

NOT ALL FORESTS ARE DISTURBED EQUALLY: POPULATION DYNAMICS
AND RESOURCE SELECTION OF BLACK-BACKED WOODPECKERS IN THE
BLACK HILLS, SOUTH DAKOTA

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By

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

NOT ALL FORESTS ARE DISTURBED EQUALLY: POPULATION DYNAMICS
AND RESOURCE SELECTION OF BLACK-BACKED WOODPECKERS IN THE
BLACK HILLS, SOUTH DAKOTA

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ABSTRACT

Western North American forests are shaped by natural disturbances, which are an important driver of habitat heterogeneity and species diversity. Wildfire and bark beetle infestations are of particular interest to resource managers because of their widespread occurrence and potential economic impacts. These naturally occurring disturbances create habitat for numerous wildlife species, which benefit from abundant food resources in the form of beetle larvae, increased nesting opportunities in dead and dying trees, and increased forage production through reductions in canopy cover. Despite these benefits, wildfire and mountain pine beetle infestations reduce timber value and have historically been considered undesirable. As a result, much effort has been put into preventing or mitigating the effects of these disturbances through fire suppression, post-fire salvage logging, and sanitation logging.

Black-backed Woodpeckers are emblematic of the important role these natural disturbances play in creating wildlife habitat, since they are almost completely restricted to recently killed forests. Black-backed Woodpeckers are strongly associated with recently burned forests throughout their range. Black-backed Woodpeckers are also associated with mountain pine beetle infestations, particularly in isolated portions of their range. Finally, recent evidence suggests that Black-backed Woodpeckers will use habitat created by prescribed fire. Black-backed Woodpeckers are attracted to these disturbed forests because of beetle larvae associated with dead and dying trees. Beetle larvae typically occur in recently killed forest for only a short period, and disturbance-killed forests therefore represent ephemeral habitats for Black-backed Woodpeckers. Black-

backed Woodpeckers are considered a sensitive species by Region 2 of the U.S. Forest Service and a Species of Greatest Conservation Concern by the State of South Dakota. In addition, the Black-backed Woodpecker has recently been petitioned for listing as a Threatened or Endangered species under the Endangered Species Act.

Identifying effective conservation strategies for Black-backed Woodpeckers requires understanding the role of each of these major disturbances in maintaining regional populations. However, considerable uncertainty exists regarding the relative value of wildfire, prescribed fire, and mountain pine beetle infestations to Black-backed Woodpeckers. This dissertation evaluates the relative role of each of these major disturbances on population growth rates, home range size and resource selection, food resources, and movements of Black-backed Woodpeckers in the Black Hills, South Dakota. Understanding how population growth rates vary across each of these major disturbances is a cornerstone to developing effective conservation strategies for this sensitive species. An evaluation of habitat-specific population growth rates is complemented by an understanding of spatial requirements and vegetation conditions within the home range of Black-backed Woodpeckers, which will enable managers to target specific vegetation conditions when developing conservation strategies. Both population dynamics and space use can be affected by available food resources, and an evaluation of foraging behavior can provide insight into mechanisms driving patterns of population growth and space use across habitats. Finally, understanding factors affecting Black-backed Woodpecker movements among ephemeral habitat patches will provide insight into how this species persists in a spatially and temporally dynamic environment.

We evaluated population growth rates of Black-backed Woodpeckers in habitat created by summer wildfire, mountain pine beetle infestations, and fall prescribed fire by studying habitat-specific demographic rates. We studied adult and juvenile survival probabilities and reproductive rates between April 2008 and August 2012 in the Black Hills, South Dakota. We estimated habitat-specific adult ($n = 137$ adults) and juvenile ($n = 73$ juveniles) survival probability using Bayesian multi-state models and habitat-specific reproductive success using Bayesian nest survival models ($n = 95$ nests). We used these estimated demographic rates to calculate asymptotic population growth rates using matrix projection models. Adult and juvenile survival and nest success were highest in habitat created by summer wildfire, intermediate in mountain pine beetle infestations, and lowest in habitat created by fall prescribed fire. Additionally, mean adult and juvenile survival probability and mean nest success declined slightly with increasing number of years post-fire. Consequently, mean population growth in habitat created by summer wildfire was positive, while mean population growth was negative in fall prescribed fire and mountain pine beetle infestations. Population growth rates were most sensitive to variation in adult and juvenile survival, and were least sensitive to variation in nest success and the number of young fledged per successful nest.

We evaluated resource selection of Black-backed Woodpeckers by comparing vegetation conditions at trees used by woodpeckers within their home range to trees considered available to woodpeckers. We first estimated home range size using fixed kernel density techniques ($n = 28$ in habitat created by summer wildfire, $n = 19$ in habitat created by fall prescribed fire, and $n = 27$ in mountain pine beetle infestations). We then

evaluated resource selection using a Bayesian random-effects discrete choice model ($n = 5$ woodpeckers in habitat created by summer wildfire, $n = 16$ in habitat created by fall prescribed fire, and $n = 8$ in habitat created by mountain pine beetle infestations). Home range size was smallest in 1 - 2 year post summer wildfire habitat (mean home range size = 79 ha) and 2-year post fall prescribed fire habitat (mean home range size = 143 ha). Home range size was intermediate in mountain pine beetle infestations (mean home range size = 307 ha) and was greatest in 3-4 year post fire habitat (mean summer wildfire home range size = 430 hectares, mean fall prescribed fire home range size = 460 ha). The relative probability that a Black-backed Woodpecker used a tree within its home range increased with increasing diameter at breast height (DBH) and basal area, and was greatest on disturbance-killed trees.

The differences in population growth rates and home range size among summer wildfire, mountain pine beetle infestations, and fall prescribed fire may occur as a result of differences in food resources among these habitats. We thus asked whether apparent foraging success of Black-backed Woodpeckers differed among habitats created by summer wildfire, mountain pine infestations, and fall prescribed fire. We counted the number of successfully captured wood-boring beetle and 'small' prey on each tree a Black-backed Woodpecker used for foraging and modeled these counts as a function of habitat (summer wildfire, fall prescribed fire, or mountain pine beetle infestation), tree diameter, number of years post-fire, and tree disturbance category (burn severity and age of mountain pine beetle infestation). Apparent foraging success for wood-boring beetles was greatest in habitat created by summer wildfire relative to fall prescribed fire and

mountain pine beetle infestations. In contrast, apparent foraging success for small prey was greatest in habitat created by mountain pine beetle infestations relative to summer wildfire. Assuming apparent foraging success reflects underlying differences in wood-boring beetle larvae abundance, Black-backed Woodpeckers may have greater food resources in habitat created by summer wildfire relative to fall prescribed fire.

Additionally, assuming food resources scale with prey size, Black-backed Woodpeckers foraging in habitat created by summer wildfire may acquire more food resources per tree relative to mountain pine beetle infestations.

We studied movement dynamics of Black-backed Woodpeckers by tracking long-distance movements with aerial telemetry. We modeled movement dynamics with Bayesian multi-state models that allowed for movements between burned forest and mountain pine beetle infestations. We collected movement data between April 2008 and August 2011 from 122 adult Black-backed Woodpeckers that collectively totaled 771 months of observations. We observed a total of 18 dispersal events ranging from 4 – 60 km. We found that the probability of dispersing during a single time step (1 month) was associated with nest failure the previous time step and increased with increasing time post-fire, regardless of nest fate. We also found that dispersing Black-backed Woodpeckers were most likely to move to a burned forest relative to the amount of burned forest available.

The combination of results from all study components indicate that habitat created by summer wildfires holds the greatest relative value to Black-backed Woodpeckers in the Black Hills. Mean population growth rates were positive only in habitat created by

summer wildfires, home range sizes were smallest in 1-2 year post-summer wildfire habitat, foraging woodpeckers consistently captured the most wood-boring beetles in habitat created by summer wildfires, and dispersing woodpeckers were most likely to move to burned forest relative to availability. However, habitat created by summer wildfire is ephemeral for Black-backed Woodpeckers. We found declining demographic rates, increasing home range size, and increasing probability of dispersing away from habitat created by summer wildfire as the time since disturbance increased. Our results suggest 1-2 year post summer wildfire habitat may have the greatest relative value to Black-backed Woodpeckers. We recommend the most efficient strategy for maintaining regional populations of Black-backed Woodpeckers is to retain patches of 1-2 year post summer wildfire habitat by exempting portions of recently burned forest from salvage logging. Recently burned forest patches should be at least 40 – 200 hectares and primarily composed of $\geq 27 \text{ m}^2$ basal area / ha of trees that burned at moderate or high severity, with at least 40% of the basal area composed of trees $\geq 27 \text{ cm DBH}$.

Mountain pine beetle infestations may become more important to Black-backed Woodpeckers as burned forests age. Indeed, population growth rates in mountain pine beetle infestations are likely intermediate between recently burned forests and completely undisturbed forests, potentially buffering population declines when recently burned forests are not available. The decreased mean population growth rates in mountain pine beetle infestations relative to habitat created by summer wildfire is likely driven by reduced adult and juvenile survival. Predators of Black-backed Woodpeckers may forage more efficiently in mountain pine beetle infestations, which have more canopy cover

relative to recently burned forests. Additionally, unburned trees may afford less camouflage to foraging Black-backed Woodpeckers, exposing them to more predators.

The low population growth rates estimated in habitat created by fall prescribed fire suggest, under the conditions we evaluated, that this habitat holds little value to Black-backed Woodpeckers. The low growth rates in this habitat may be attributed to timing, extent, and severity of fall prescribed fire relative to summer wildfire. Prescribed fires in this study occurred during fall months, while wildfires occurred during summer months. This may impact the ability of wood-boring beetles to immediately colonize fall prescribed fires and may consequently lead to reduced food resources we observed in fall prescribed fires. Additionally, prescribed fires tend to burn at lower severity and over a smaller spatial extent relative to wildfires, which may alter predator communities between the two disturbance types.

CHAPTER 1: THE ROLE OF WILDFIRE, PRESCRIBED FIRE, AND MOUNTAIN PINE BEETLE INFESTATIONS ON THE POPULATION DYNAMICS OF A DISTURBANCE-DEPENDENT SPECIES

ABSTRACT

Wildfire and mountain pine beetle infestations are naturally occurring disturbances in western forests that benefit numerous wildlife species. Black-backed Woodpeckers are emblematic of the important role these natural disturbances play in creating wildlife habitat, since they are almost completely restricted to disturbed-killed forests. However, management practices aimed at reducing the economic impact of natural disturbances can result in habitat loss for this sensitive species. Although Black-backed Woodpeckers occupy habitat created by wildfire, prescribed fire, and mountain pine beetle infestations, the relative value of these habitats in maintaining regional populations remains unknown. We studied habitat-specific adult and juvenile survival probabilities and reproductive rates between April 2008 and August 2012 in the Black Hills, South Dakota. We estimated habitat-specific adult ($n = 137$ adults) and juvenile ($n = 73$ juveniles) survival probability using Bayesian multi-state models and habitat-specific reproductive success using Bayesian nest survival models ($n = 95$ nests). We then used these estimated demographic rates to calculate asymptotic population growth rates with matrix projection models. Adult and juvenile survival and nest success were highest in habitat created by summer wildfire, intermediate in MPB infestations, and lowest in habitat created by fall prescribed fire. Consequently, mean population growth in habitat created by summer wildfire was positive, while mean population growth was negative in fall prescribed fire and mountain pine beetle infestations. Our finding that mean population growth rates were positive only in habitat created by summer wildfire underscores the need to

maintain early post-wildfire habitat across the landscape. The timing of prescribed fire, coupled with reduced size and lower severity relative to wildfire, may affect food and predator communities, contributing to lower population growth in this habitat.

Introduction

Western North American forests are shaped by natural disturbances. From small-scale canopy gaps to stand-replacing fires, disturbances are an important source of heterogeneity and species diversity in western landscapes (Connell 1978). Wildfire and mountain pine beetle (*Dendroctonus ponderosae*, hereafter MPB) infestations are of particular interest to land managers because of their widespread occurrence and economic impacts. Wildfires burned an average of 2.7 million ha annually in the decade between 2001 and 2011 (NIFC 2013) and may be increasing in size and frequency (Westerling et al. 2006). Many species benefit from wildfires, from xylophagous insects that reproduce in dead and dying trees (Saint-Germain et al. 2004) to mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*), which may benefit from improved forage (Keay and Peek 1980, Zimmerman et al. 2006). Widespread MPB infestations occur irregularly in western forests, though eruptions often impact millions of hectares and last for several years at a time (Allen et al. 2001, Raffa et al. 2008, Man 2010). Benefits of MPB infestations include a superabundant food resource (beetle larvae) that is exploited by many vertebrate and invertebrate species (Raffa et al. 2008, Drever et al. 2009, Edworthy et al. 2011) and wildlife habitat in the form of standing dead trees (Raffa et al. 2008).

Black-backed Woodpeckers (*Picoides arcticus*) have become emblematic of the positive and regenerative role these natural disturbances play in western forests. Black-backed woodpeckers are associated with habitat created by wildfire (Hutto 1995, Murphy and Lehnhausen 1998, Dudley and Saab 2007, Nappi and Drapeau 2009, Dudley et al. 2012), prescribed fire (Russell et al. 2009), and mountain pine beetle (MPB) infestations (Goggans et al. 1989, Bonnot et al. 2008, 2009). Wildfire and MPB infestations reduce timber value and have historically been considered undesirable. As a result, much effort has been put into preventing or mitigating the effects of these disturbances through fire suppression, post-fire salvage logging, and sanitation logging. Continued efforts to reduce the impacts of natural disturbance in western forests can result in habitat loss for the Black-backed Woodpecker, which is considered a sensitive species by Region 2 of the U.S. Forest Service and a Species of Greatest Conservation Concern by the State of South Dakota (South Dakota Department of Game, Fish & Parks 2006). In addition, the Black-backed Woodpecker has recently been petitioned for listing as a Threatened or Endangered species under the Endangered Species Act (Hanson et al. 2012).

Identifying effective conservation strategies for Black-backed Woodpeckers requires understanding the role of each of these major disturbances in maintaining regional populations. However, considerable uncertainty exists regarding the relative value of wildfire, prescribed fire, and MPB infestations to Black-backed Woodpeckers. Many authors consider Black-backed Woodpeckers a fire-dependent species (Dixon and Saab 2000, Hoyt and Hannon 2002, Dudley and Saab 2007, Hutto 2008, Nappi and Drapeau 2011, Dudley et al. 2012). In a survey of all major northern Rocky Mountain vegetation classes, Hutto (1995) found the Black-backed Woodpecker nearly restricted to

post-fire habitat, which led to the hypothesis that burned forest acts as a population source for Black-backed Woodpeckers while unburned forest acts as a population sink. Within post-wildfire habitat, Black-backed Woodpeckers appear to be further restricted to early post-fire conditions (Murphy and Lehnhausen 1998, Nappi and Drapeau 2009) and forest that burned at moderate or high severity (Hanson and North 2008, Hutto 2008).

Despite potential benefits to wildlife species, forest managers often focus on reducing the incidence of high severity wildfires. Prescribed fire is one tool forest managers use to meet this objective (Graham et al. 2004). An attractive feature of using prescribed fire to reduce the incidence of high-severity fire is that Black-backed Woodpeckers are known to use forests treated with prescribed fire (Russell et al. 2009), potentially allowing managers to simultaneously meet multiple management objectives. However, prescribed fire can differ from wildfire in important ways. Prescribed fires often burn at low severity, while Black-backed Woodpeckers are often associated with high-severity burns (Hanson and North 2008, Hutto 2008). Another important difference is the timing of prescribed fire. Forests are typically treated with prescribed fire during seasons when burns are easier to control, such as spring or fall months (Knapp et al. 2009), while wildfires typically burn during summer months (Brown and Hull Sieg 1996). Such differences in timing of fire can impact post-fire arthropod communities (Ferrenberg et al. 2006, Johnson et al. 2008), potentially affecting food resources for Black-backed Woodpeckers. Therefore, while habitat created by prescribed fire may appear superficially similar to habitat created by wildfire, the value of prescribed fire to Black-backed Woodpeckers remains unknown.

Although typically associated with post-fire habitat, a growing body of literature suggests Black-backed Woodpeckers are attracted to MPB infestations as well. Black-backed Woodpeckers have been documented using MPB infestations in lodgepole pine (*Pinus contorta*) forests in the Cascade Mountains of Oregon (Goggans et al. 1989) and are known to successfully reproduce in MPB infestations in ponderosa pine (*Pinus ponderosa*) forests the Black Hills of South Dakota (Bonnot et al. 2008, 2009). However, apparent use of MPB infestations is not uniform across their range. For example, Cilimburg et al. (2006) rarely detected Black-backed Woodpeckers in MPB infestations in lodgepole pine forests in the northern Rocky Mountains, despite considerable survey effort. Additionally, in a 15-year study of woodpecker responses to MPB infestations in lodgepole pine / Douglas fir (*Pseudotsuga menziesii*) forests in British Columbia, Edworthy et al. (2011) describe Black-backed Woodpeckers as ‘rare’, and subsequently excluded them from analysis. Such apparent discrepancies create uncertainty regarding the value of MPB infestations in various forest types to Black-backed Woodpeckers.

For this study, we evaluated the role of habitat created by summer wildfire, fall prescribed fire, and MPB infestations on the population dynamics of Black-backed Woodpeckers in the Black Hills, South Dakota. We first estimated adult survival, juvenile survival, and reproductive rates of Black-backed Woodpeckers occupying each of these disturbance types. We then derived habitat-specific growth rates as a function of underlying demographic parameters. By evaluating habitat-specific population growth rates, we attempt to clarify the role each of these disturbance types play in maintaining regional populations of Black-backed Woodpeckers.

Methods

Study Sites

This study was divided among several study sites in the Black Hills, South Dakota representing habitat created by wildfire, prescribed fire, and MPB infestations (Table 1.1). All wildfire sites burned during the months of June or July (hereafter we use the term wildfire and summer wildfire synonymously) and all prescribed fire sites burned during the months of September or October (hereafter we use the term prescribed fire and fall prescribed fire synonymously). All study sites were predominately monotypic stands of ponderosa pine (*Pinus ponderosa*) forest, with quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*) occurring less frequently (Hoffman and Alexander 1987). All sites were also composed of a heterogeneous mix of disturbed trees. All burned study sites (prescribed fire and wildfire) contained a mix of trees that burned at low, moderate, and high severity, although the relative proportion of trees burned at each severity category varied by study site. Similarly, all MPB study sites contained trees that had been infested < 1 year, 1-2 years, and > 2 years. All study sites also contained live, undisturbed trees. Field work began in April 2008 and continued year-round through August 2011. Additional field work at prescribed fire study sites occurred from May through August 2012.

Capture and Radio-telemetry

We used very high frequency (VHF) radio-transmitters to collect survival data from adult and juvenile Black-backed Woodpeckers. We captured adult woodpeckers using mist nets, hoop nets, and netguns. Mist nets were used with limited success only

during the 2009 and 2010 breeding seasons and were quickly abandoned in favor of the more efficient hoop net and netgun capture approach (Lehman et al. 2011).

We initially targeted adult black-backed woodpeckers for capture by searching potential study sites for signs of woodpeckers. Once captured, all adults were weighed and a 3.0 – 3.3 g transmitter was attached (Rappole and Tipton 1991). Adult black-backed woodpeckers captured weighed an average of 75g (sd = 5g), so transmitters weighed < 5% of an average adult bird's mass (Fair et al. 2010). We also marked each bird with a unique combination of colored leg bands and a uniquely numbered USFWS aluminum leg band. As VHF radio-transmitter batteries failed, we attempted to recapture previously marked individuals and replace transmitters. We supplemented recaptured birds with unmarked birds that were captured opportunistically. Adult woodpeckers with active transmitters were relocated at least once per month, though most woodpeckers were relocated more frequently (mean number of telemetry locations per month = 6).

We captured black-backed woodpecker nestlings at the nest cavity using a 'chick-snagging' device and by accessing the nest with a hole saw (Ibarzabal and Tremblay 2006). 'Chick-snagging' devices were constructed by looping fishing line through ½ inch plastic tubing. At approximately 3-days post-hatching, we attempted to capture nestlings with the chick-snagging device by entangling them in the looped fishing line and pulling them from the nest. All nestlings captured with the chick-snagging device were fitted with a unique combination of one USFWS aluminum leg band and three colored leg bands, but were not fitted with radio-transmitters. We only used the chick-snagging device during the 2009 breeding season. We captured the rest of the nestlings by using a 3-inch hole-saw to drill into the side of the cavity. Nestlings were captured

with the hole-saw method approximately 3 days prior to fledging. All nestlings captured with the hole-saw method were weighed and fitted with a unique combination of one USFWS aluminum leg band and three colored leg bands. During the 2010 breeding season, all nestlings ($n = 25$) were fitted with a 2.2 g transmitter (Rappole and Tipton 1991). During the 2011 breeding season, one randomly selected nestling from each nest was fitted with a 2.2 g transmitter until all available transmitters were used ($n = 6$). Nestlings weighed an average of 57g (sd = 10g) and transmitters weighed <5% of an average nestling's mass (Fair et al. 2010). Fledglings with active transmitters were relocated as soon as possible after emerging from the nest and every-other week thereafter. Fledglings that were not given transmitters were relocated by observing radio-marked parents provisioning individually-marked young.

Reproductive Success and Number of Young Fledged

We located nests by systematically searching study areas, by following birds to their nests (Martin and Geupel 1993), and opportunistically while collecting field data (e.g., hearing nestlings while collecting field data). We visited nests every 3-4 days during the 2009 – 2011 breeding seasons until either the nest failed or fledged young. Because of logistic constraints, nest visits were less regular during the 2008 and 2012 field seasons and the mean interval between nest visits was 4 days. During nest visits, we examined nest contents using a nest camera attached to a telescoping pole (Proudfoot 1996, Huebner and Hurteau 2007). We assumed the number of young fledged was the number of nestlings present in the nest during our last visit prior to fledging.

