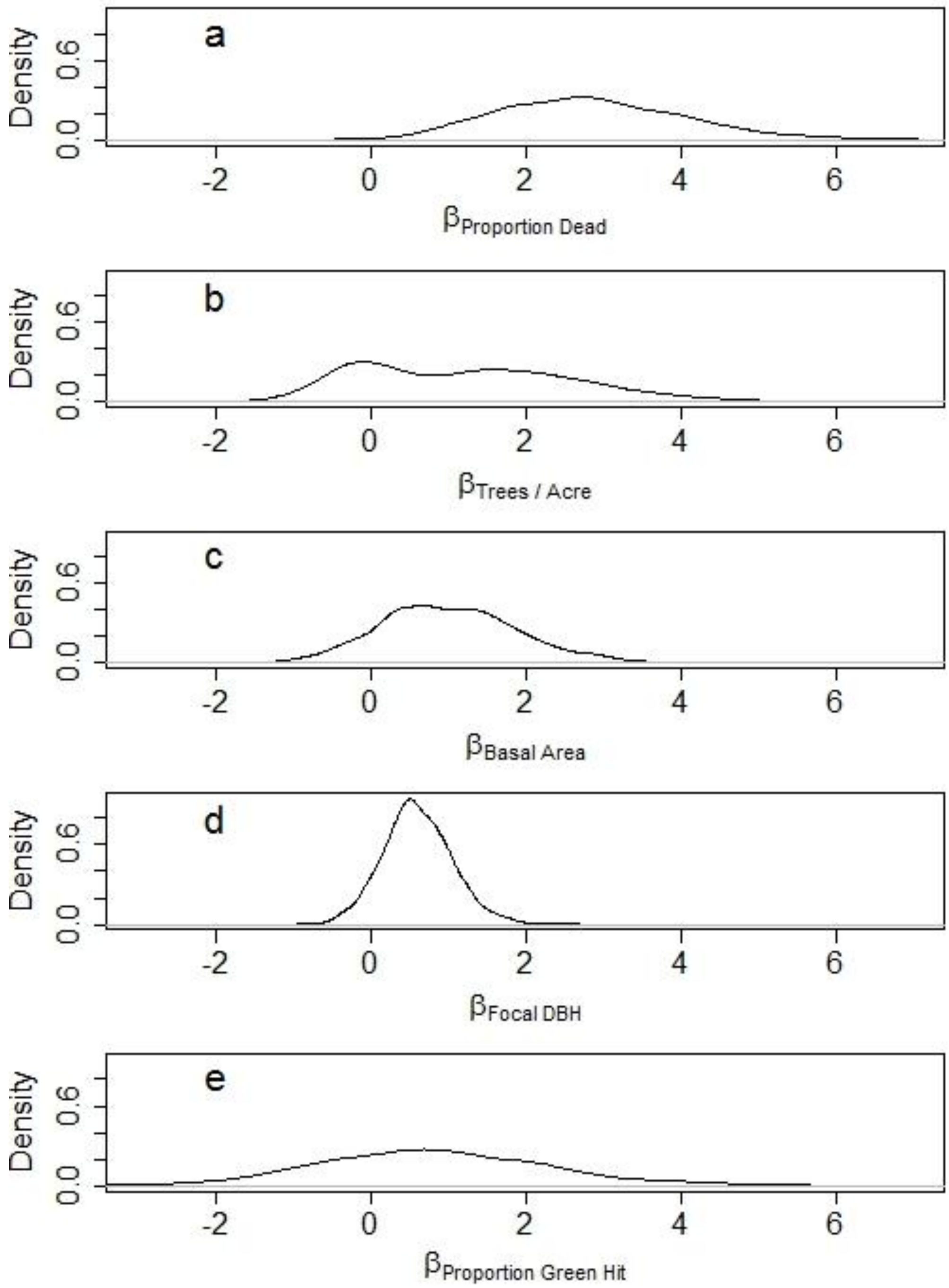

Figure 3 Posterior density estimates for regression coefficients describing Black-backed Woodpecker resource selection a) as a function of the proportion of dead trees surrounding the focal tree, b) as a function of trees per acre c) as a function of basal area, d) as a function of the diameter of the focal tree and e) as a function of the proportion of green hit trees surrounding the focal tree. Greater values of the regression coefficients (β) on the x-axis represent stronger selection. Note that the area under each curve must sum to 1, so tall, narrow curves represent relatively precise posterior density estimates while low wide curves represent relatively imprecise posterior density estimates.