Estimating Adult and Juvenile Survival

We estimated adult and juvenile survival probabilities using a Bayesian multi-state mark recapture (MSMR) model (Williams et al. 2002, Converse et al. 2011). We considered a 3-state model where adult woodpeckers were classified as ‘detected alive’ (state 1), ‘detected dead’ (state 2), or ‘undetected’ (state 3). This 3-state model allowed us to include woodpeckers with both active and inactive transmitters in the same analysis. We assumed the following state-transition matrix:

		state at time t		
		1	2	3
state at time $t - 1$	1	$p_{it}\phi_{it}$	$p_{it}(1 - \phi_{it})$	$(1 - p_{it})[\phi_{it} + (1 - \phi_{it})]$
	2	0	1	0
	3	$p_{it}\phi_{it}$	$p_{it}(1 - \phi_{it})$	$(1 - p_{it})[\phi_{it} + (1 - \phi_{it})]$

where woodpeckers transition from the state along the row (the state at time $t - 1$) to the state along the column (the state at time t) with the associated cell probability. Detection probability, denoted p_{it} , is the probability woodpecker i is detected by the end of timestep t . Survival probability, denoted ϕ_{it} , is the probability woodpecker i is alive at the end of timestep t . We thus modeled a woodpecker’s state at time t as a multinomial random variable:

$$state_t \sim \text{multinomial}(\mathbf{M}_{t-1}, 1)$$

where \mathbf{M}_{t-1} is the row of the state transition matrix associated with a woodpecker’s state at time $t - 1$.

We modeled adult and juvenile detection and survival probability during each time step as a function of covariates. We assumed a 1-month time step for adult detection and survival probability and a 2-week time step for juvenile detection and survival probability. We modeled adult and juvenile detection probability as a function of whether woodpecker i had an active transmitter during timestep t (Appendix 1, *Detection Probability*). Juveniles that were color-banded but did not receive a transmitter were coded as having an inactive transmitter. We modeled monthly adult survival probability as a function of sex, season, habitat (wildfire, prescribed fire, and MPB infestation), and number of years post-fire (Appendix 1, *Adult Survival Probability*). Similarly, we estimated bi-weekly juvenile survival probability as a function of habitat, the number of years post-fire, and the number of two-week time intervals since fledging (Appendix 1, *Juvenile Survival Probability*). Juvenile detection histories began the last time interval before they fledged (i.e. the last full two-week interval they remained in the nest) and lasted through the end of March the following year. Thus, the first transition included the period when juveniles fledged from the nest.

Estimating Nest Success

We estimated daily nest survival probabilities using a Bayesian adaptation of Dinsmore et al.'s (2002) nest survival model. We modeled daily survival probability as a function of habitat and time since fire (Appendix 1, *Daily Nest Survival Probability*). Detection histories for all nests started the first day a nest was found. Detection histories for successful nests continued until the last date the nest was observed active (Stanley 2004) and detection histories for unsuccessful nests ended the first date nest failure was observed. For failed nests, we treated the days between the last observation of an active

nest and the first observation of a failed nest as missing data and imputed the response variable during this period.

Estimating the Expected Number of Young Fledged

We modeled the number of young fledged from each successful nest using a zero-truncated Poisson model. A zero-truncated Poisson model is appropriate when a count cannot be 0 (successful nests fledge at least 1 young by definition). We modeled the number of young fledged per successful nest as a function of habitat (Appendix 1, *Expected Number of Young Fledged*).

Estimating Habitat-specific Population Growth Rates

We calculated habitat-specific annual population growth rates for Black-backed Woodpeckers occupying habitat created by wildfire, prescribed fire, and MPB infestations using a 2-stage female-based pre-breeding projection matrix (Caswell 2001):

$$\mathbf{A}_h = \begin{bmatrix} m_h P_h^{Juv} & m_h P_h^{Juv} \\ P_h^{Ad} & P_h^{Ad} \end{bmatrix}$$

where m_h is habitat specific fecundity, P_h^{Juv} is the habitat-specific probability a juvenile will survive to the adult stage, and P_h^{Ad} is habitat specific annual female adult survival probability (Appendix 1, *Scaling Demographic Rates*). We evaluated how sensitive population growth rates were to variation in component demographic rates using life stage simulation analysis (Wisdom et al. 2000). Using this approach, we calculated the proportion of variation in population growth rates explained by variation in component demographic rates by regressing estimates of population growth rate against the value of the component demographic rate for each of the 300,000 simulations and calculating the coefficient of determination (r^2) from simple linear regression.

Results

Adult and Juvenile Survival

Prior to analysis, we censored detection histories of adult birds with inadequate data or whose mortality was possibly a result of capture. In total, we censored complete detection histories for 7 adults (1 that died the same month as initial capture and 6 that were recovered dead the first observation after their initial capture) and censored mortality events for 4 adults that were recovered dead the first observation after a recapture. After censoring, we estimated survival based on detection histories of 140 adult woodpeckers. Detection histories for adult birds consisted of 369, 406, and 164 cumulative months at risk of dying in habitat created by wildfire, MPB infestations, and prescribed fire, respectively. We were unable to determine the source of mortality for the majority of adult birds recovered dead, though one transmitter was recovered in the vicinity of a Northern Goshawk (*Accipiter gentilis*) nest and apparent Cooper's Hawk (*Accipiter cooperii*) feathers were recovered close to another transmitter.

Mean annual adult survival probability was greatest in habitat created by wildfire, intermediate in habitat created by MPB infestations, and lowest in habitat created by prescribed fire. For example, mean annual adult female survival probability was 0.75 (95% CI = [0.54, 0.91]) in 2-year post-wildfire habitat, 0.65 (95% CI = [0.45, 0.83]) in MPB infestations, and 0.50 (95% CI = [0.20, 0.79]) in 2-year post-prescribed fire habitat (Fig. 1.1). Mean annual adult survival probability was nearly identical between sexes and declined slightly as time since fire increased. Finally, mean monthly survival probability was slightly greater during the breeding season relative to the non-breeding season (Fig. 1.2).

Prior to analysis, we censored the detection history for 1 juvenile that died before fledging. After censoring, we estimated juvenile survival from detection histories of 72 woodpeckers. Detection histories for juvenile woodpeckers consisted of 119, 139, and 44 cumulative time steps (2-week intervals) at risk of dying in habitat created by wildfire, MPB infestations, and prescribed fire, respectively. We were unable to determine the source of mortality for the majority of juvenile birds recovered dead, though one transmitter (and color bands) was recovered from a Great Horned Owl (*Bubo virginianus*) pellet, another was found in the vicinity of a Red-tailed Hawk (*Buteo jamaicensis*) nest, and another was recovered in a squirrel midden.

Patterns of juvenile survival probability closely tracked patterns of adult survival probability. The mean probability of juvenile Black-backed woodpeckers surviving to the adult stage class was greatest in habitat created by wildfire, intermediate in habitat created by MPB infestations, lowest in habitat created by prescribed fire, and declined as the time since fire increased. For example, the mean probability a juvenile survived to the adult stage class (which we assumed took 42 weeks, Appendix 1) was 0.64 (95% CI = [0.25, 0.91]) in 2-year post-wildfire habitat, 0.35 (95% CI = [0.11, 0.62]) in MPB infestations, and 0.15 (95% CI = [0, 0.55]) in 2-year post-prescribed fire habitat (Fig. 1.3). The mean probability of juvenile survival was lowest immediately after fledging, and increased as the number of time steps fledged increased (Fig. 1.4).

Nest Success and Number of Young Fledged

We suspected some nest failures were related to capture at the nest cavity with the hoop net. We thus censored 14 nest failures (13 that occurred the first visit following capture with the hoop net and 1 that occurred because of capture-related adult mortality),

though we retained detection histories through the last day each nest was observed active. We estimated the probability of a nest successfully fledging at least one young from 95 nests: 40 in habitat created by wildfire; 35 in MPB infestations; and 20 in habitat created by prescribed fire. We were unable to determine the cause of most nest failures, though a prairie rattlesnake (*Crotalus viridis*) was observed in one failed nest and a pair of adult Black-backed Woodpeckers was observed defending a nest from a squirrel on a separate occasion.

Patterns of nest success followed similar patterns as adult and juvenile survival in relation to habitat. The mean probability of a nest fledging at least one young was greatest in habitat created by wildfire, intermediate in habitat created by MPB infestations, lowest in habitat created by prescribed fire, and decreased as time since fire increased. For example, the mean probability of successfully fledging at least 1 young was 0.72 (95% CI = [0.55, 0.86]) in 2-year post-wildfire habitat, 0.59 (95% CI = [0.40, 0.77]) in MPB infestations, and 0.45 (95% CI = 0.23, 0.67]) in 2-year post-prescribed fire habitat (Fig. 1.5).

We estimated the expected number of young fledged per successful nests from 50 successful nests: 23, 18, and 9 in habitat created by wildfire, MPB infestations, and prescribed fire, respectively. The expected number of young fledged per successful nest was greatest in habitat created by prescribed fire (mean fledged = 2.05, 95% CI = [1.44, 2.95]) and nearly identical between habitat created by wildfire (mean fledged = 1.80, 95% CI = [1.44, 2.28]) and MPB infestations (mean fledged = 1.81, 95% CI = 1.41, 2.35]).

Habitat-specific Population Growth Rates

Mean population growth rates were positive only in habitat created by wildfire. For example, $\bar{\lambda} = 1.16$ in 2-year post-wildfire habitat and 84% of the posterior density of estimated population growth rates was > 1 (Fig. 1.6). Mean population growth rates were negative in habitat created by MPB infestations ($\bar{\lambda} = 0.84$) and 10% of the posterior density of estimated population growth rates in MPB infestations was > 1 . Mean population growth rates were also negative in habitat created by prescribed fire. For example, $\bar{\lambda} = 0.57$ in 2-year post-prescribed fire habitat and $< 1\%$ of the posterior density of estimated population growth rates was > 1 . Variation in adult survival rates consistently explained the most variation in population growth rates (Table 1.2) and the probability a juvenile survived to the adult stage class was also an important source of variation in population growth rates. Fecundity parameters explained very little variation in population growth rates, particularly in habitat created by prescribed fire.

Discussion

This study helps clarify the relative value of wildfire, prescribed fire, and MPB infestations in maintaining regional populations of Black-backed Woodpeckers in the Black Hills, South Dakota. Mean population growth rates were positive only in habitat created by summer wildfire, while mean population growth rates were negative in habitats created by MPB infestations and fall prescribed fire. These findings support long-standing hypotheses that recently burned forests are population sources for Black-backed Woodpeckers, while unburned forests, such as MPB infestations, may be population sinks (Hutto 1995). Further, the negative population growth we observed in

habitat created by fall prescribed fire indicate this management tool, under the conditions we evaluated, is not a viable substitute for summer wildfire.

Habitat created by prescribed fire differed from habitat created by wildfire at our study sites in two primary ways, both of which may harbor important biological consequences. First, managers treated sites with prescribed fire in September or October. In contrast, wildfire sites burned during June and July. This difference in timing may affect post-fire arthropod communities. For example, some species of wood-boring beetles have sensors capable of detecting compounds emitted from burning wood (Schütz et al. 1999) and can rapidly colonize a recently burned forest. However, these beetles may not be active during autumn months and thus may not be able to immediately colonize late-season prescribed burns. As a consequence, wood-boring beetle abundance in habitat created by prescribed fire may be low relative to habitat created by wildfire, leading to different food resources for Black-backed Woodpeckers (*Chapter 3*). Second, the prescribed fire study sites tended to be smaller in area and burned at lower severity relative to the wildfire study sites. This may result in different predator communities between the two types of disturbed forest because many species respond differently to different burn severities (Smucker et al. 2005). These potential differences between habitats created by prescribed fire and wildfire may impact demographic rates of Black-backed Woodpeckers.

Our sensitivity analysis provides insight into how these potential differences may lead to the lower growth rates observed in habitat created by prescribed fire. In all habitats, Black-backed Woodpecker population growth rates were most sensitive to changes in adult and juvenile survival. If the timing of prescribed fire affects wood-

boring beetle abundance, this may affect the food resources available to Black-backed Woodpeckers, which in turn may impact survival rates. This may particularly affect juvenile survival rates, since recently fledged woodpeckers rely on provisioning from adults for several weeks post-fledging. Adult and juvenile survival rates may also be affected by potential differences in predator communities between habitats. For example, Northern Goshawks, a known predator of Black-backed Woodpeckers in the Black Hills (C.T. Rota, *unpublished data*), preferentially nest in closed canopy forest (Squires and Reynolds 1997) and may be less abundant in severely burned forest relative to unburned forest or forest that burned at low severity. Such sit-and-wait predators may also forage less effectively in low canopy-cover forest because they have fewer opportunities for concealment.

We were surprised that mean population growth rates were negative in habitat created by MPB infestations, since woodpeckers readily occupy such habitat in ponderosa pine forests in the Black Hills and have been demonstrated to successfully breed in such habitat (Bonnot et al. 2008, 2009). However, our finding is consistent with previous hypotheses that Black-backed Woodpeckers are a fire-dependent species and that unburned forest may act as sink habitat when recent forest burns are not available (Hutto 1995). Our findings may also help explain regional differences in the propensity for Black-backed Woodpeckers to use MPB infestations. Black-backed Woodpeckers are only documented using MPB infestations in lodgepole pine forests in the Cascade Mountains of Oregon (Goggans et al. 1989) and in ponderosa pine forests in the Black Hills of South Dakota (Bonnot et al. 2008, 2009). Both of these populations are isolated (Pierson et al. 2010) and recently burned forest may be relatively rare across the

landscape, forcing the Oregon and Black Hills populations to settle in MPB infestations. In contrast, Black-backed Woodpeckers rarely use MPB infestations in more contiguous portions of their range, such as lodgepole pine forests in the northern Rocky Mountains (Cilimburg et al. 2006) and lodgepole pine / Douglas fir forests in British Columbia (Edworthy et al. 2011), perhaps because recently burned forest is more plentiful.

Habitat created by MPB infestations likely harbors some value to Black-backed Woodpeckers, even if mean population growth rates in this habitat were negative. Indeed, 95% credible intervals of estimated growth rates overlapped 1, suggesting the potential for positive population growth in this habitat during some years. We suggest that, on average, Black-backed Woodpecker population growth rates in MPB infestations are intermediate between early post-wildfire habitat and undisturbed forest. Our models of adult, juvenile, and nest survival probability all predicted declines in these demographic rates as a function of years post-fire, which will lead to decreased population growth rates as post-wildfire habitat ages. Mountain pine beetle infestations may thus improve in relative value to Black-backed Woodpeckers as post-wildfire habitat ages and may help buffer population declines when recent forest burns are not available.

The differences in Black-backed Woodpecker population growth rates between habitat created by wildfire and MPB infestations reflects likely historic disturbance patterns in the Black Hills. Allen et al. (2001) describe 7 discrete MPB outbreaks in the Black Hills during the 20th century, including the current infestation. The extent of individual outbreaks can be larger than the total forest area burned in any given year. However, during most years, MPBs exist at ‘endemic’ levels, which Allen et al. (2001) describe as < 1 tree killed per acre per year. In contrast, Brown and Hull Sieg (1996)

predicted a 16 year pre-settlement mean fire-return interval for ponderosa pine forests in Jewel Cave National Park, South Dakota. A mean fire-return interval reflects the average time between fires at any given location, though fires probably burned different portions of the Black Hills during most years. Evidence suggests these fires likely burned at mixed severity, killing some trees while allowing others to live. The 16 year mean fire return interval estimated in the Black Hills is longer than in many ponderosa pine forests in the western US (Agee 1993, Brown and Hull Sieg 1996), which may allow greater accumulation of ladder fuels and subsequent greater levels of tree mortality during wildfires. Additional evidence for a mixed-severity fire regime comes from early timber surveys in the Black Hills, which documented extensive areas of fire-killed trees (Shinneman and Baker 1997). Finally, recent research suggests ponderosa pine forests in general were probably subject to mixed-severity fire regimes (Baker et al. 2007, Hessburg et al. 2007). Thus, wildfires that resulted in at least minimal tree mortality were probably much more predictable than widespread MPB infestations in the Black Hills.

Wildfire and MPB infestations are naturally occurring disturbances, but prescribed fire is a human-caused disturbance that may result in post-fire conditions that differ significantly from naturally occurring wildfires. Such human caused disturbances may result in ecological traps if settlement cues are decoupled from the ultimate fitness consequences of settling in a particular habitat (Hildén 1965, Schlaepfer et al. 2002). Indeed, forests treated with prescribed fire appear superficially similar to post-wildfire conditions, and Black-backed Woodpeckers have been documented using such habitat (Russell et al. 2009). Robertson and Hutto (2006) provide two criteria to demonstrate

that a habitat is an ecological trap. One criterion is that a reasonable surrogate of fitness differs between two or more habitats. We believe population growth rates are a reasonable surrogate for individual fitness because this measure is a function of both survival probability and reproductive success, both demographic parameters that impact the genetic contribution of individuals to future generations (Brommer et al. 2004). Consequently, fitness is likely lower in habitat created by prescribed fire relative to habitat created by wildfire. The other criterion Robertson and Hutto (2006) outline is that individuals demonstrate an equal or greater preference for trap habitat relative to other habitats that provide greater fitness benefits, which we did not measure. However, we envision three scenarios regarding the role of prescribed fire for Black-backed Woodpeckers. In one scenario, wildfire is preferred over prescribed fire, in which case forest treated with prescribed fire may simply act as a sink habitat. In the other two scenarios, prescribed fire is preferred over wildfire, or Black-backed Woodpeckers settle in prescribed fire or wildfire with equal preference. In either case, habitat created by prescribed fire could act as an ecological trap. Although population growth rates were negative in habitat created by prescribed fire, more work is needed to determine the potential impact on overall Black-backed Woodpecker population growth in the Black Hills, since prescribed fires tend to cover a smaller spatial extent relative to wildfire.

We do not wish to completely discard the utility of either prescribed fire or MPB infestations as important disturbance agents for Black-backed Woodpeckers. Large, severe wildfires are not likely to gain widespread acceptance on public lands, and prescribed fire may be the only way to introduce fire into the landscape at a large scale. Prescribed fire is a flexible management tool that can be applied in a variety of ways. For

example, managers can vary factors including timing, severity, and extent. We recommend further research to determine the mechanisms leading to negative population growth of Black-backed Woodpeckers in habitat created by prescribed fire so forests can be treated in an appropriate manner. In particular, we suggest further research to understand how the timing of prescribed fire may impact post-fire wood-boring beetle abundance. In addition, we recommend further research examining how predator communities may change in response to burn size and severity.

Our finding that Black-backed Woodpecker mean population growth rates were positive only in habitat created by wildfire demonstrates the importance of early post-fire habitat. While this study focused on how Black-backed Woodpecker population growth rates vary across disturbance types, they are but one member of a community of post-fire species. An important member of early post-fire communities are wood boring beetles (Buprestidae, Cerambycidae), which eat the cambium of trees weakened and killed by fire (Saint-Germain et al. 2004). Wood-boring beetles, in turn, are an important food source for many insectivores that occupy early post-fire habitat, including Black-backed Woodpeckers (Murphy and Lehnhausen 1998, Costello et al. 2011). Black-backed Woodpeckers do not just rely on other members of post-fire communities for food: they also create conditions that allow other species to colonize post-fire habitat. Many bird species in general, and woodpeckers in particular, are increasingly recognized as ecosystem engineers because of their propensity to build cavities that are subsequently used by other species (Sekercioglu 2006). Indeed, many species that occupy relatively old post-wildfire forest, such as Lewis's Woodpeckers (*Melanerpes lewis*), a species of management concern (South Dakota Department of Game, Fish & Parks 2006), re-use

cavities created by primary cavity excavators such as Black-backed Woodpeckers (Gentry and Vierling 2008). Thus, conservation actions focused on maintaining Black-backed Woodpecker habitat will undoubtedly benefit many other species.

Our study is the first to evaluate the demographic response of Black-backed Woodpeckers to a range of disturbance conditions. Our results indicate this sensitive species is dependent on early post-wildfire habitat in the Black Hills, South Dakota, underscoring the importance of ensuring recently burned forest is present across the landscape. Ensuring the existence of early post-wildfire habitats will benefit not just Black-backed Woodpeckers, but a whole suite of fire-adapted species.

Table 1.1: Study sites used to evaluate Demography of Black-backed Woodpeckers in the Black Hills, South Dakota, USA.

Site	Habitat	Coordinates	Size (Ha) ^a	Month / Year Disturbed ^b	Years Included in Study
Ricco	Wildfire	44°13'N, 103°25'W	1,602	July 2005	2008, 2010
Box Elder	Wildfire	44°9'N, 103°24'W	129	July 2007	2008, 2009
4-Mile	Wildfire	43°41'N, 103°26'W	955	June 2007	2008 - 2011
Bullock	Rx Fire	44°0'N, 103°30'W	486	Sept. 2008	2010 – 2012
Bitter	Rx Fire	43°58'N, 103°26'W	304	Oct. 2010	2012
Headquarters West	Rx Fire	43°34'N, 103°30'W	255	Sept. 2009	2011
American Elk	Rx Fire	43°61'N, 103°49'W	1376	Oct. 2010	2012
Norbeck	MPB	43°50'N, 103°30'W	> 213 ^c	1998	2008
Bear Mountain	MPB	43°51'N, 103°45'W	> 48 ^c	Before 1995	2008 – 2011
East Slate Creek	MPB	43°58'N, 103°44'W	> 1,303 ^d	Before 1995	2008 - 2011
Deerfield Lake	MPB	44°00'N, 103°49'W	> 169 ^c	Before 1995	2008
Medicine Mountain	MPB	43°52'N, 103°42'W	> 1,748 ^d	Before 1995	2009 – 2011

- ^a Size of MPB infestations Calculated from FHP Aerial Detection Surveys, available at <http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3_041629> (accessed Feb. 13, 2013). This is an estimate of the minimum total area impacted by MPBs in each study site in a given year.
- ^b The first year MPB infestations were detected in FHP Aerial Detection Surveys. Note there is no aerial detection data prior to 1995.
- ^c calculated from 2008 FHP Aerial Detection Survey
- ^d calculated from 2010 FHP Aerial Detection Survey

Table 1.2: Proportion of variation in Black-backed Woodpecker population growth rates in habitat created by wildfire, prescribed fire, and mountain pine beetle (MPB) infestations explained by adult survival, juvenile survival, nest success, and number of young fledged.

Demographic Rate	Variation Explained (r^2)		
	Wildfire	MPB Infestation	Prescribed Fire
Adult Survival	0.34	0.59	0.79
Juvenile Survival	0.48	0.31	0.17
Nest Success	0.08	0.05	0.01
No. Young Fledged	0.09	0.04	0.01

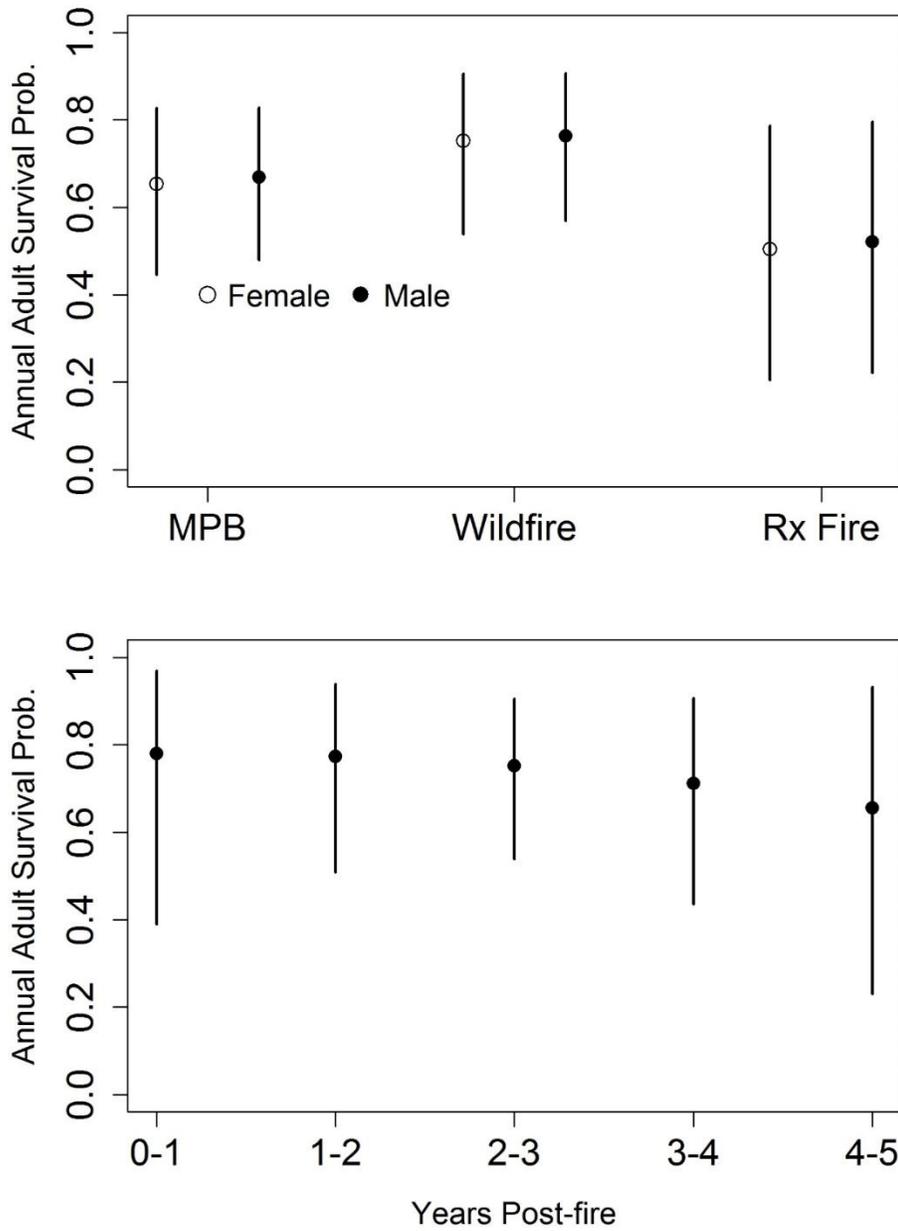


Figure 1.1: *Upper panel:* mean posterior distribution \pm 95% credible intervals of adult male and female Black-backed Woodpecker annual survival rates in habitat created by wildfire, prescribed (Rx) fire, and mountain pine beetle (MPB) infestations in the Black Hills, SD, USA. Plots of annual survival rates assume habitat created by wildfire and prescribed fire are both 2 years post-fire. *Lower panel:* mean posterior distribution \pm 95% credible intervals of annual survival probability as a function of time since wildfire. This figure assumes an adult female in habitat created by wildfire, but the trend is similar in habitat created by prescribed fire.

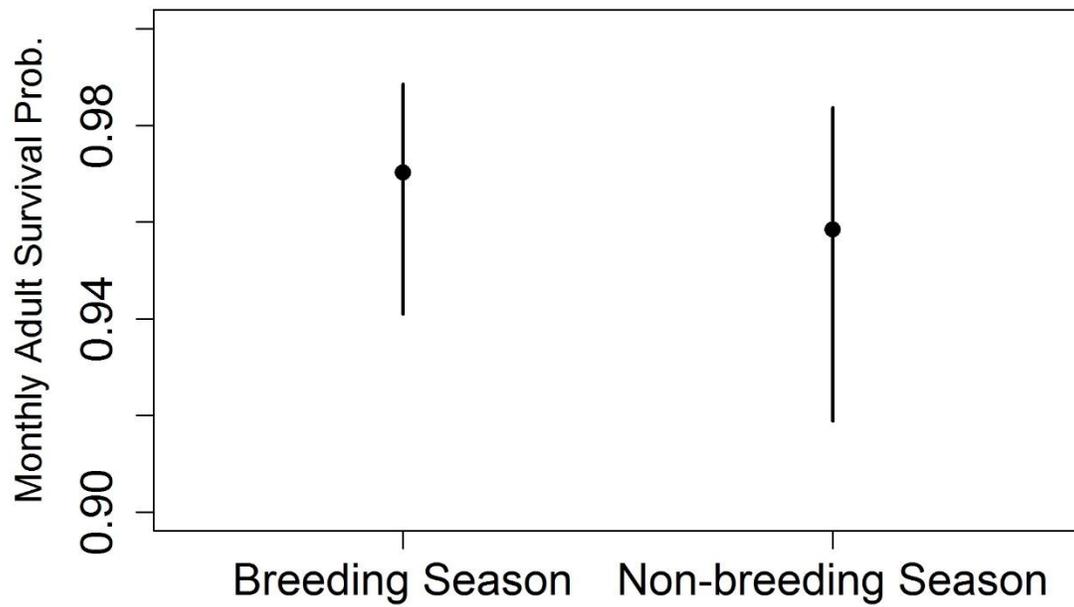


Figure 1.2: Mean posterior distribution \pm 95% credible intervals of adult Black-backed Woodpecker monthly survival probability as a function of season in the Black Hills, SD, USA. The breeding season is defined as April – September and the non-breeding season is defines as October – March. This figure assumes an adult female in habitat created by mountain pine beetle infestations, but the trend is similar across habitats.

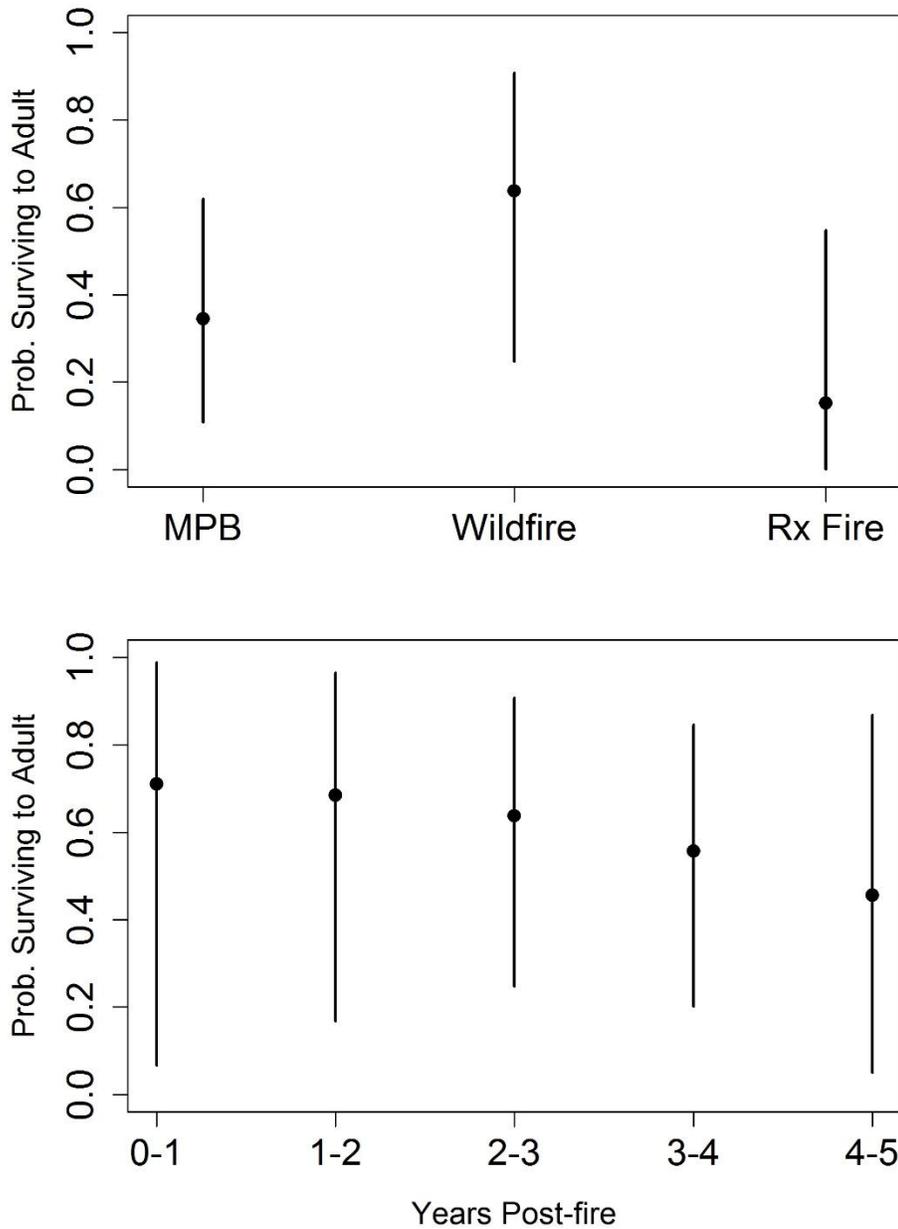


Figure 1.3: *Upper panel:* mean posterior distribution \pm 95% credible intervals of the probability juvenile Black-backed Woodpeckers survive to the adult age-class in habitat created by wildfire, prescribed (Rx) fire, and mountain pine beetle (MPB) infestations in the Black Hills, SD, USA. Plots of survival probabilities assume habitat created by wildfire and prescribed fire are both 2 years post-fire. *Lower panel:* mean posterior distribution \pm 95% credible intervals of the probability a juvenile Black-backed Woodpecker survives to the adult age-class as a function of time since wildfire. This figure assumes a juvenile in habitat created by wildfire, but the trend is similar in habitat created by prescribed fire.

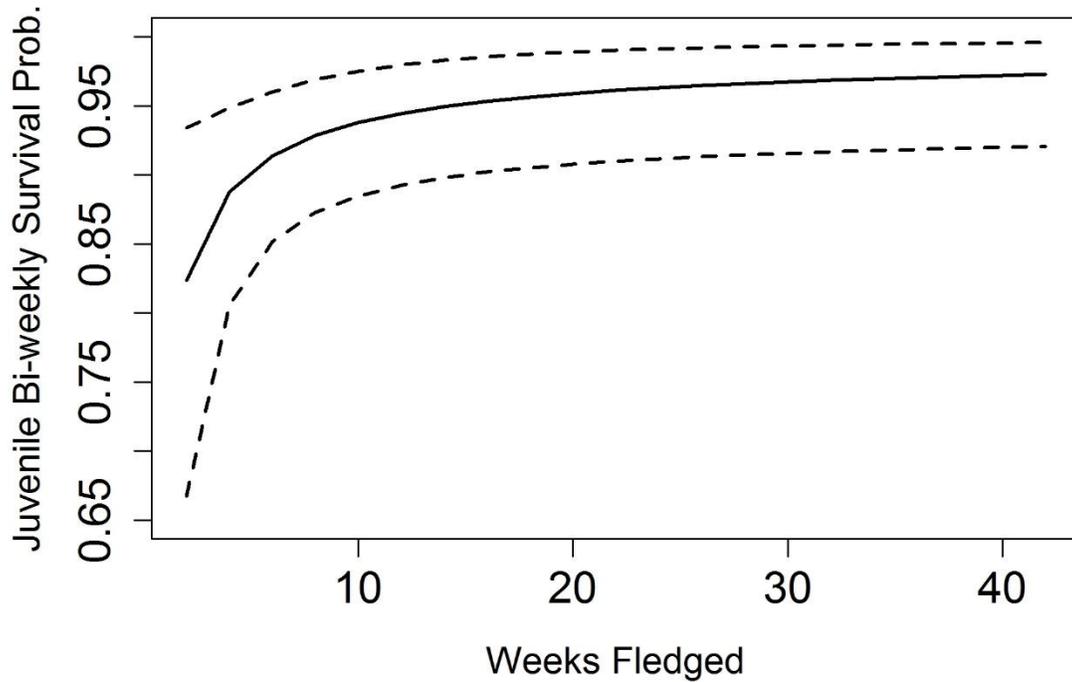


Figure 1.4: Mean posterior distribution \pm 95% credible intervals of biweekly juvenile Black-backed Woodpecker survival probability as a function of the number of weeks fledged (1 time step = 2 weeks) in the Black Hills, SD, USA. This figure shows that recently fledged young have the lowest survival probability and that survival probability increases the longer a juvenile has been fledged from the nest. This figure assumes juvenile woodpeckers occupying habitat created by MPB infestations, but the trend is similar in habitat created by wildfire and prescribed fire.

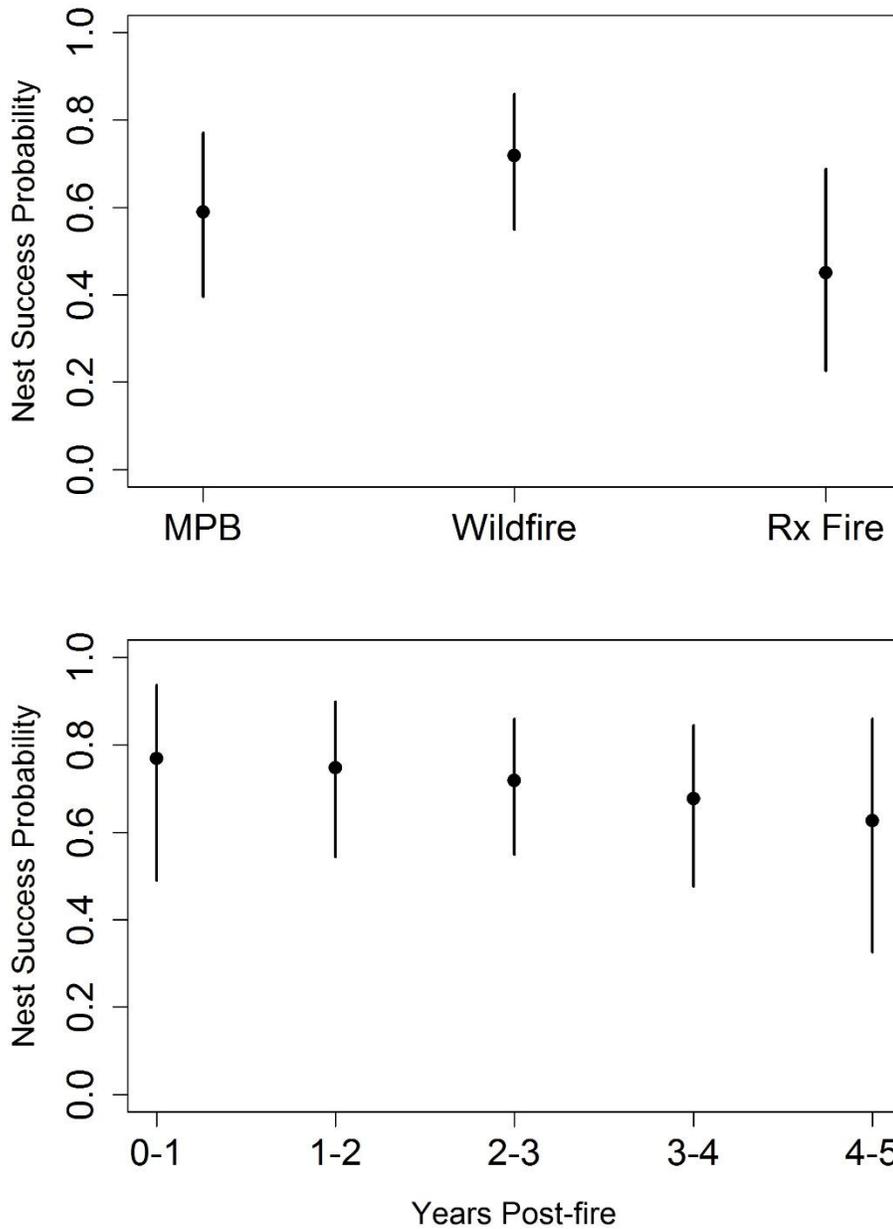


Figure 1.5: *Upper panel:* mean posterior distribution \pm 95% credible intervals of the probability a Black-backed Woodpecker nest successfully fledged at least 1 young in habitat created by wildfire, prescribed (Rx) fire, and mountain pine beetle (MPB) infestations in the Black Hills, SD, USA. This plot assumes nests in habitat created by wildfire and prescribed fire are both 2 years post-fire. *Lower panel:* mean posterior distribution \pm 95% credible intervals of the probability a nest successfully fledges at least 1 young as a function of time since fire. This figure assumes a nest in habitat created by wildfire, but the trend is similar in habitat created by prescribed fire.

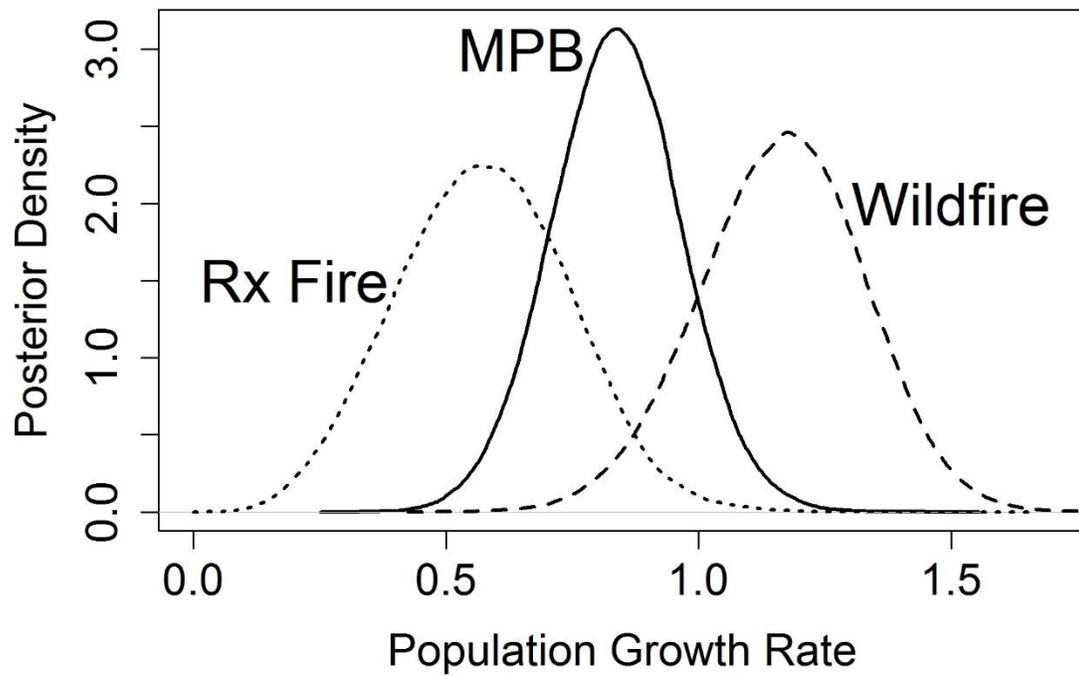


Figure 1.6: Posterior densities of population growth rates estimated from Black-backed Woodpeckers occupying habitat created by wildfire, mountain pine beetle (MPB), and prescribed (Rx) fire in the Black Hills, SD.

CHAPTER 2: SPACE USE AND HABITAT ASSOCIATIONS OF BLACK-BACKED WOODPECKERS (*PICOIDES ARCTICUS*) OCCUPYING DISTURBED FORESTS IN THE BLACK HILLS, SOUTH DAKOTA

ABSTRACT

Black-backed Woodpeckers (*Picoides arcticus*) are a disturbance-dependent species that occupy recently burned forest and mountain pine beetle (MPB) infestations. Forest management practices that reduce the amount of disturbance-killed forest may lead to habitat loss for Black-backed Woodpeckers, which have recently been petitioned for listing under the Endangered Species Act. Effective conservation action requires knowledge of habitat associations and spatial requirements of this sensitive species. We studied home range size and resource selection of Black-backed Woodpeckers occupying habitat created by summer wildfire, fall prescribed fire, and MPB infestations in the Black Hills, South Dakota. We studied home range size and resource selection by attaching radio-transmitters to adult Black-backed Woodpeckers. We estimated home range size using fixed kernel density techniques ($n = 28$ in habitat created by summer wildfire, $n = 19$ in habitat created by fall prescribed fire, and $n = 27$ in MPB infestations). We evaluated resource selection by comparing vegetation characteristics at used and available trees within each woodpecker's home range using a Bayesian random-effects discrete choice model ($n = 5$ in habitat created by summer wildfire, $n = 16$ in habitat created by fall prescribed fire, and $n = 8$ in habitat created by MPB infestations). Home range size was smallest in 1 - 2 year post summer wildfire habitat (mean home range size = 79 ha) and 2-year post fall prescribed fire habitat (mean home range size = 143 ha). Home range size was intermediate in MPB infestations (mean home range size = 307 ha) and was greatest in 3-4 year post fire habitat (mean summer wildfire home range size =

430 hectares, mean fall prescribed fire home range size = 460 ha). The relative probability that a Black-backed Woodpecker used a tree within its home range increased with increasing diameter at breast height (DBH) and basal area, and was greatest on disturbance-killed trees. These results suggest 1-2 year post summer wildfire habitat may have the greatest relative value to Black-backed Woodpeckers, and that MPB infestations may be more important as post-fire habitats age. Black-backed Woodpeckers were rarely located in 1-year post fall prescribed fire habitat, suggesting that prescribed fires conducted during autumn months may have little value to Black-backed Woodpeckers. We recommend the most efficient strategy for maintaining regional populations of Black-backed Woodpeckers is to retain patches of 1-2 year post summer wildfire habitat by exempting portions of recently burned forest from salvage logging. Recently burned forest patches should be at least 40 – 200 hectares and primarily composed of $\geq 27 \text{ m}^2$ basal area / ha of trees that burned at moderate or high severity, with at least 40% of the basal area composed of trees $\geq 27 \text{ cm DBH}$.