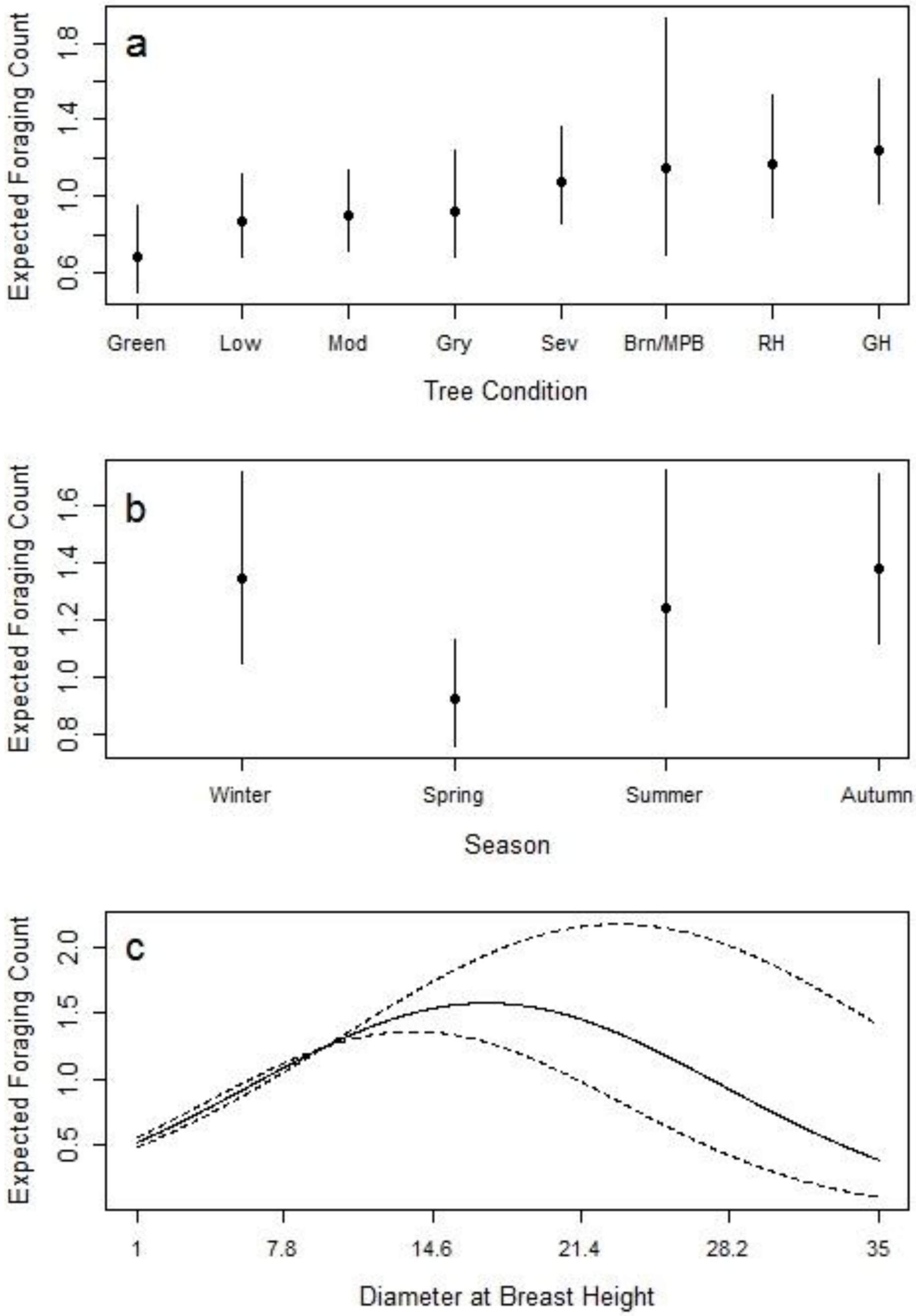

Figure 4 Expected counts ± 95% confidence intervals of foraging rates as a function of a) tree condition (Green = tree not burned or infested with mountain pine beetles, Low = low severity burn, Mod = moderate severity burn, Gry = >3 year old mountain pine beetle infestation, Sev = high severity burn, Brn/MPB = tree both burned and infested with mountain pine beetles, RH = 1-3 year old mountain pine beetle infestation, GH = <1 year old mountain pine beetle infestation), b) season, and c) tree diameter at breast height.