Introduction

Black-backed woodpeckers (*Picoides arcticus*) are a disturbance dependent species that rely on recently killed forest habitat. Throughout their range, Black-backed Woodpeckers are most strongly associated with habitat created by wildfire (Bock and Lynch 1970, Hutto 1995, Murphy and Lehnhausen 1998, Hobson and Schieck 1999, Hoyt and Hannon 2002, Nappi et al. 2003, Nappi and Drapeau 2009). Additionally, Black-backed Woodpeckers are attracted to habitat created by prescribed fire (Russell et al. 2009), though recent research suggests prescribed fire may act as an ecological trap

under certain circumstances (*Chapter 1*). Despite this burn-centric association, mountain pine beetle (*Dendroctonus ponderosae*, MPB) infestations also play an important role in creating habitat for Black-backed Woodpeckers, particularly in isolated populations occurring in the Black Hills (Bonnot et al. 2008, 2009) and the Cascade Mountains (Goggans et al. 1989). Finally, Black-backed Woodpeckers occupy undisturbed forest (Mohren 2002, Tremblay et al. 2009), though often only when recently burned forest is not available (Hoyt and Hannon 2002). Even in these situations, Black-backed Woodpeckers may often be associated with small patches of recently killed forest (Hutto 1995, S. Mohren, *personal communication*).

Although disturbances such as wildfire and beetle infestations are naturally occurring in most western forests, these disturbances reduce the quality and quantity of timber and have historically been considered undesirable. As a result, much effort has been put into preventing or mitigating the effects of natural disturbances through fire suppression, post-fire salvage logging, or sanitation logging in insect infestations. Continued efforts to reduce the impacts of natural disturbance in western forests may result in habitat loss for Black-backed Woodpeckers, which is now considered a species of management concern throughout its range. In particular, Black-backed Woodpeckers are considered a sensitive species by Region 2 of the U.S. Forest Service and a Species of Greatest Conservation Concern by the State of South Dakota (South Dakota Department of Game, Fish & Parks 2006). In addition, the Black-backed Woodpecker has recently been petitioned for listing as Threatened or Endangered under the Endangered Species Act (Hanson et al. 2012).

Effective conservation strategies require detailed knowledge of resource selection patterns of this sensitive species. Many studies have evaluated resource selection in Black-backed Woodpeckers, particularly in response to burn severity, pre-burn forest conditions, and snag density. Black-backed Woodpeckers select foraging habitat (Murphy and Lehnhausen 1998, Hanson and North 2008) and occur with greater probability (Hutto 2008) and abundance (Koivula and Schmiegelow 2007) in forests that burned at high severity. Black-backed Woodpeckers also respond to pre-disturbance forest conditions and disproportionately forage on the largest diameter trees available (Nappi et al. 2003, Nappi and Drapeau 2011, Dudley et al. 2012). Finally, in unburned forest, Black-backed Woodpeckers are most likely to occur (Goggans et al. 1989) and are more abundant (Settingington et al. 2000, Mohren 2002) in areas with relatively high snag densities.

Most of this research has focused on understanding patterns of Black-backed Woodpecker resource selection in recently burned forest. Consequently, little is known about resource selection patterns in MPB infestations or in habitat created by prescribed fire. For example, although Bonnot et al. (2009) determined that nest site selection was correlated with food resources in MPB infestations, the extent to which foraging woodpeckers select recently infested trees relative to older beetle-killed trees remains unknown. Further insight into resource selection patterns may be gained by studying how resource selection varies among individuals. For example, low variation in the strength and direction of selection for a particular resource among individuals may indicate that a particular resource is consistently used. Such knowledge may guide

development of silvicultural treatments that both limit the economic impact of natural disturbances while simultaneously conserving critical Black-backed Woodpecker habitat.

An understanding of which resources are selected by Black-backed Woodpeckers is complemented by an understanding of the spatial requirements of these woodpeckers. Black-backed Woodpeckers are a highly mobile species with potentially large home ranges, making estimation of home range size challenging. Despite these challenges, Dudley and Saab (2007) report home range size for 4 woodpeckers in 6-8 year post-fire habitat and Goggans et al. (1989) report home range size for 3 woodpeckers in habitat created by MPB infestations. However, home range size is likely to vary across habitats and through time, particularly as the time since fire increases. Knowledge of such variation will enable managers to include spatial components into silvicultural prescriptions.

For this study we evaluated resource selection and home range size in Black-backed Woodpeckers occupying habitat created by wildfire, prescribed fire, and MPB infestations in the Black Hills, South Dakota. We evaluated resource selection at the individual level, effectively treating individual woodpeckers as the sample unit, and scaled individual-level selection to the population level. In this way, we evaluated population-level patterns of resource selection and evaluate variation in resource selection patterns across woodpeckers. We also estimated home range size of Black-backed Woodpeckers and evaluated how home range size varied among habitats and as burned forests age.

Methods

Study Sites

This study was divided among numerous study sites in the Black Hills, South Dakota representing habitat created by wildfire, prescribed fire, and MPB infestations (Table 2.1). All wildfire sites burned in June or July (hereafter we use the term wildfire and summer wildfire synonymously) and all prescribed fire sites were treated during September or October (hereafter we use the term prescribed fire and fall prescribed fire synonymously). All study sites were composed primarily of monotypic ponderosa pine forest (*Pinus ponderosa*) forest, with quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*) occurring less frequently (Hoffman and Alexander 1987).

Capture and Radio-telemetry

We collected Black-backed Woodpecker home range data by fitting VHF radio-transmitters to adult birds. We initially targeted Black-backed woodpeckers for capture by playing audio recordings of territorial calls at potential study sites. Once found, we captured woodpeckers with mist nets, hoop nets, and netguns. Mist nets were used with limited success only during the 2009 and 2010 breeding seasons and were quickly abandoned in favor of the more efficient hoop net and netgun capture approach (Lehman et al. 2011). Hoop nets were an efficient capture method only during the breeding season when woodpeckers were actively attending cavities. Alternatively, the netgun allowed capture away from nest cavities and outside the breeding season. Once captured, we weighed all birds and fitted a small (3.0 – 3.3 g) transmitter (Rappole and Tipton 1991). 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 (Fair et al. 2010). Additionally, we fit all birds with a unique combination of colored leg bands, including a uniquely numbered U.S. Fish & Wildlife Service aluminum leg band. As VHF radio-transmitters died, we attempted to recapture previously marked individuals and replace transmitters. We supplemented recaptured birds with unmarked birds that were captured opportunistically during trapping events.

We located woodpeckers at least 2 times weekly to ensure ≥ 30 telemetry locations necessary to estimate home range size before transmitters failed (Seaman et al. 1999). All telemetry locations were spaced ≥ 4 hours apart. We assumed spacing telemetry locations ≥ 4 hours apart was adequate to ensure independence between successive locations because woodpeckers could (and did) traverse even the largest home range during this time interval. We located woodpeckers via homing and all trees physically occupied by woodpeckers (hereafter 'used' trees) were visually confirmed. During the nesting period, we excluded all telemetry observations made at the nest cavity to address resource selection patterns beyond the nest cavity and to ensure home range size estimates were not biased because of repeated observations at the nest cavity. Whenever woodpeckers were located, we recorded spatial coordinates (Universal Transverse Mercator Zone 13) using a hand-held GPS unit and flagged the tree for future vegetation sampling.

Estimating Home Range Size

We collected home range data on Black-backed Woodpeckers between April 2008 and August 2011, and again between May 2012 and August 2012. We only included woodpeckers in the home range analysis if we obtained ≥ 30 telemetry locations

during a 12-month period, which we defined as April 1 through March 31. We classified the number of years post-fire based on this 12 month period, with the 1st year post-fire occurring the 1st April following a burn. For example, we considered telemetry locations gathered in the 4-Mile study site between April 1, 2008 and March 31, 2009 as 1-year post-fire (4-Mile burned in June 2007). We began the 12-month period on April 1 because this is the approximate date woodpeckers begin excavating cavities (recognizing that Black-backed Woodpeckers make territorial settlement decisions year-round, C.T. Rota, *personal observation*). We clumped winter and summer telemetry locations during the same 12-month period together because there was no clear difference in space use between seasons and because of small sample sizes during winter months ($n = 3$ wildfire winter home ranges and $n = 3$ prescribed fire winter home ranges). We did not attempt to classify the age of MPB infestations because infestations were not one discrete disturbance and woodpeckers often used infestations of several different ages.

We estimated home-range size using kernel density techniques (Worton 1989). We estimated home ranges using the ‘ks’ package in Program R (R Core Team 2012), which assumes a bivariate normal density fixed kernel. We used the ‘plug-in’ method for calculating the bandwidth parameter (Millsbaugh et al. 2006). Home range size estimates were based on 99% home range contours.

Vegetation Measurements

We collected vegetation data at used and available focal trees within the home range of individual Black-backed Woodpeckers. We define focal trees as either the tree on which we observed the woodpecker (a used focal tree) or the tree closest to a randomly generated point (an available focal tree, see below). We observed woodpeckers

using saplings (woodpeckers used trees as small as 4.3 cm), so we assumed any tree >1 cm DBH was available. We defined the area available to each woodpecker based on the 99% home range contour. We paired each used tree with a randomly available tree, which were selected by generating random points within 99% home range boundaries and then selecting the tree closest to each randomly generated point. At all used and available trees, we recorded diameter at breast height (DBH), whether the tree was alive, and categorized trees based on burn severity or age of MPB infestations. We classified burned trees as low severity (scorching restricted to below breast height), moderate severity (scorching above breast height but some canopy left unburned), high severity (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 1-2 years old) or ‘gray hits’ (beetle-killed trees that have lost all of their needles, generally >2 years old). In addition to measuring characteristics of used and available trees, we also measured 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 and proportion of dead trees. We collected vegetation data from home ranges used by woodpeckers from May 2010 to August 2011 and from May 2012 to August 2012. Consequently, we collected vegetation data in 3-4 year post-wildfire and 2-4 year post-prescribed fire habitat.

Modeling Resource Selection

We modeled the relative probability a tree within a woodpecker's home range would be used with a Bayesian random-effects discrete choice model (Cooper and Millsbaugh 1999, Thomas et al. 2006). We assumed choice sets were composed of 2 trees: the used tree and a randomly available tree from within the home range of woodpecker j . We modeled the 'utility' of each used tree in choice set i as a linear function of vegetation characteristics and individual-level regression coefficients:

$$U_i^{used} = \beta_{1j_i} DBH_i^{used} + \beta_{2j_i} DEAD_i^{used} + \beta_{3j_i} BA_i^{used} + \beta_{4j_i} LS_i^{used} + \beta_{5j_i} MH_i^{used} \\ + \beta_{6j_i} GH_i^{used} + \beta_{7j_i} RG_i^{used} + \beta_{8j_i} BMPB_i^{used} + \beta_{9j_i} PDEAD_i^{used}$$

where DBH_i^{used} is the diameter of the used tree in choice set i , $DEAD_i^{used}$ is a dummy variable = 1 if the used tree is dead, 0 otherwise, BA_i^{used} is the basal area of the stand immediately surrounding the used tree, LS_i^{used} , MH_i^{used} , GH_i^{used} , RG_i^{used} , $BMPB_i^{used}$ are dummy variables = 1 if the used tree is categorized as low severity burn, moderate or high severity burn, green hit, red hit or gray hit, or burned and infested with MPBs, respectively, 0 otherwise, $PDEAD_i^{used}$ is the proportion of dead trees in the stand immediately surrounding the used tree, and $\beta_{1j_i}, \dots, \beta_{9j_i}$ are the individual-level regression coefficients corresponding to woodpecker j ($j \in (1, 2, \dots, W)$, where W is the total number of woodpeckers included in the model). We modeled the utility of each available tree in choice set i in an identical manner, substituting vegetation variables at used trees for vegetation variables at available trees. Finally, we used the utility functions defined above to model the relative probability each used tree in choice set i was used as:

$$\psi_i^{used} = \frac{\exp(U_i^{used})}{\exp(U_i^{used}) + \exp(U_i^{avail})}.$$

Since choice-sets contained 2 trees, the relative probability the available tree was used is $(1 - \psi_i^{used})$.

We modeled population-level resource selection by assuming individual-level regression coefficients for woodpecker j arise from normal population-level distributions (Thomas et al. 2006). For example, we assume

$$(\beta_{11}, \dots, \beta_{1W}) \sim N(\mu_1, \sigma_1^2).$$

Hereafter, we refer to the set of parameters governing each population-level distribution $([\mu_1, \sigma_1^2], \dots, [\mu_9, \sigma_9^2])$ as population-level parameters. Note that individual-level regression coefficients describe how a unit change in the value of a corresponding vegetation variable changes the ‘utility’ of a tree for woodpecker j , with greater utility leading to a higher relative probability of use, while population-level parameters describe the mean and variation of individual-level regression coefficients across all j woodpeckers. Hereafter, we refer to each population-level distribution by the name of the associated vegetation covariate. For example, we refer to the population-level distribution that describes the mean and variation of individual-level regression coefficients associated with tree DBH (β_1) simply as the DBH population-level distribution.

We used population-level distributions to evaluate relations between vegetation variables and the relative probability a tree would be used and to rank the relative importance of each vegetation variable. We evaluated the functional relation between vegetation variables and the relative probability a tree would be used with population-level mean parameters. We evaluated the relative importance of each vegetation variable

in influencing the relative probability a tree was used by calculating the absolute value of the coefficient of variation (CV) for each population-level distribution. The CV is a ratio of the standard deviation to the mean for each population-level distribution. A low CV (e.g., < 1) can arise from two distinct population-level resource selection patterns. A low CV can arise if mean selection for a resource is ‘weak’ (i.e., the absolute value of the population-level mean is ‘small’) and the population-level standard deviation is correspondingly ‘small’ (i.e., $<$ the population-level mean). This suggests weak, but consistent, selection for a particular resource among individuals, which may occur if a vital resource is only required in small quantities. A low CV can also arise if the population-level standard deviation for a particular resource is ‘high’, but the population-level mean is correspondingly ‘high’ (provided the population-level variation $<$ the population-level mean). This suggests high variability in resource selection patterns among individuals (perhaps a resource is not available to all individuals), but strong selection when that resource is available. We interpret CVs of population-level distributions as an index of relative variable importance, with low relative CVs indicating high relative importance.

We selected vague prior distributions for all model parameters. We assumed vague normal, $N(\mu = 0, \sigma^2 = 100)$ prior distributions on all population mean hyper-parameters μ_1, \dots, μ_9 and we assumed vague *Uniform*(0, 10) prior distributions of all population standard deviation hyper-parameters $\sigma_1, \dots, \sigma_9$. We assume uniform prior distributions for standard deviation hyper-parameters because the inverse gamma distribution, which is often used as a prior distribution for variance hyper-parameters, can have a strong influence on posterior distributions (Gelman 2006).

We fit discrete choice models in WinBUGS (Gilks et al. 1994) via the R2WinBUGS interface (Sturtz et al. 2005). We simulated posterior distributions of each model parameter from 3 Markov chains. We ran each chain for 51,000 iterations, discarding the first 1,000 as burn-in. There was evidence of correlation between successive draws for some Markov chains, so we kept every 50th iteration after the initial burn-in period. Estimated posterior distributions for each model parameter were thus composed of 3,000 random draws. The Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998) indicated adequate convergence for all hyperparameters ($\hat{R} = 1$).

We assessed the goodness of fit of the discrete choice model using Estrella's (1998) R^2 . We calculated Estrella's R^2 as:

$$1 - \left(\frac{\log(L)}{\log(L_0)} \right)^{-\left(\frac{2}{N}\right)\log(L_0)}$$

where $\log(L)$ is the log-likelihood of the fully parameterized model, $\log(L_0)$ is the likelihood of a null model with all coefficients = 0, and N is the total number of choice sets ($N = 1,104$). Since there were only two choices per choice-set, the null model assumes each tree is selected with 50% probability. Values of Estrella's $R^2 = 0$ indicate the discrete choice model predicts use at random, while values of $R^2 = 1$ indicates perfect fit.

Results

Home Range Size

We collected ≥ 30 telemetry locations over at least 1 12-month period for 70 individual Black-backed Woodpeckers. We collected ≥ 30 telemetry locations over 2 12-month periods for 4 individual woodpeckers, so we analyzed a total of 74 different home ranges. Estimated home range size was highly variable between disturbance categories (minimum estimated home range size = 20 ha, maximum estimated home range size = 1,248 ha, Table 2.2). Average estimated home range size was the smallest in 1-year post-wildfire habitat and was slightly larger in 2-year post-wildfire and post-prescribed fire habitat. We rarely observed Black-backed Woodpeckers in 1-year post prescribed fire habitat, so we were unable to estimate home range size in this disturbance category. Home range size was largest in ≥ 3 -year post-fire habitats (both wildfire and prescribed fire). Home range size in MPB infestations were intermediate between 1-2 year post-fire habitats and ≥ 3 year post-fire habitats.

Resource Selection

We modeled resource selection from 1,104 pairs of used and available trees (hereafter called resource selection data) collected from 29 Black-backed Woodpeckers: 5 woodpeckers were in habitat created by wildfire, 8 were in habitat created by MPB infestations, and 16 were in habitat created by prescribed fire. On average, resource selection data were collected over a period of 118 days (range = 41 – 434 days). Most of the used locations were the only point collected in a day (55% of all telemetry locations), though 42% of telemetry locations used to model resource selection were 1 of 2 locations collected from a single bird in 1 day and 3% of telemetry locations used to model

resource selection were 1 of 3 locations collected from a single bird in 1 day. We collected resource selection data in 3-4 year post-wildfire habitat and 2-4 year post-prescribed fire habitat. The mean posterior distribution of Estrella's $R^2 = 0.68$ (95% credible interval = [0.66, 0.70]). This mean value of 0.68 indicates performance that is better than random, so we assume an adequate goodness-of-fit for the discrete choice model.

The relative probability a Black-backed Woodpecker used a tree was influenced by characteristics of the tree and the surrounding stand. The relative probability of using a tree was positively associated with the tree's DBH (Fig. 2.1a, mean DBH of used trees = 27 cm, mean DBH of available trees = 24 cm) and was greater for dead trees than for live trees (Fig. 2.1b). Within burned forests (both wildfire and prescribed fire), Black-backed Woodpeckers exhibited the greatest relative probability of using trees that were both burned and infested with MPBs, followed by intermediate relative probabilities of using trees that burned at moderate / high severity and trees that burned at low severity (Fig. 2.2a). The relative probability of using an unburned tree was almost 0 when any category of burned tree was available. Within forest infested with MPBs, Black-backed Woodpeckers exhibited the greatest relative probability of using green hit trees, followed by intermediate relative probabilities of using trees that were both burned and infested with MPB infestations and trees that were infested with MPBs > 1 year. As with woodpeckers occupying burned forests, the relative probability of using an undisturbed tree was almost 0 when any category of MPB infested tree was available.

Black-backed Woodpeckers also exhibited selection at the level of the forest immediately surrounding a tree. The relative probability of using a tree increased as the

basal area of the surrounding stand increased (Fig. 2.1c, mean basal area surrounding used trees = 27.7 m² / ha, mean basal area surrounding available trees = 20.8 m² / ha). The relative probability of using a tree also increased slightly as the proportion of dead trees in the surrounding stand increased (Fig. 2.1d, mean proportion dead trees surrounding used trees = 0.62, mean proportion dead trees surrounding available trees = 0.28).

The mean CV of all population-level distributions was < 1, indicating variation in individual-level regression coefficients was small relative to population-level means. The mean CV and corresponding 95% credible intervals of the DBH (diameter at breast height), MH (moderate-high severity burn), RG (red hit / gray hit), and BA (basal area) population-level distributions were all < 1 (Table 2.3), indicating that these vegetation variables may have the strongest influence on Black-backed Woodpecker resource selection. However, the mean CVs of the LS (low severity), PD (proportion dead), GH (green hit), BMPB (burn / MPB) and DEAD (focal tree dead) population-level distributions were also < 1 (though 95% credible intervals overlap 1), suggesting these vegetation variables may have a strong influence on Black-backed Woodpecker resource selection as well.

Discussion

Our evaluation of Black-backed Woodpecker resource selection revealed consistent selection for several vegetation characteristics within the home range of individual birds, regardless of the disturbance type occupied by individual woodpeckers. Across all disturbance types, Black-backed Woodpeckers were most likely to use

relatively large, disturbance-killed trees in relatively high basal area stands. Further, the low CVs of all population-level distributions indicates that Black-backed Woodpeckers use of trees within a home range is not driven by a few specific resources, but is instead driven by a suite of vegetation characteristics.

Variation in population-level responses to vegetation characteristics and home range size are likely driven by underlying variation in food resources. At the most basic level, the consistently high relative probability of Black-backed Woodpeckers using disturbance-killed trees of any category probably reflects the food resources harbored in these trees. Black-backed Woodpeckers also exhibited consistently high relative probability of using the largest diameter trees available, which is likely a result of higher beetle abundance in large diameter trees (Nappi et al. 2003, Saint-Germain et al. 2004). Finally, Black-backed Woodpeckers exhibited consistently high probability of using trees situated in relatively high basal area stands. While this may reflect conditions that lead to high tree mortality following fire or MPB infestations (Graham et al. 2004, Negrón et al. 2008), high basal area stands may also contain high densities of beetle-rich trees. Variation in home range size may also reflect variation in food resources between disturbance types. Wood-boring beetles of the families Cerambycidae and Buprestidae are strongly attracted to fire-killed trees (Saint-Germain et al. 2004, Costello et al. 2011) and the larvae of these beetles are the primary prey items of Black-backed Woodpeckers occupying recently burned forest (Murphy and Lehnhausen 1998). Wood-boring beetle larvae are much larger than MPB larvae and likely provide a greater food resource. Indeed, results from *Chapter 3* suggest Black-backed Woodpeckers may acquire more food per tree while foraging in post-wildfire habitat relative to MPB infestations. This

potentially greater food resource in recently burned forest may explain why home range sizes were consistently smaller in 1-2 year post-wildfire habitat relative to home ranges in habitat created by MPB infestations and ≥ 3 year post-fire forest.

Although home range sizes were smallest in the 1-2 year post-fire category, Black-backed Woodpeckers only consistently occupied habitat created by wildfires for both years. We rarely observed Black-backed Woodpeckers occupying 1-year post prescribed fire habitat and were unable to estimate home range size in this disturbance category. The rare occurrence of Black-backed Woodpeckers in 1-year post prescribed fire habitat may occur because of a difference in timing of disturbance, since all of our wildfire study sites burned during June or July and all of our prescribed fire study sites were treated in September or October. Indeed, Vierling (2004) failed to detect Black-backed Woodpecker nests the first year following the Jasper wildfire in the Black Hills, which burned in late August 2000. This suggests that the timing of fire, rather than whether a fire is wild or prescribed, may play the biggest role in determining whether Black-backed Woodpeckers occupy burned forest the first post-fire breeding season.

Differences between the timing of wildfire and prescribed fire in our study may have affected the ability of wood-boring beetles to colonize post-fire forests. Many species of wood-boring beetles are capable of detecting compounds in smoke (Schütz 1999), but may be unable to rapidly colonize burns if they occur in the fall months when beetles are inactive. This is consistent with recent surveys (M. A. Rumble, *unpublished data*) indicating abundant wood-boring beetle activity the first autumn following a summer wildfire, but little wood-boring beetle activity the first autumn following a fall prescribed fire. This is also consistent with the results of *Chapter 3*, which indicated

Black-backed Woodpeckers successfully captured nearly twice as many wood-boring beetles in habitat created by summer wildfire relative to fall prescribed fire.

We were surprised that woodpeckers occupying post-fire habitat (both wildfire and prescribed fire) were not most likely to use trees that burned at moderate or high severity, since most studies of Black-backed Woodpeckers in recently burned forest indicate strong selection for this disturbance category (Murphy and Lehnhausen 1998, Koivula and Schmiegelow 2007, Hanson and North 2008, Hutto 2008). Instead, we found that Black-backed Woodpeckers occupying post-fire habitat were most likely to use trees that were both burned and infested with MPBs (Fig. 2.2). This may be a result both of the age of post-wildfire habitat we evaluated and low relative abundance of wood-boring beetles in habitat created by prescribed fire. We only modeled resource selection of woodpeckers that occupied 3-4 year post-wildfire habitat. This timing coincided with a large increase in average home range size in post-wildfire habitat (Table 2.2) that likely coincided with most wood-boring beetle larvae emerging as adults (Murphy and Lehnhausen 1998). Woodpeckers in these older post-wildfire habitats were observed foraging in MPB infestations along the periphery of burn boundaries, which is similar to observations made by Dudley and Saab (2012) in 6-8 year post-wildfire habitat. In wildfire study sites, the woodpeckers may need to forage on MPB infestations along burn peripheries as wood-boring beetle abundance declines ≥ 3 years post-fire, which may account for the apparent preference for trees that were burned and infested with MPBs. In habitat created by prescribed fire, autumn burns may prevent the immediate colonization of wood-boring beetles in fire-killed trees. Therefore, trees that burned at moderate and high severity in prescribed fire study sites may have relatively low wood-

boring beetle abundance relative to post-wildfire habitat of the same age, forcing Black-backed Woodpeckers to spend more time foraging on trees that are infested with MPBs along burn peripheries.

Management Implications

Our evaluation of habitat-specific home range size clearly demonstrates that summer wildfire is the most efficient disturbance agent for creating Black-backed Woodpecker habitat. Habitat created by summer wildfire supported smaller home ranges relative to all disturbance types and supported Black-backed Woodpeckers for more years relative to habitat created by fall prescribed fire. An ideal management strategy for maintaining regional Black-backed Woodpecker populations includes maintaining a mosaic of 1-2 year post-summer wildfire habitat. We recognize fire management policy is unlikely to allow summer wildfires to remain unsuppressed, particularly in densely populated regions like the Black Hills, and we do not advocate such an approach. However, ignitions of summer wildfires are inevitable, and we suggest management that allows summer wildfires to burn safely within a network of treated forest patches. Safety nets could include road systems in combination with mechanically treated patches and prescribed fire treatments. When summer wildfires occur, we recommend retaining 40 - 200 hectare patches of 1-2 year post-summer wildfire forest to provide high-quality habitat, which is based on estimated home range size in this habitat. Ideally, patches of recently burned forest should support more than 1 breeding pair of Black-backed Woodpeckers and we recommend exempting at least ½ the area of all forest burns > 400 hectares from salvage logging.

Results from resource selection analysis suggest that recently burned patches should contain certain structural characteristics. Black-backed Woodpeckers demonstrated consistently high probability of using trees ≥ 27 cm DBH (the mean DBH of all used trees) in stands ≥ 27.8 m² basal area / ha (the mean basal area surrounding used trees). On average, trees ≥ 27 cm DBH constituted 11.1 m² / ha (approximately 40%) of the basal area surrounding used trees. Additionally, across all habitats, Black-backed Woodpeckers exhibited the greatest probability of using disturbed trees of any category relative to undisturbed trees and dead trees relative to live trees. Although there was no strong preference for any burn severity category, increased burn severity results in greater tree mortality. We therefore recommend retaining portions of burned forest composed of ≥ 27 m² basal area / ha of trees that burned at moderate and high severity, since these stands will likely contain the greatest number of standing dead trees. Additionally, we recommend that at least 40% of the basal area of these stands be composed of trees ≥ 27 cm DBH.

We do not advocate the use of fall prescribed burns as a tool for creating Black-backed Woodpecker habitat in the Black Hills. Not only did we fail to detect many woodpeckers in 1-year post-prescribed fire habitat, but the results of *Chapter 1* suggest declining population growth rates of Black-backed Woodpeckers occupying habitat created by prescribed fire. However, we do not completely discount the utility of prescribed fire as a management tool if applied differently. More research regarding the mechanisms leading to delayed Black-backed Woodpecker colonization of habitat created by prescribed fire may increase the utility of this tool for creating woodpecker habitat. For example, spring burns may allow rapid colonization of prescribed fire sites

by wood-boring beetles, allowing Black-backed Woodpeckers to immediately occupy habitat created by prescribed fire. Additionally, prescribed fire could also be used as a tool to allow greater tolerance of summer wildfires. Prescribed fire has repeatedly been shown to reduce the severity of subsequent wildfires in ponderosa pine forests, largely by removing excessive fuels (Wagle and Eakle 1979, Pollet and Omi 2002, Prichard and Kennedy 2012). Thus, naturally ignited summer wildfires could potentially be allowed to burn in sections of forest that have been previously treated with prescribed fire.

We also do not believe MPB infestations require specific management action targeted toward Black-backed Woodpeckers. Home ranges in habitat created by MPBs were large relative to 1-2 year post-wildfire habitat. Assuming relatively large home ranges coincide with relatively low-quality habitat (e.g., Anich et al. 2010), this may suggest that MPB infestations have low value to Black-backed Woodpeckers relative to recently burned forest. This notion is consistent with previous hypotheses suggesting that unburned forest may act as sink habitat for Black-backed Woodpeckers (Hutto 1995), and is supported by the results of *Chapter 1* demonstrating that mean population growth rates of Black-backed Woodpeckers may be negative in MPB infestations. Additionally, Black-backed Woodpeckers have historically persisted in the Black Hills, despite decades without widespread MPB infestations (Allen 2001). Finally, the spatial extent of the current MPB infestation in the Black Hills, SD, coupled with an inability to fully treat the entire infestation (USDA 2011a), suggests there is unlikely to be a shortage of MPB infested habitat for Black-backed Woodpeckers in the foreseeable future.

Our study is the first to simultaneously compare resource selection and home range size of Black-backed Woodpeckers occupying habitat created by wildfire,

prescribed fire, and MPB infestations. Our study suggests that although Black-backed Woodpeckers may exploit vegetation characteristics in a similar manner across all disturbance types, woodpeckers occupying 1-2 year post-wildfire forests have smaller spatial requirements. Thus, while Black-backed Woodpeckers are clearly exploiting the ongoing MPB epidemic in the Black Hills ecoregion, we believe long-term conservation strategies should focus on ensuring a network of 1-2 year post summer wildfire patches.

Table 2.1: Study sites used to evaluate home range size and resource selection of Black-backed Woodpeckers in the Black Hills, South Dakota, USA.

Site	Habitat	Coordinates	Size (Ha) ^a	Month / Year Disturbed ^b	Years Included in Study ^a
Box Elder	Wildfire	44°9'N, 103°24'W	129	July 2007	2008, 2009
4-Mile	Wildfire	43°41'N, 103°26'W	955	June 2007	2008 - 2011
Bullock	Rx Fire	44°0'N, 103°30'W	486	Sept. 2008	2010 – 2012
5 Bitter	Rx Fire	43°58'N, 103°26'W	304	Oct. 2010	2012
Headquarters West	Rx Fire	43°34'N, 103°30'W	255	Sept. 2009	2011
American Elk	Rx Fire	43°61'N, 103°49'W	1376	Oct. 2010	2012
Norbeck	MPB	43°50'N, 103°30'W	> 213 ^c	1998	2008
Bear Mountain	MPB	43°51'N, 103°45'W	> 48 ^c	Before 1995	2008 – 2011
East Slate Creek	MPB	43°58'N, 103°44'W	> 1,303 ^d	Before 1995	2008 - 2011
Deerfield Lake	MPB	44°00'N, 103°49'W	> 169 ^c	Before 1995	2008
Medicine Mountain	MPB	43°52'N, 103°42'W	> 1,748 ^d	Before 1995	2009 - 2011

- ^a Size of MPB infestations Calculated from FHP Aerial Detection Surveys, available at <http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3_041629> (accessed Feb. 13, 2013). This is an estimate of the minimum total area impacted by MPBs in each study site in a given year.
- ^b The first year MPB infestations were detected in FHP Aerial Detection Surveys. Note there is no aerial detection data prior to 1995.
- ^c calculated from 2008 FHP Aerial Detection Survey
- ^d calculated from 2010 FHP Aerial Detection Survey

Table 2.2: Mean and range of estimated home range size (ha) of Black-backed Woodpeckers occupying habitat created by wildfire, prescribed fire, and mountain pine beetle (MPB) infestations in the Black Hills, South Dakota, USA. Home ranges in wildfire and prescribed fire are further broken down by number of years post-fire. Home range size estimates represent the area contained within 99% contours, estimated using fixed kernel techniques.

Habitat	Mean	Min	Max	<i>n</i> ^a
MPB	307	67	790	27
Prescribed Fire:				
2-year	143	44	339	13
3-year	519	150	1,248	5
4-year	164	-	-	1
Wildfire:				
1-year	70	30	187	11
2-year	88	20	226	10
3-year	439	37	825	5
4-year	408	399	416	2

^a The number of home ranges collected in each category

Table 2.3: Mean and 95% credible intervals for coefficient of variation (CV) posterior distributions. CVs are calculated from population-level distributions, which describe the mean and variation of individual-level regression coefficients across woodpeckers. Individual-level regression coefficients describe the ‘utility’ of a tree to a woodpecker as a function of diameter at breast height (*DBH*), whether a tree was burned at moderate or high severity (*MH*), whether a tree was infested with MPSs ≥ 1 year (*RG*), whether a tree was burned at low severity (*LS*), basal area surrounding a tree (*BA*), the proportion of dead trees surround a tree (*PD*), whether a tree was infested with mountain pine beetles (MPBs) < 1 year (*GH*), whether a tree was both burned and infested with MPBs (*BMPB*), and whether a tree is dead (*DEAD*). We interpret CV as an index of relative importance for each variable, with low relative CV indicating high relative importance.

Population-level Distribution ^a	Mean CV	95% Credible Interval
<i>DBH</i>	0.18	0.01, 0.52
<i>MH</i>	0.23	0.01, 0.62
<i>RG</i>	0.28	0.01, 0.90
<i>LS</i>	0.41	0.02, 1.14
<i>BA</i>	0.46	0.15, 0.85
<i>PD</i>	0.55	0.02, 1.93
<i>GH</i>	0.55	0.03, 1.50
<i>BMPB</i>	0.72	0.02, 2.52
<i>DEAD</i>	0.75	0.34, 1.40

^a Population-level distributions are referred to by the name of the vegetation covariate they are associated with.

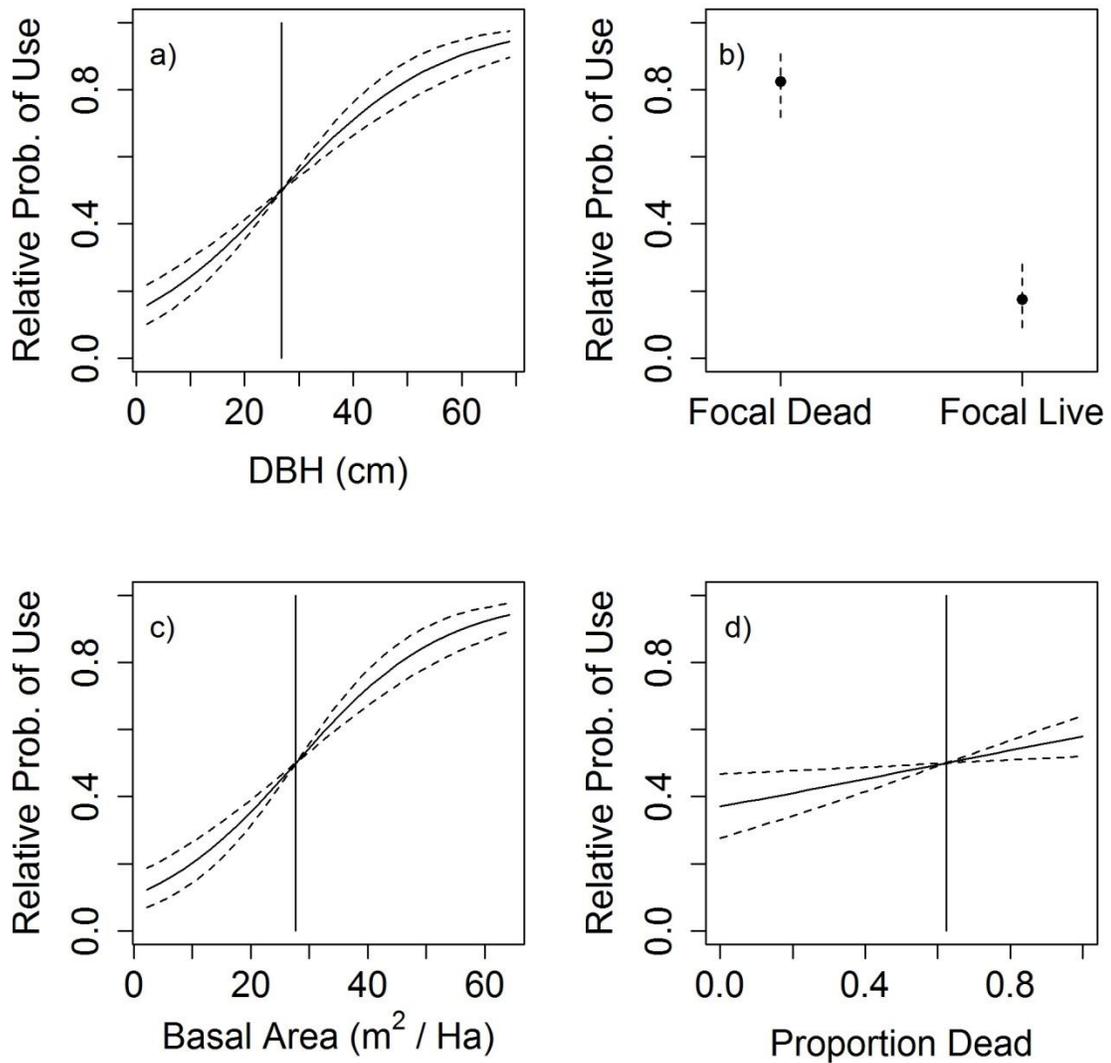


Figure 2.1: Estimated relative probability (\pm 95% credible intervals) of a Black-backed Woodpecker using a tree as a function of a) tree diameter at breast height (DBH), b) whether a tree is alive or dead, c) basal area surrounding tree, and d) proportion of dead trees surrounding the focal tree. All figures assume a woodpecker is faced with two choice sets. For continuous predictors (DBH, basal area, proportion dead, panels a, c, and d, respectively), one choice set is always represented by the value of the vertical line and the other choice set is represented as the value of the x -axis. Figure b) assumes a woodpecker is faced with a choice of a dead or live focal tree. There is no variation around the vertical lines because, under the assumptions of the discrete choice model, woodpeckers will always choose 1 of 2 identical trees with 50% probability.

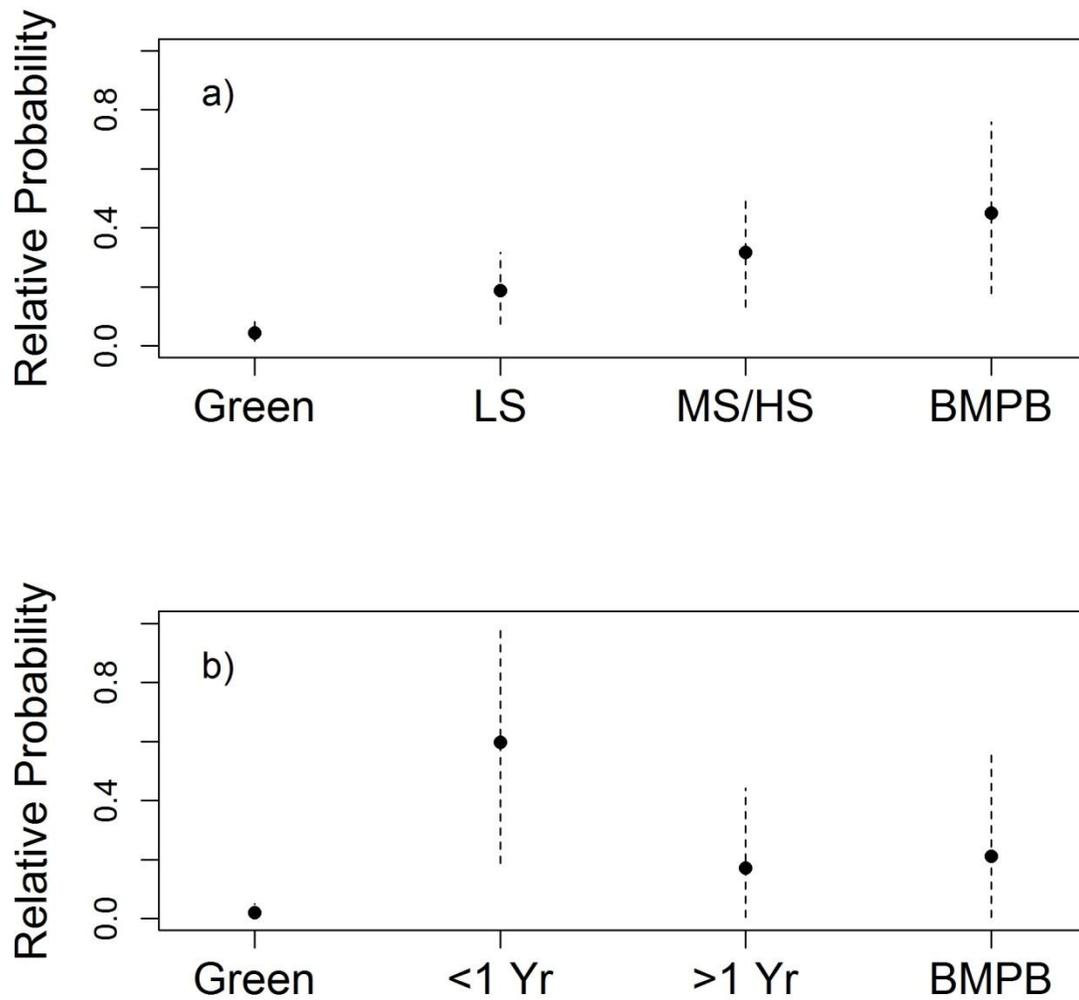


Figure 2.2: Estimated relative probability of a Black-backed Woodpecker using a tree as a function of disturbance categories typical to a) burned forest and b) mountain pine beetle (MPB) infestations. Green refers to trees not disturbed by either fire or MPBs, LS refers to trees burned at low severity, MS / HS refers to trees burned at moderate or high severity, <1 yr refers to trees infested with MPBs < 1 year, >1 yr refers to trees infested with MPBs for ≥ 1 year, and BMPB refers to trees that are both burned and infested with mountain pine beetles. In both disturbance types, Black-backed Woodpeckers are assumed to be faced with a choice set of 4 trees, one of each disturbance category listed on the x -axis.

CHAPTER 3: DO BLACK-BACKED WOODPECKER FOOD RESOURCES VARY AMONG WILDFIRE, PRESCRIBED FIRE, AND MOUNTAIN PINE BEETLE INFESTATIONS?

ABSTRACT

Black-backed Woodpeckers are a disturbance-dependent species that occupy habitat created by wildfire, prescribed fire, and mountain pine beetle (MPB) infestations. Recent research has suggested that population growth rates of Black-backed Woodpeckers in the Black Hills, South Dakota may be positive only in habitat created by summer wildfire, and may be negative in habitat created by fall prescribed fire and MPB infestations. Lower growth rates in fall prescribed fires may be related in part to low wood-boring beetle abundance relative to summer wildfires, while lower growth rates in MPB infestations may be related in part to different prey bases, since bark beetle larvae are smaller than wood-boring beetle larvae. We evaluated the hypothesis that apparent foraging success of Black-backed Woodpeckers differ among habitats created by summer wildfire, fall prescribed fire, and MPB infestations in the Black Hills, South Dakota. We counted the number of successfully captured wood-boring beetle and ‘small’ prey on each tree a Black-backed Woodpecker used for foraging and modeled these counts as a function of habitat (summer wildfire, fall prescribed fire, or MPB infestation), tree diameter, number of years post-fire, and tree disturbance category (burn severity and age of MPB infestation). Apparent foraging success for wood-boring beetles was greater in habitat created by summer wildfire relative to fall prescribed fire and MPB infestations. In contrast, apparent foraging success for small prey was greater in habitat created by MPB infestations relative to summer wildfire. Assuming apparent foraging success reflects underlying differences in wood-boring beetle larvae abundance, Black-backed

Woodpeckers may have greater food resources in habitat created by summer wildfire relative to fall prescribed fire. Additionally, assuming food resources scale with prey size, Black-backed Woodpeckers foraging in habitat created by summer wildfire may gain more food resources per tree relative to MPB infestations.