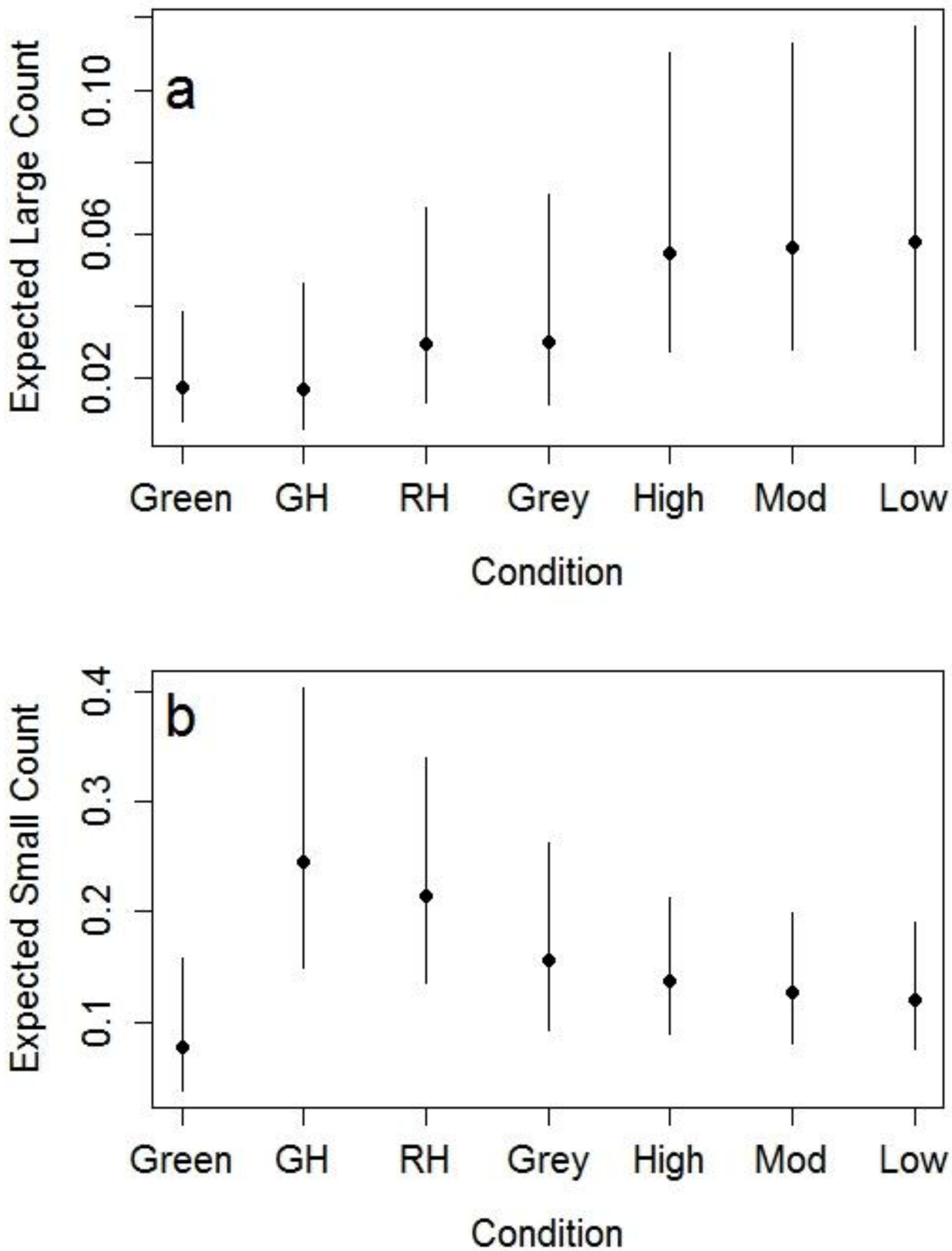

Figure 5 Expected count ± 95% confidence intervals of a) the number of large prey items and b) the number of small prey items as a function of disturbance type captured by black-backed woodpeckers in the Black Hills, South Dakota. Green = tree not burned or infested with mountain pine beetles, Low = low severity burn, Mod = moderate severity burn, Grey = >3 year old mountain pine beetle infestation, High = high severity burn, Brn/MPB = tree both burned and infested with mountain pine beetles, RH = 1-3 year old mountain pine beetle infestation, GH = <1 year old mountain pine beetle infestation

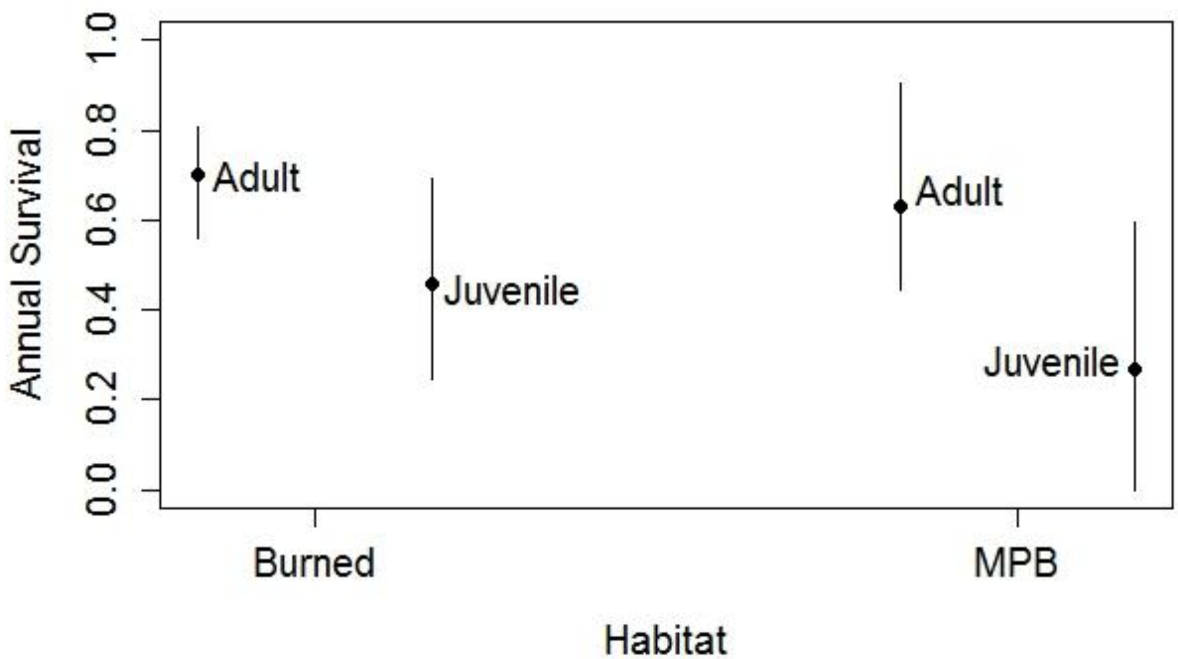

Figure 6 Estimated annual survival probabilities ± 95% confidence intervals of adult and juvenile black-backed woodpeckers occupying burned forests or mountain pine beetle infestations.