Introduction

Black-backed Woodpeckers (*Picoides arcticus*) are a disturbance-dependent species that respond opportunistically to pulses in prey resources, particularly wood-boring beetles and bark beetles in recently killed trees. In general, Black-backed Woodpeckers are considered an irruptive species and have been documented exploiting various kinds of insect outbreaks throughout their range (Yunick 1985, Dixon and Saab 2000). In particular, Black-backed Woodpeckers are strongly associated with early post-fire habitat because of high concentrations of wood-boring beetles (Cerambycidae and Buprestidae) that are attracted to recently burned forest (Hutto 1995, Murphy and Lehnhausen 1998). Black-backed Woodpeckers are also associated with mountain pine beetle (*Dendroctonus ponderosae*, hereafter MPB) infestations (Goggans et al. 1989, Bonnot et al. 2008, 2009) because of high abundances of both bark beetles and wood-boring beetles. Finally, Black-backed Woodpeckers are known to use undisturbed forest (Mohren 2002, Tremblay et al. 2009), particularly when recently burned habitat is not available (Hoyt and Hannon 2002), though such use is often associated with small patches of recently killed trees (Hutto 1995, S Mohren, *Personal Communication*).

Resources in these recently killed forests are not likely to be of equal value to Black-backed Woodpeckers. Two broadly different disturbance types that may differ in

value to Black-backed Woodpeckers are recently burned forests and MPB infestations. Black-backed woodpeckers were rarely detected in MPB infestations in areas where extensive early post-fire habitat occurred (Cilimburg et al. 2006, Edworthy et al. 2011). In contrast, Black-backed Woodpeckers readily use MPB infestations in the margins of their range where early post-fire habitat may be relatively rare (Goggans et al. 1989, Bonnot et al. 2008, 2009, Pierson et al. 2010). Thus, MPB infestations may have low value to Black-backed Woodpeckers relative to early post-fire habitat. This hypothesis was supported by the results of *Chapter 1*, which suggested negative population growth rates of Black-backed Woodpeckers occupying MPB infestations in the Black Hills, South Dakota. Two disturbance types that differ more subtly are habitats created by wildfire and prescribed fire. Habitat created by prescribed fire appears visually similar to habitat created by wildfire and Black-backed Woodpeckers occupy both habitats (Russell et al. 2009). However, the results of *Chapter 1* suggest negative population growth rates of Black-backed Woodpeckers occupying forests treated by fall prescribed fire in the Black Hills, South Dakota. Indeed, the results of *Chapter 1* suggested positive population growth rates only in habitat created by summer wildfire, suggesting this habitat may be of the greatest relative value to Black-backed Woodpeckers.

Differences in population growth rates among woodpeckers occupying these distinct habitats may arise, in part, from differences in food resources. Food availability can be a major determinant of habitat quality (Lyons 2005, Johnson 2007). Differences in food availability among habitats may affect reproduction and survival, which in turn impact population growth rates and fitness. For example, Siikamäki (1998) demonstrated food availability may impact the weight of Pied Flycatcher (*Ficedula hypoleuca*)

nestlings at fledging and Strong and Sherry (2000) demonstrated that body condition indices of Ovenbirds (*Seiurus aurocapilla*) wintering in Jamaica were correlated with changes in prey across habitats and through time. There are likely to be differences in food resources available to Black-backed Woodpeckers among habitats created by wildfire, MPB infestations, and prescribed fire. Differences in food resources between habitats created by wildfire and prescribed fire may arise through differences in abundance of wood-boring beetles owed to seasonality of fire. Wildfires are most likely to occur in dry summer months, while forests are often treated with prescribed fire during months when fire is easiest to control, such as spring or autumn (Knapp et al. 2009). Treating forests with prescribed fire during autumn months may affect the ability of wood-boring beetles to immediately colonize treated forests, resulting in reduced abundance.

Differences in food resources between habitats created by wildfire and MPB infestations may be related to differences in the primary prey item between habitats. Wood-boring beetles of the families Cerambycidae and Buprestidae are attracted to early post-wildfire habitat (Costello et al. 2011) and feed on the moist phloem of recently-killed or dying trees (Saint-Germain et al. 2004). In contrast, the mountain pine beetle is primarily responsible for the current beetle infestation in the Black Hills (Negrón et al. 2008), although wood-boring beetles and other bark beetles (*Ips* species) occur in both MPB infestations and wildfires (Hull-Sieg et al. 2006). In general, wood-boring beetles are much larger than bark beetles (Arnett et al. 2002), suggesting Black-backed Woodpeckers may have access to greater food resources in recently burned forests relative to MPB infestations.

For this study, we evaluated apparent foraging success of Black-backed Woodpeckers among habitats created by summer wildfire, fall prescribed fire, and MPB infestations in the Black Hills, South Dakota. We define apparent foraging success as the count of successfully captured prey from each tree used for foraging. We evaluated whether apparent foraging success for wood-boring beetles was greater in habitat created by wildfire relative to habitat created by prescribed fire. We also evaluated whether apparent foraging success for wood-boring beetles was greater in habitat created by wildfire than MPB infestations, and whether apparent foraging success for small prey items (including bark beetles) was greater in MPB infestations than habitat created by wildfire.

Methods

Study Sites

This study occurred between 2008 and 2012 in the Black Hills, South Dakota at study sites representing habitat created by wildfire, prescribed fire, and MPB infestations (Table 3.1). All wildfire sites burned during the months of June or July (hereafter we use wildfire synonymously with summer wildfire), and all prescribed fire sites were ignited during the months of September or October (hereafter we use prescribed fire synonymously with fall prescribed fire). All study sites were composed primarily of ponderosa pine (*Pinus ponderosa*) forest, with quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*) trees occurring less frequently within monotypic ponderosa pine stands (Hoffman and Alexander 1987).

All study sites were composed of a heterogeneous mix of disturbance types. The prescribed fire and wildfire sites contained a mix of trees that burned at low, moderate, and high severity, although the relative proportion of trees burned at each severity category varied by study site. All MPB study sites contained a mix of trees that had been infested < 1 year (hereafter called ‘green hits’), trees that had been infested 1-2 years (hereafter called ‘red hits’), and trees that had been infested for > 2 years (hereafter called ‘gray hits’). Further, although each study site was predominantly composed of one disturbance type (wildfire, prescribed fire, or MPB infestations), most study sites had components of both fire and MPB infestations. For example, most wildfire and prescribed fire study sites had small MPB infestations close to the burn periphery, while many of the MPB study sites contained small patches of burned forest. We classified each study site based on the dominant disturbance present (wildfire, prescribed fire, or MPB infestation).

Capture and Radio-telemetry

We studied apparent foraging success of Black-backed Woodpeckers by observing individuals fitted with VHF radio-transmitters. We captured woodpeckers using mist nets, hoop nets, and netguns. We captured birds with mist nets by luring them into nets with decoy woodpeckers and recordings of territorial vocalizations or by placing nets along known flight paths. Mist nets were used with limited success only during the 2009 and 2010 breeding seasons and were quickly abandoned in favor of the more efficient hoop net and netgun capture methods (Lehman et al. 2011). We captured birds with hoop nets by waiting for a bird to enter a nest cavity and placing the net over the cavity entrance. Hoop nets were an efficient capture method during the breeding season,

but were only effective when woodpeckers were actively attending cavities. Finally, we used the netgun to capture woodpeckers by luring them in with territorial recordings or by stalking foraging woodpeckers. The netgun allowed capture away from nest cavities and outside the breeding season.

Once captured, all birds were weighed and a small (3.0 – 3.3 g) transmitter was attached (Rappole and Tipton 1991). 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 (Fair et al. 2010). Additionally, all birds were banded with a unique combination of colored leg bands and a uniquely numbered U.S. Fish & Wildlife Service aluminum leg band. We attempted to recapture previously marked individuals and replace transmitters as batteries expired. We supplemented recaptured birds with unmarked birds that were captured opportunistically during trapping events.

Foraging Observations

This project was part of a larger study evaluating habitat-specific demography (*Chapter 1*) and resource selection (*Chapter 2*) of Black-backed Woodpeckers in the Black Hills, South Dakota. Our schedule for locating radio-marked Black-backed Woodpeckers thus reflected sampling requirements for each study component and radio-marked woodpeckers were observed as often as once every 4 hours and as infrequently as once every month.

Observers conducted 10-minute foraging observations on radio-marked woodpeckers when they were located. During foraging observations, observers counted the number of apparent 'large' and 'small' prey items a woodpecker extracted from each tree it used for foraging. We define 'large' prey as items that were approximately the

length of a woodpecker's bill and we define 'small' prey as items that were $<1/2$ the length of a woodpecker's bill. We assumed large prey items were wood-boring beetle larvae, since wood-boring beetle larvae (e.g. *Cerambycidae*) are typically 15 or more mm in length (Arnett et al. 2002, p. 568). We did not attempt to further classify small prey items, since small prey could be a variety of species (e.g., MPB, *Ips*, small wood-boring beetle larvae, or wasp larvae). There is a large size discrepancy between wood-boring beetles and the 'small' prey the woodpeckers were foraging on. For example, bark beetle larvae (e.g. *Scolytinae*) are typically 1-3 mm in length (Arnett et al. 2002, p. 793). Therefore, we assume observers were able to correctly distinguish between wood-boring beetle larvae and other smaller prey items. Observations were typically conducted within 10 – 20 m of foraging woodpeckers. Black-backed Woodpeckers are generally tolerant of approaching humans (e.g., Lehman et al. [2011] describe approaching Black-backed Woodpeckers to within 3 m), so we assume foraging behavior was not biased by proximity of observers. Occasionally, observers were unable to complete 10 minutes of observation (e.g., a radio-telemetry signal may be lost after a long flight), though this occurred during $< 5\%$ of observations. When foraging observations were truncated, counts of successfully extracted prey from those trees a woodpecker used for foraging were still included in the analysis.

Observers recorded several variables to characterize each tree a woodpecker used for foraging. Observers classified burn severity as low if scorch height was approximately breast height or lower, moderate if scorch height extended above approximate breast height, but did not burn the entire canopy, and high if the entire tree canopy was consumed by fire. Trees were classified as 'green hits' if boles exhibited

fresh pitch tubes (pitch tubes indicate a tree has been attacked by MPBs) and needles were still green, ‘red hits’ if pitch tubes were present but the needles were red, and ‘gray hits’ if there were few or no needles but pitch tubes were present on trees. Trees were further classified as ‘Burn/MPB’ if they were both burned and infested with MPBs and ‘undisturbed’ if trees were neither burned nor infested with MPBs. Note that there were not enough observations of birds foraging on trees both burned and infested with MPBs to simultaneously classify by burn severity and age of infestation, so all such trees were classified as ‘Burn/MPB’. Observers visually estimated the diameter at breast height (DBH) of each tree a woodpecker used for foraging. Observers measured the DBH of the final tree included in foraging observations to ensure estimates of tree DBH were reasonably accurate. Estimated DBH was correlated ($r = 0.90, n = 381, p < 0.01$) with measured DBH, so we assumed estimated DBH was a reasonable representation of tree diameter. We classified the number of years post-fire based on a 12 month period starting the 1st April following a burn. For example, we considered foraging observations conducted in the 4-Mile study site between April 1, 2008 and March 31, 2009 as 1-year post-fire (4-Mile burned in June 2007). We began this 12-month period on April 1 because this is the approximate beginning of the breeding season (recognizing that Black-backed Woodpeckers make territorial settlement decisions year-round). Thus, the number of years post-fire reflects the number of breeding seasons post-fire.

Statistical Methods

We modeled apparent foraging success for wood-boring beetle larvae and small prey items with Bayesian negative binomial generalized linear mixed models:

$$y_{ijk} \sim \text{Neg. Binomial}(\pi_{ijk}, r)$$

$$\pi_{ijk} = \frac{r}{r + \lambda_{ijk}}$$

where y_{ijk} is the count of successfully captured prey observer i made of woodpecker j foraging on tree k , π_{ijk} and r are the ‘probability of success’ and ‘dispersion’ parameters, respectively, of a negative binomial distribution, and λ_{ijk} is the expected count of successfully captured prey observer i made of woodpecker j foraging on tree k . We included a random woodpecker effect in all models to account for lack of independence in counts due to observations of individual woodpeckers foraging on multiple trees. We included a random observer effect in all models to account for systematic variation in counts among observers.

We evaluated whether foraging success for wood-boring beetle larvae was greater in habitat created by wildfire than in prescribed fire by modeling counts of successfully captured wood-boring beetle larvae on burned trees in these two habitats. We assumed the expected count of successfully extracted wood-boring beetle larvae was a linear function of fixed and random effects:

$$\log(\lambda_{ijk}) = (\beta_0 + Obs_i + Bird_j) + \beta_1 LS_k + \beta_2 MS_k + \beta_3 Wild_k + \beta_4 Yr2_k + \beta_5 Yr3_k + \beta_6 Yr4_k + \beta_7 DBH_k$$

where LS_k and MS_k are dummy variables = 1 if tree k burned at low or moderate severity, respectively, 0 otherwise; $Wild_k$ is a dummy variable = 1 if tree k was located in habitat created by summer wildfire, 0 otherwise; $Yr2_k$, $Yr3_k$, and $Yr4_k$ are dummy variables = 1 if tree k was located in 2-year, 3-year, or 4-year post-fire habitat, respectively, 0 otherwise; DBH_k is the estimated diameter at breast height of tree k ; Obs_i and $Bird_j$ are random effects associated with observer i and bird j , respectively; and β_0, \dots, β_7 are

fixed-effects parameters. We were primarily interested in how apparent foraging success for wood-boring beetle larvae varied by habitat, but included the variables tree diameter, tree condition, and burn age to account for additional sources of variation.

We next modeled apparent foraging success for wood-boring beetle larvae and small prey in wildfire and MPB infestations. We fit two separate models evaluating apparent foraging success in wildfire and MPB infestations; one with counts of successfully captured wood-boring beetle larvae as the response variable and the other with counts of successfully captured small prey as the response variable. We assumed the expected count of both wood-boring beetle larvae and small prey were linear functions of fixed and random effects:

$$\begin{aligned} \log(\lambda_{ijk}) = & (\beta_0 + Obs_i + Bird_j) + \beta_1 LS_k + \beta_2 MS_k + \beta_3 HS_k + \beta_4 GH_k + \beta_5 RH_k \\ & + \beta_6 GR_k + \beta_7 BM_k + \beta_8 Wild_k + \beta_9 Yr2_k + \beta_{10} Yr3_k + \beta_{11} Yr4_k \\ & + \beta_{12} DBH_k \end{aligned}$$

where HS_k , GH_k , RH_k , GR_k , and BM_k are dummy variables = 1 if tree k is severely burned, green hit, red hit, gray hit, or burn/MPB, respectively, 0 otherwise. We were primarily interested in how apparent foraging success varied by habitat, but included tree diameter, tree condition, and number of years post-fire to account for additional sources of variation.

Finally, we calculated the ratio of food resources provided by wood-boring beetle larvae relative to small prey required for total food resources per tree to be equal in habitat created by wildfire and MPB infestations. We make no assumptions about what ‘food resources’ woodpeckers may acquire, and note this may include calories, protein, or any combination of other nutrients. We first calculated the ratio of expected count of

small prey to expected count of wood-boring beetle larvae in MPB infestations as:

$\delta_{mpb} = e^{\beta_0^{sm}} / e^{\beta_0^{wb}}$, where β_0^{sm} and β_0^{wb} are the intercept parameters for the small prey

and wood-boring foraging models, respectively. Similarly, we calculated the ratio of

expected count of small prey to expected count of wood-boring beetle larvae in habitat

created by wildfire as: $\delta_{wild} = e^{\beta_0^{sm} + \beta_{wild}^{sm}} / e^{\beta_0^{wb} + \beta_{wild}^{wb}}$, where β_{wild}^{sm} and β_{wild}^{wb} are the

parameters associated with the wildfire covariate for the small prey and wood-boring

foraging models, respectively. We calculated δ_{mpb} and δ_{wild} so counts of successfully

extracted prey are directly comparable across habitats. We then calculated the ratio of

food-resources provided by wood-boring beetle larvae relative to food resources provided

by small prey necessary for food resources to be equal between habitats as:

$$x = \frac{\delta_{mpb} - e^{\beta_{wild}^{wb}} \delta_{wild}}{e^{\beta_{wild}^{wb}} - 1} \quad \text{Eqn. 3.1}$$

Derivation of equation 3.1 can be found in Appendix 2. Note that this calculation

requires two assumptions. One assumption is that successful wood-boring beetle larvae

captures are detected with the same probability as successful captures of small prey. The

other assumption is that the energy required to capture prey scales with prey size. For

example, if a wood-boring beetle larva is approximately 5× larger than a small prey, we

assume it requires 5× the energy to acquire a wood-boring beetle larva. These

assumptions allow ratios of food resources provided by wood-boring beetle larvae to food

resources provided by small prey to remain unbiased, even if detection probability is < 1

and the absolute energy required to acquire prey is unequal.

We fit all three models in WinBUGS (Gilks et al. 1994) via the R2WinBUGS

interface (Sturtz et al. 2005). We only included data from individual woodpeckers or

observers if there were at least 10 observations in each group to aid in model convergence. We assumed $normal(0, 1000)$ prior distributions for all fixed-effects parameters and $gamma(0.001, 0.001)$ prior distributions for r (the negative binomial dispersion parameter). We assumed $Obs \sim normal(0, \sigma_{obs}^2)$ and $Bird \sim normal(0, \sigma_{bird}^2)$ and we assumed $uniform(0, 100)$ prior distributions for both σ_{obs} and σ_{bird} . We assume uniform prior distributions for standard deviation hyper-parameters because the inverse gamma distribution, which is often used as a prior distribution for variance hyper-parameters, can have a strong influence on posterior distributions (Gelman, 2006). We simulated marginal posterior distributions of parameters for the model fit to counts of wood-boring beetle larvae in wildfire and prescribed fire from 3 Markov chains. We ran each chain for 51,000 iterations, discarding the first 1,000 iterations as burn-in and keeping every 50th iteration thereafter to reduce autocorrelation between successive draws. Estimated marginal posterior distributions of parameters for the model fit to counts of wood-boring beetle larvae in wildfire and prescribed fire are thus based on 3,000 random draws. We simulated marginal posterior distributions of parameters for the models fit to counts of wood-boring beetles and small prey in wildfire and MPB infestations from 3 Markov chains. We ran each chain for 4.2 million iterations, discarding the first 200,000 iterations as burn-in and keeping every 400th iteration thereafter to reduce autocorrelation between successive draws. Estimated marginal posterior distributions of parameters for the models fit to counts of wood-boring beetles and small prey in wildfire and MPB infestations are thus based on 30,000 random draws. The Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998) indicated adequate convergence for all parameters ($\hat{R} = 1$).

Results

Wildfire vs. Prescribed Fire

We modeled apparent foraging success for wood-boring beetle larvae from 2,625 observations of woodpeckers foraging on burned trees in habitat created by wildfire and prescribed fire. The dataset included observations from 61 different woodpeckers collected by 14 different observers.

We found evidence that apparent foraging success for wood-boring beetle larvae was greater in habitat created by wildfire relative to prescribed fire. For example, Black-backed Woodpeckers were expected to capture 90 (95% CI = [34, 175]) wood-boring beetle larvae for every 1,000 24-cm DBH severely burned trees in 1-year post-wildfire habitat relative to 51 (95% CI = [18, 108]) wood-boring beetle larvae on identical trees in 1-year post-prescribed fire habitat. Additionally, 94% of the posterior density of the ratio of the expected count of wood-boring beetle larvae captured in wildfire to prescribed fire was > 1 (Fig. 3.1), suggesting more wood-boring beetle larvae were captured in habitat created by wildfire than in habitat created by prescribed fire.

Apparent foraging success for wood-boring beetle larvae also varied as a function of tree diameter and time since fire. Apparent foraging success for wood-boring beetle larvae was positively associated with estimated tree DBH and negatively associated with time since fire, with the lowest counts occurring 3-years post-fire (Fig. 3.2). Apparent foraging success for wood-boring beetle larvae did not vary appreciably as a function of burn severity.

Wildfire vs. MPB Infestations

We modeled apparent foraging success for wood-boring beetle larvae and small prey from 3,534 observations of woodpeckers foraging in habitat created by wildfire and MPB infestations. These datasets include observations from 73 different woodpeckers collected by 12 different observers.

We found evidence that apparent foraging success for wood-boring beetle larvae was greater in habitat created by wildfire relative to habitat created by MPB infestations. For example, Black-backed Woodpeckers were expected to capture 105 (95% CI = [20, 321]) wood-boring beetle larvae for every 1,000 24-cm DBH red-hit trees in 1-year post-wildfire habitat, relative to 34 (95% CI = [12, 76]) wood-boring beetle larvae on identical trees in MPB infestations. Additionally, 97% of the posterior density of the ratio of the expected count of wood-boring beetle larvae captured in wildfire to MPB infestations was > 1 (Fig. 3.3), suggesting more wood-boring beetle larvae were captured in habitat created by wildfire than in habitat created by MPB infestations.

Apparent foraging success for wood-boring beetle larvae also varied as a function of estimated tree DBH, time since fire, and tree condition. Apparent foraging success for wood-boring beetle larvae was positively associated with estimated tree DBH and was greatest in trees that burned at low severity. Additionally, apparent foraging success for wood-boring beetle larvae was greatest in 4-year post wildfire habitat (Fig. 3.4).

We found evidence that apparent foraging success for small prey was greater in habitat created by MPB infestations relative to habitat created by wildfire. For example, Black-backed Woodpeckers were expected to capture 139 (95% CI = [38, 369]) small prey for every 1,000 24-cm DBH red-hit trees in 1-year post-wildfire habitat, relative to

267 (95% CI = [102, 600]) small prey on identical trees in MPB infestations.

Additionally, 96% of the posterior density of the ratio of the expected count of small prey captured in wildfire to MPB was < 1 (Fig. 3.5), suggesting more small prey were captured in habitat created by MPB infestations than in habitat created by wildfire.

Apparent foraging success for small prey varied as a function of tree condition and estimated tree DBH. Expected counts of successfully captured small prey items were greatest on trees that burned at low, moderate and high severity, green hit, and red hit trees, and increased with increasing estimated DBH. Apparent foraging success for small prey did not vary appreciably as a function of time since fire (Fig. 3.6).

We found that total apparent foraging success (i.e., the sum of expected counts of successfully captured wood-boring beetle larvae and small prey) was greater in MPB infestations relative to post-wildfire habitat because Black-backed Woodpeckers were observed successfully capturing more small prey in MPB infestations (Table 3.2). Black-backed Woodpeckers captured 10.9 (95% CI = [2.3, 32.1]) small prey for every 1 wood-boring beetle larvae ($\bar{\delta}_{mpb} = 10.9$) in MPB infestations and captured 2.1 (95% CI = [0.3, 7.6]) small prey for every 1 wood-boring beetle in post-wildfire habitat ($\bar{\delta}_{wild} = 2.1$). Black-backed Woodpeckers captured 3.1 (95% CI = [0.9, 7.4]) wood-boring beetles in post-wildfire habitat for every 1 wood-boring beetle in MPB infestations. The median value of the posterior distribution of $x = 2.75$, suggesting wood-boring beetle larvae needed to provide approximately 175% more food resources than small prey for Black-backed Woodpeckers to gain equal food resources per tree in habitat created by wildfire and MPB infestations (Fig. 3.7). Additionally, 70% of the posterior density of x was < 5 ,

which is the threshold where wood-boring beetles provide 5 units of food resources for every 1 unit of food resources provided by small prey.

Discussion

We found that apparent foraging success for wood-boring beetle larvae was greater in habitat created by wildfire relative to habitat created by prescribed fire. Assuming apparent foraging success is related to the underlying abundance of wood-boring beetles, this result suggests a greater abundance of wood-boring beetles in habitat created by wildfire relative to habitat created by prescribed fire. Similarly, we found greater apparent foraging success for wood-boring beetle larvae in habitat created by wildfire relative to MPB infestations, and greater apparent foraging success for small prey in habitat created by MPB infestations relative to wildfire. Although Black-backed Woodpeckers were observed eating more individual larvae in MPB infestations, our results suggest wood-boring beetles only needed to provide 175% more food resources than small prey for apparent food resources per tree to be equal between habitats created by wildfire and MPB infestations. Assuming acquired food resources scales approximately with the size of the prey, wood-boring beetle larvae, which are generally $\geq 5\times$ larger than many small prey woodpecker were eating (e.g., bark beetle larvae, Scolytinae, Arnett et al. 2002), likely provide $> 175\%$ more food resources than small prey. This suggests Black-backed Woodpeckers may acquire more food resources per tree while foraging in habitat created by wildfire relative to habitat created by MPB infestations. Together, these results may help explain the differences in population growth rates among disturbed habitats in the Black Hills suggested in *Chapter 1* and the

strong association between Black-backed Woodpeckers and early post-fire habitat (Hutto 1995, Murphy and Lehnhausen 1998).

The lower apparent foraging success for wood-boring beetle larvae in habitat created by prescribed fire relative to habitat created by wildfire may occur as a result of differences in timing between these two disturbances. All of our wildfire study sites burned during the months of June or July, while forests were treated with prescribed fire during the months of September and October. Such differences in timing may affect the ability of wood-boring beetles to colonize recent prescribed burns. Some species of wood-boring beetle are capable of detecting chemicals present in wildfire smoke (Schütz et al. 1999) and can rapidly colonize recent burns. However, if prescribed fires burn during months that wood-boring beetles are inactive, these beetles may not be able to immediately colonize prescribed fire sites. This is supported by recent surveys suggesting high relative wood-boring beetle abundance the first autumn following a summer wildfire, but almost no wood-boring beetle activity the first autumn following a fall prescribed fire (M.A. Rumble, *unpublished data*). Furthermore, wood-boring beetles eat the moist cambium of recently killed and dying trees (Saint-Germain et al. 2004). The effects of delayed colonization may therefore be exacerbated if trees killed by prescribed fire are allowed to dry through the fall and winter months. Further research is needed to clarify the relationship between wood-boring beetle abundance and the timing of fire.

The greater apparent foraging success for wood-boring beetle larvae in habitat created by wildfire and small prey in habitat created by MPB infestations suggests woodpeckers are exploiting different prey bases between these two habitats. We found

these differences even after controlling for tree disturbance condition, such as burn severity or age of MPB infestation, suggesting a real difference between habitats in the primary prey consumed, and not just an artifact of the predominant disturbance type in each habitat. Such differences may be caused by different prey types aggregating in each type of disturbed forest. For example, wood-boring beetles may have aggregated in greater density in wildfire study sites, which were much larger than the small patches of burned forest present in some MPB study sites. These differences in apparent foraging success may also result from different foraging behaviors Black-backed Woodpeckers develop in each habitat. For example, Black-backed Woodpeckers forage for bark beetles by excavating just under the bark layer, while they often must excavate into heartwood to extract wood-boring beetle larvae. Woodpeckers foraging in MPB infestations may thus not spend much time foraging deep enough to find and capture wood-boring beetle larvae.

This potential difference in prey base between habitat created by wildfire and MPB infestations, coupled with potential differences in food resources between wood-boring beetle larvae and small prey, suggests Black-backed Woodpecker may gain fewer food resources per tree while foraging in MPB infestations. Black-backed Woodpeckers foraging in MPB infestations could potentially acquire the necessary food resources by foraging over a greater spatial area relative to 1-2 year post-fire habitat. This hypothesis is consistent with our observations (*Chapter 2*) that home ranges of Black-backed Woodpeckers were nearly 4-times larger in MPB infestations relative to 1-2 year post-fire habitat. This need to search for food over a greater area could increase exposure to

potential predators while foraging, contributing to the low growth rates observed in habitat created by MPB infestations relative to habitat created by wildfire.

We found that apparent foraging success for both wood-boring beetle larvae and small prey in all habitats was positively associated with tree diameter, suggesting relatively large diameter trees may be an important foraging resource for Black-backed Woodpeckers. Nappi et al. (2003) and Saint-Germain et al. (2004) found wood-boring beetle abundance was positively associated with tree diameter. Similarly, Negrón et al. (2008) found that the probability a tree was attacked by MPBs in the Black Hills, South Dakota was positively associated with tree diameter. Our observation is also consistent with the results of *Chapter 2* and Dudley et al. (2012), who found that Black-backed Woodpeckers selected relatively large-diameter trees within their home range. Together, this suggests that large diameter trees likely contain abundant food resources for Black-backed Woodpeckers.

We also found that apparent foraging success for wood-boring beetles in habitat created by wildfire and prescribed fire was lowest 3-years post-fire, suggesting a potential decline in food resources after the first two years post-fire. This decline in apparent foraging success for wood-boring beetles was concomitant with an increase in home range size over the same time period, with 4-fold increases in home range size in 3-4 year post-fire habitat (both prescribed fire and wildfire) relative to 1-2 year post-fire habitat (*Chapter 2*). This timing is also consistent with changes in nest success observed by Nappi and Drapeau (2009), who observed declines in nest success 3-years post-fire, and with Murphy and Lehnhausen (1998), who found declines in densities of Black-backed Woodpeckers in 3-year post-fire habitat. These dramatic changes in apparent

foraging success, home range size, nest success, and density that occur 3-years post-fire likely reflect life history patterns of wood-boring beetle larvae, which typically emerge from host trees 2-3 years after eggs are initially deposited (Murphy and Lehnhausen 1998). Thus, we conclude that 1-2 year post-wildfire habitat that burns during summer months are important for maintaining Black-backed Woodpecker populations.

Our calculation of the ratio of food resources provided by wood-boring beetle larvae to food resources provided by small prey necessary for equal food resources between wildfire and MPB infestations relies on assumptions that the probability of detecting a successful capture is identical for wood-boring beetle larvae and small prey and that the energy required to capture prey scales with prey size. Successful captures of small prey are likely more difficult to detect than successful wood-boring beetle larvae captures, given the difference in prey size. Such a violation of the detectability assumption would result in an underestimation of the ratio of food resources provided by wood-boring beetle larvae to food resources provided by small prey necessary for equal food resources across habitats (i.e., if woodpeckers were observed capturing more small prey relative to wood-boring beetle larvae, each wood-boring beetle larvae would need to provide more food resources for total food resources across habitats to be equal). Given the median ratio of 2.75 units of food resources provided by wood-boring beetle larvae to units food resources provided by small prey necessary for equal food resources across habitats, detectability would have to differ by a factor of 1.8 for wood-boring beetle larvae to provide 5 units of food resources for every 1 unit of food resources provided by small prey (because $5 / 2.75 = 3.47$). In general, Black-backed Woodpeckers were tolerant of approaching humans and observers were generally able to conduct

observations within 10 – 20 m with high-powered binoculars. While the probability of detecting a successful capture of small prey was likely lower than the probability of detecting a successful wood-boring beetle larvae capture, we don't believe successful captures of wood-boring beetle larvae were twice as detectable. Thus, although we may have underestimated the ratio of food resources provided by wood-boring beetle larvae to food resources provided by small prey necessary for food resources to be equal across habitats, our results suggest that woodpeckers may gain more food resources per tree in post-wildfire habitat relative to MPB infestations. Our other assumption was that the energy required to capture prey scaled with prey size. Black-backed Woodpeckers typically need to excavate into the heartwood to capture wood-boring beetle larvae, while they only need to forage directly under the bark to capture most small prey. Thus, more energy is likely required to capture wood-boring beetles relative to small prey. The energetic costs associated with capturing each of these prey is unknown, and likely depends on factors beyond simply depth of excavation. For example, search time is an important energetic cost. Although wood-boring beetles are typically excavated from heartwood, they are also audible from a great distance (C. T. Rota *personal observation*) and thus may be easier to locate than small prey. While we do not know the absolute difference in energy required to successfully extract different prey types, we believe our assumption that energy expenditure scales with prey size is a reasonable approximation. This is the first study to quantify potential differences in Black-backed Woodpecker food resources among habitats created by wildfire, prescribed fire, and MPB infestations. Our finding that apparent foraging success for wood-boring beetle larvae was greater in habitat created by wildfire compared to habitat created by prescribed fire and MPB

infestations may help explain observed differences in population growth rates among these habitats in the Black Hills (*Chapter 1*). Indeed, this study helps confirm a long-standing hypothesis (Hutto 1995) that Black-backed Woodpeckers are an early post-fire specialist.

Table 3.1: Study sites used to evaluate apparent foraging success of Black-backed Woodpeckers in the Black Hills, South Dakota, USA.

Site	Habitat	Coordinates	Size (Ha) ^a	Month / Year Disturbed ^b	Years Included in Study ^a
Box Elder	Wildfire	44°9'N, 103°24'W	129	July 2007	2008, 2009
4-Mile	Wildfire	43°41'N, 103°26'W	955	June 2007	2008 - 2011
Bullock	Rx Fire	44°0'N, 103°30'W	486	Sept. 2008	2010 – 2012
84 Bitter	Rx Fire	43°58'N, 103°26'W	304	Oct. 2010	2012
Headquarters West	Rx Fire	43°34'N, 103°30'W	255	Sept. 2009	2011
American Elk	Rx Fire	43°61'N, 103°49'W	1376	Oct. 2010	2012
Norbeck	MPB	43°50'N, 103°30'W	> 213 ^c	1998	2008
Bear Mountain	MPB	43°51'N, 103°45'W	> 48 ^c	Before 1995	2008 – 2011
East Slate Creek	MPB	43°58'N, 103°44'W	> 1,303 ^d	Before 1995	2008 - 2011
Deerfield Lake	MPB	44°00'N, 103°49'W	> 169 ^c	Before 1995	2008
Medicine Mountain	MPB	43°52'N, 103°42'W	> 1,748 ^d	Before 1995	2009 - 2011

- ^a Size of MPB infestations Calculated from FHP Aerial Detection Surveys, available at <http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3_041629> (accessed Feb. 13, 2013). This is an estimate of the minimum total area impacted by MPBs in each study site in a given year.
- ^b The first year MPB infestations were detected in FHP Aerial Detection Surveys. Note there is no aerial detection data prior to 1995.
- ^c calculated from 2008 FHP Aerial Detection Survey
- ^d calculated from 2010 FHP Aerial Detection Survey

Table 3.2: Relative expected counts of Black-backed Woodpecker apparent foraging success for wood-boring beetle larvae and small prey in habitats created by wildfire and MPB infestations. Expected counts are relative to a baseline of 1 apparent wood-boring beetle capture in habitat created by MPB infestations. Black-backed Woodpeckers capture 10.87 small prey for every 1 wood-boring beetle larvae in MPB infestations, and Black-backed Woodpeckers capture 3.09 wood-boring beetle larvae in post-wildfire habitat for every 1 wood-boring beetle in MPB infestations.

	MPB Infestation	Post-Wildfire Habitat
Wood-boring Beetles	1.00	3.09
Small Prey	10.87	6.64

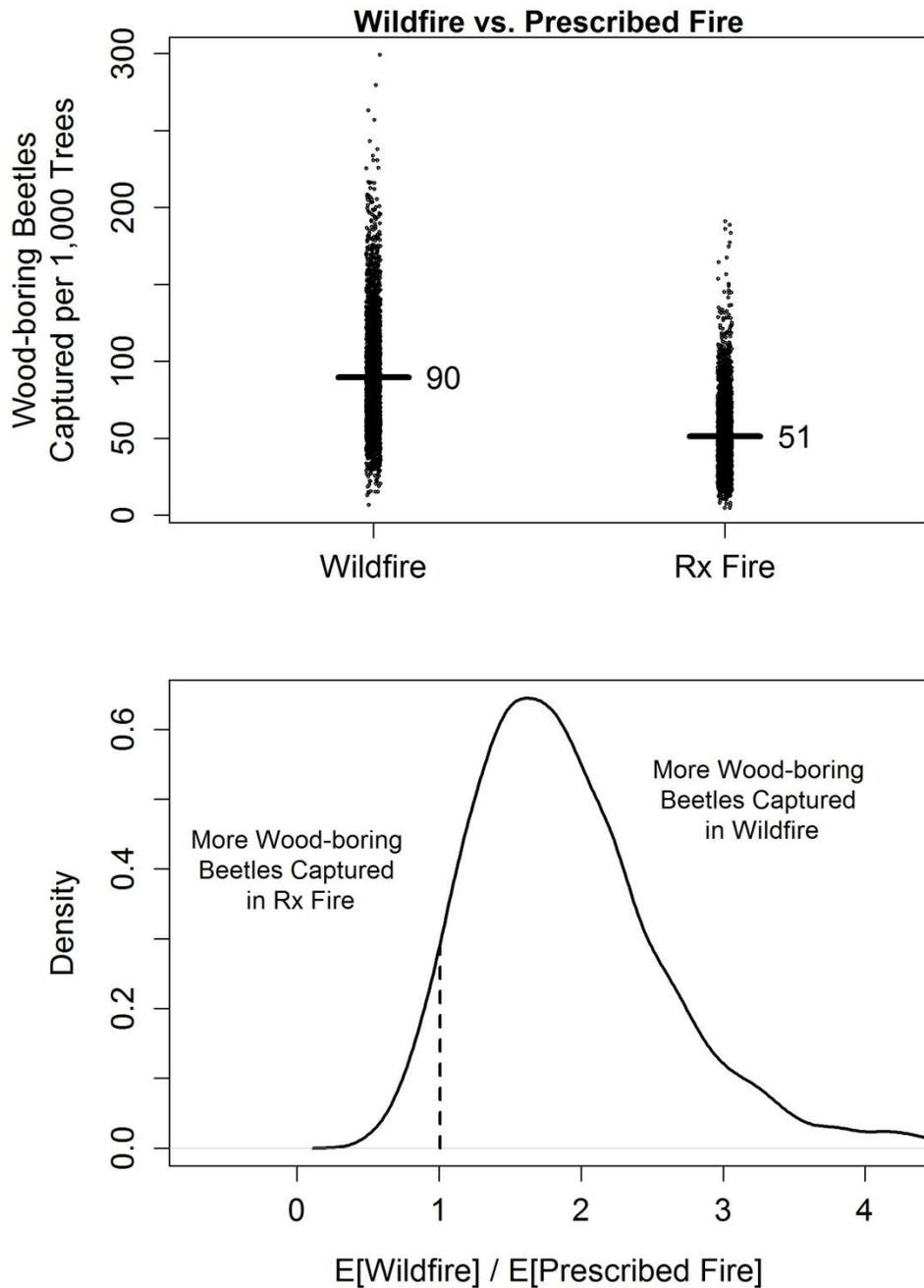


Figure 3.1: *Upper panel:* Realized results from the posterior distributions of expected counts of successfully captured wood-boring beetle larvae per 1,000 trees in habitat created by wildfire and prescribed fire. This figure assumes woodpeckers are foraging on 24-cm DBH severely burned trees in 1-year post-fire forest. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution. *Lower panel:* Posterior density of the ratio of expected counts of successfully captured wood-boring beetle larvae in habitat created by wildfire to habitat created by prescribed fire. Values > 1 , indicated by the vertical dashed line, means more wood-boring beetle larvae are captured in habitat created by wildfire.

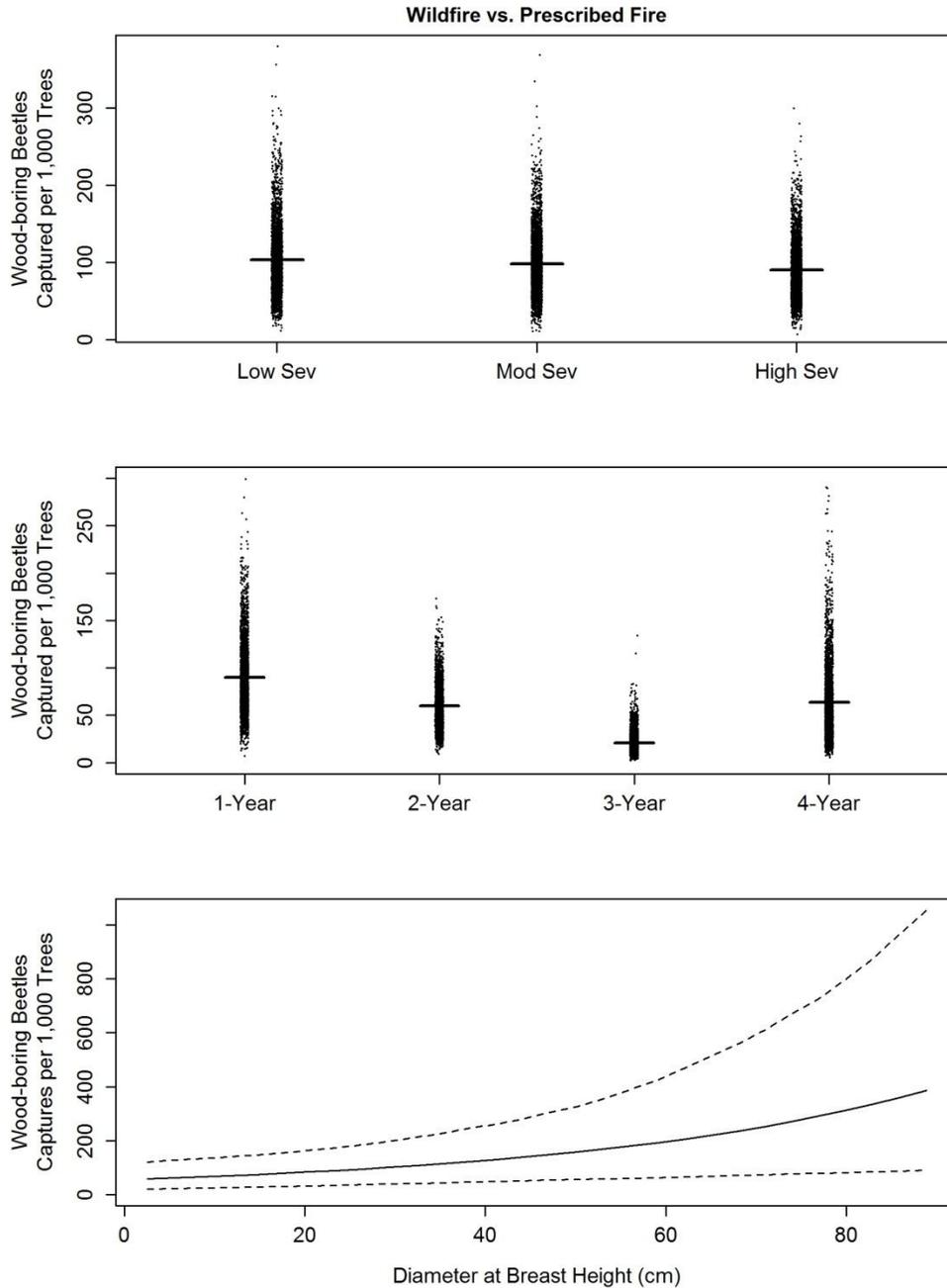


Figure 3.2: Posterior distributions from the model fit to counts of successfully captured wood-boring beetle larvae by woodpeckers foraging on burned trees in habitat created by wildfire and prescribed fire. *Upper panel:* Realized results from the posterior distributions of expected counts of successfully captured wood-boring beetle larvae per 1,000 trees that burned at low severity, moderate severity, and high severity. This figure assumes woodpeckers foraging on 24-cm DBH trees in 1-year post wildfire forest. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution. *Middle panel:* Realized results from the posterior distributions of expected counts of successfully captured wood-boring beetle larvae per 1,000 trees in 1, 2, 3, and 4-year post-fire habitat. This figure assumes

woodpeckers foraging on 24-cm DBH severely burned trees in post-wildfire forest. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution. *Lower panel:* Mean (solid line) and 95% credible intervals (dashed line) of the expected count of successfully captured wood-boring beetle larvae per 1,000 trees as a function of tree diameter at breast height. This figure assumes a woodpecker foraging on a severely burned tree in 1-year post-wildfire habitat.

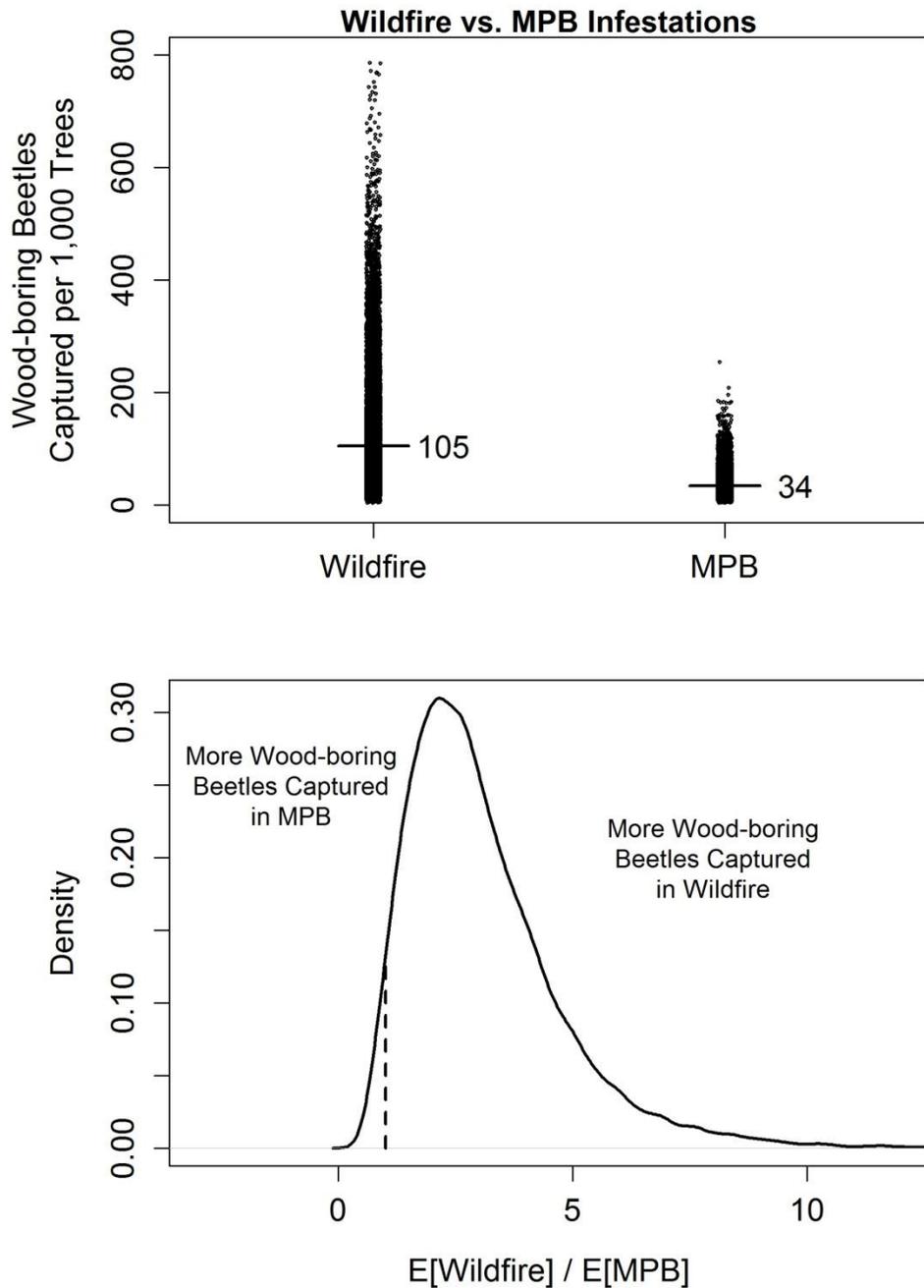


Figure 3.3: *Upper panel:* Realized results from the posterior distributions of expected counts of successfully captured wood-boring beetle larvae per 1,000 trees in habitat created by wildfire and mountain pine beetle infestations. This figure assumes woodpeckers foraging on 24-cm DBH red hit trees and that wildfire habitat is 1-year post-fire. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution. *Lower panel:* Posterior density of the ratio of expected counts of successfully captured wood-boring beetle larvae in habitat created by wildfire to habitat created by mountain pine beetle infestations. Values > 1 , indicated by the vertical dashed line, means more wood-boring beetle larvae are captured in habitat created by wildfire.

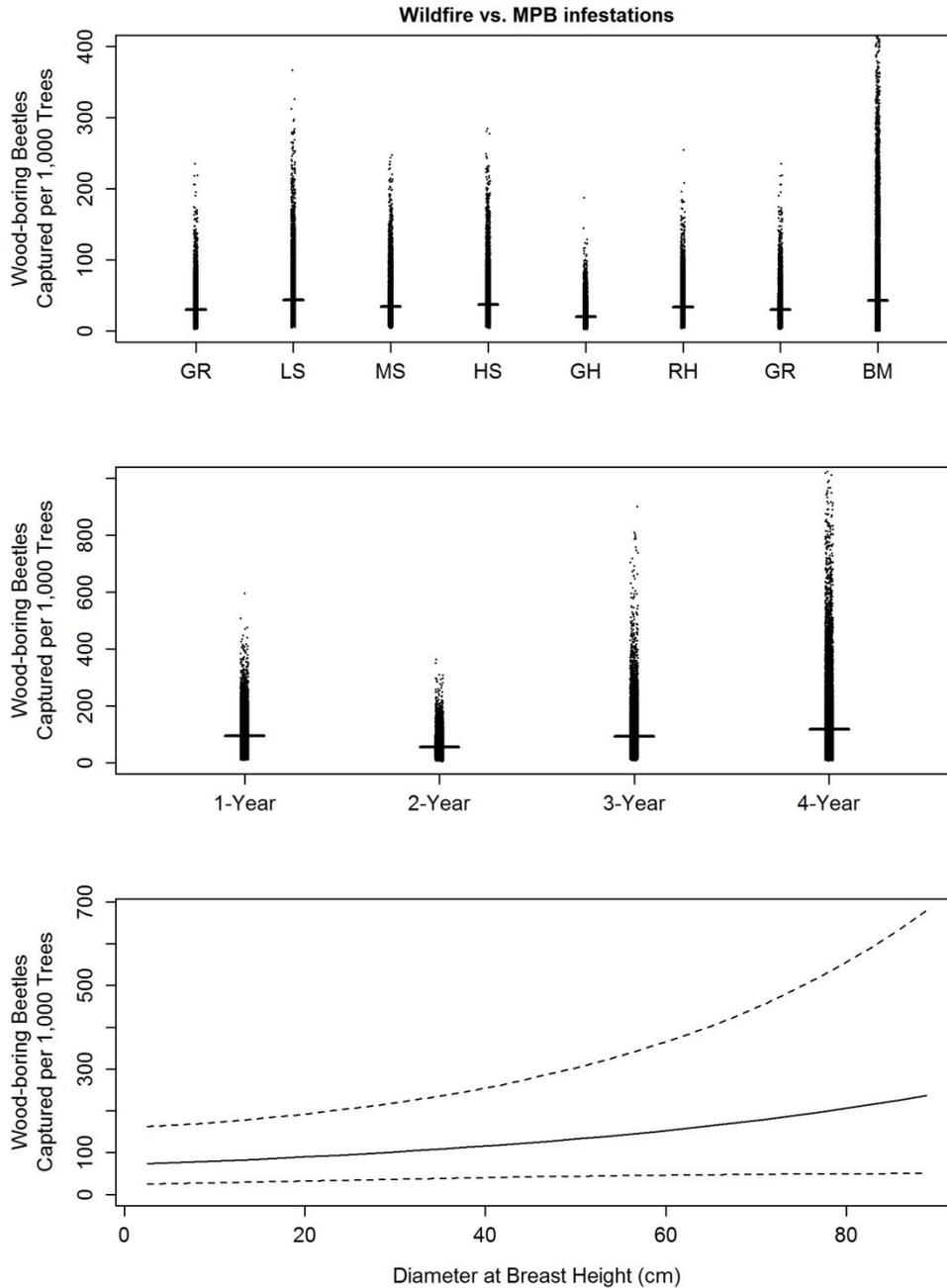


Figure 3.4: Posterior distributions from the model fit to counts of successfully captured wood-boring beetle larvae by woodpeckers foraging on trees in habitat created by wildfire and mountain pine beetle infestations. *Upper panel:* Realized results from the posterior distributions of expected counts of successfully captured wood-boring beetle larvae per 1,000 trees that were undisturbed (GR), burned a low severity (LS), burned at moderate severity (MS), burned at high severity (HS), green hit (GH), red hit (RH), gray hit (GR) or both burned and infested with mountain pine beetles (BM). This figure assumes woodpeckers foraging on 24-cm DBH trees in MPB infestations. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution. *Middle panel:* Realized results from the posterior

distributions of expected counts of successfully captured wood-boring beetle larvae per 1,000 trees in 1, 2, 3, and 4-year post wildfire habitat. This figure assumes woodpeckers foraging on 24-cm DBH severely burned trees. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution. *Lower panel:* Mean (solid line) and 95% credible intervals (dashed line) of the expected count of successfully captured wood-boring beetle larvae per 1,000 trees as a function of tree diameter at breast height. This figure assumes a woodpecker foraging on a severely burned tree in 1-year post-wildfire habitat.

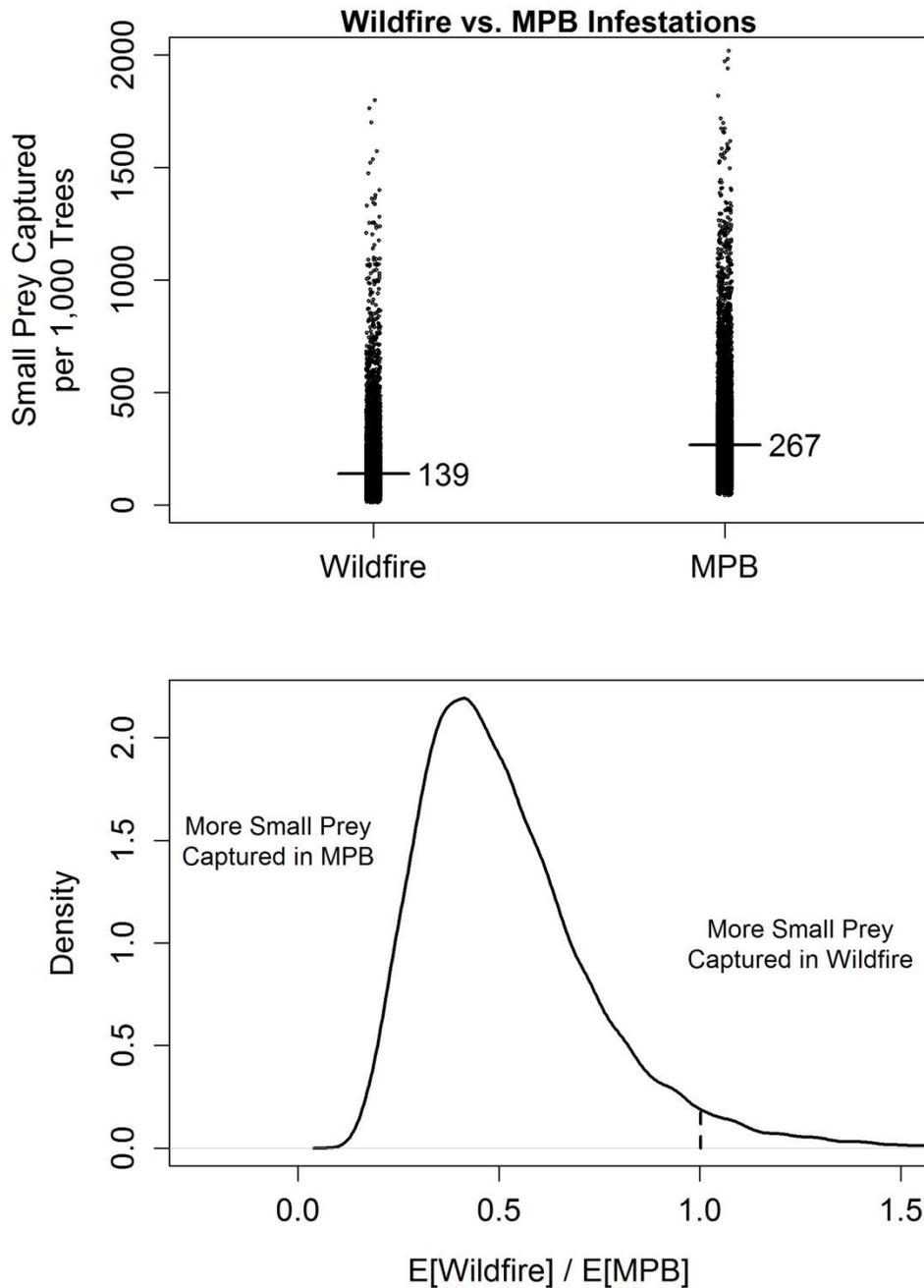


Figure 3.5: *Upper panel:* Realized results from the posterior distributions of expected counts of successfully captured small prey per 1,000 trees in habitat created by wildfire and mountain pine beetle infestations. This figure assumes woodpeckers foraging on 24-cm DBH red hit trees and wildfire habitat is 1-year post-fire. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution. *Lower panel:* Posterior density of the ratio of expected counts of successfully captured small prey in habitat created by wildfire to habitat created by mountain pine beetle infestations. Values < 1 , indicated by the vertical dashed line, means more small prey are captured in habitat created by mountain pine beetle infestations.

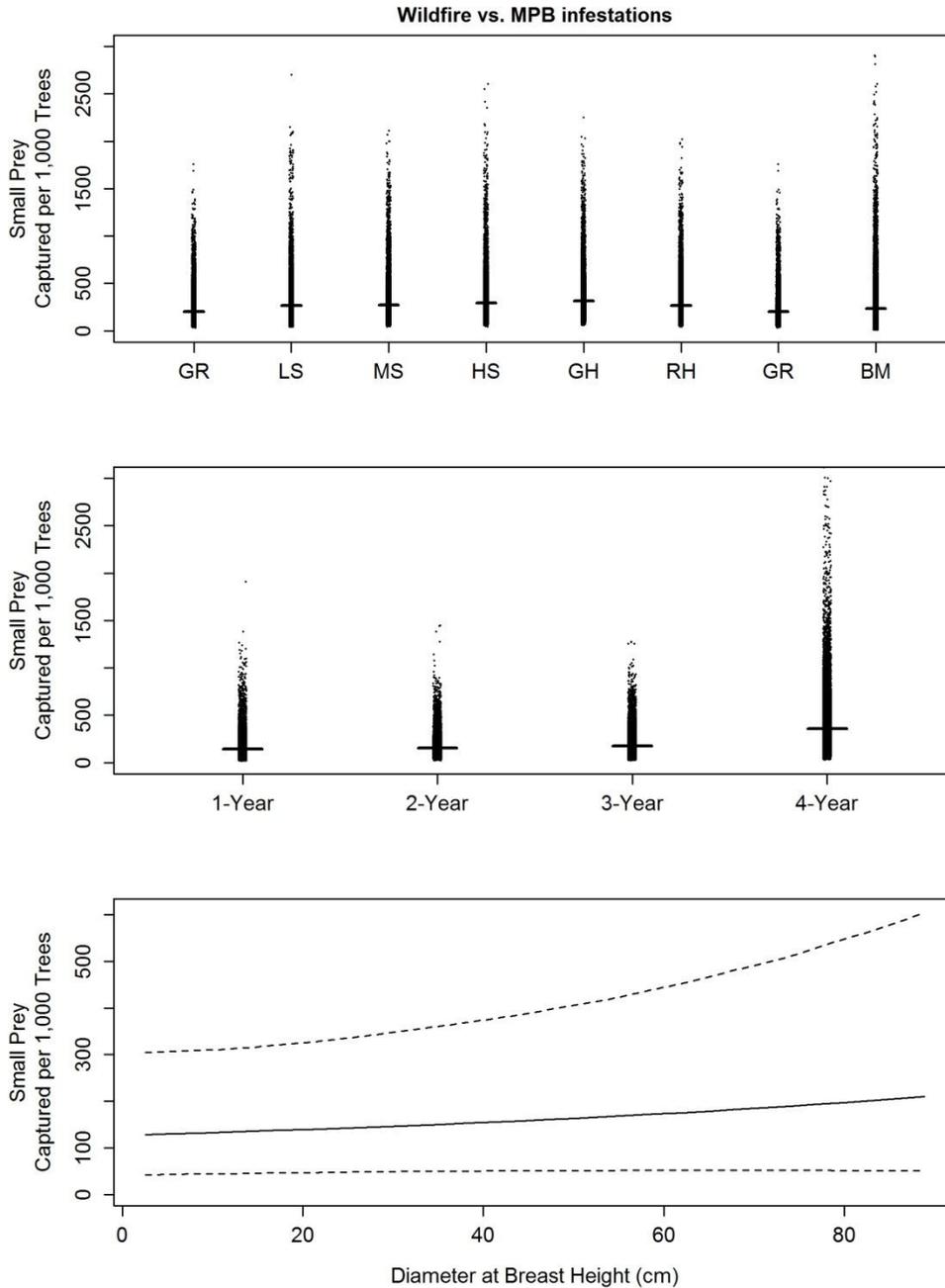


Figure 3.6: Posterior distributions from the model fit to counts of successfully captured small prey by woodpeckers foraging on trees in habitat created by wildfire and mountain pine beetle infestations. *Upper panel:* Realized results from the posterior distributions of expected counts of successfully captured small prey per 1,000 trees that were undisturbed (GR), burned a low severity (LS), burned at moderate severity (MS), burned at high severity (HS), green hit (GH), red hit (RH), gray hit (GR) or both burned and infested with mountain pine beetles (BM). This figure assumes woodpeckers foraging on 24-cm DBH trees mountain pine beetle infestations. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution. *Middle panel:* Realized results from the posterior distributions of expected

counts of successfully captured small prey per 1,000 trees in 1, 2, 3, and 4-year post wildfire habitat. This figure assumes woodpeckers foraging on 24-cm DBH severely burned trees. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution. *Lower panel:* Mean (solid line) and 95% credible intervals (dashed line) of the expected count of successfully captured small prey per 1,000 trees as a function of tree diameter at breast height. This figure assumes a woodpecker foraging on a severely burned tree in 1-year post-wildfire habitat.

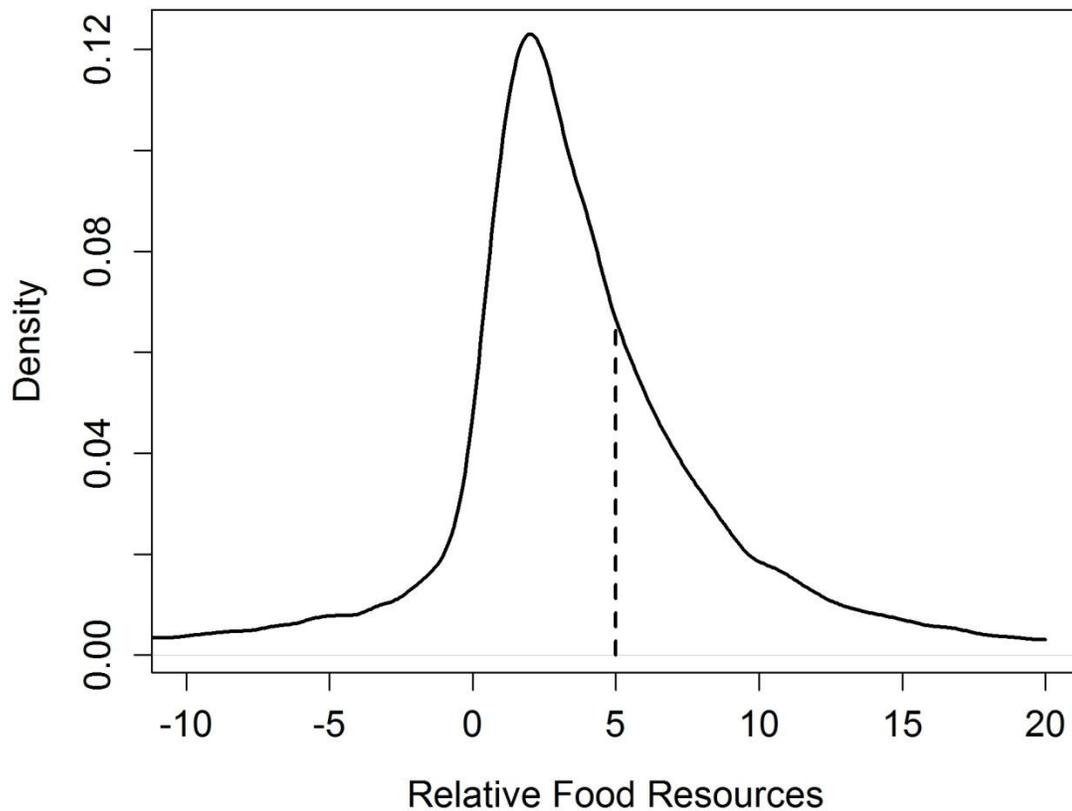


Figure 3.7: Posterior density of the ratio of food resources provided by wood-boring beetle larvae relative to small prey necessary for apparent food resources per tree to be equal in habitat created by summer wildfire and mountain pine beetle infestations. A value of 1 indicates wood-boring beetle larvae needs to identical equal food resources as small prey for apparent food resources per tree to be equal between habitats, while a value > 1 indicates wood-boring beetle larvae need to provide greater food resources relative to small prey for apparent food resources per tree to be equal between habitats. A value of 5, indicated by the vertical dashed line, is the point where wood-boring beetle larvae provide 5 units of food resources to every 1 unit of food resources provided by small prey.

CHAPTER 4: MOVEMENT DYNAMICS OF BLACK-BACKED WOODPECKERS AMONG DISTURBED HABITATS IN THE BLACK HILLS, SOUTH DAKOTA

ABSTRACT

An ephemeral habitat is a habitat patch that is suitable for an organism for only a short period relative to that organism's lifespan. Movements among ephemeral habitats play an important role in the population dynamics of species that rely on such habitats. Black-backed Woodpeckers are a disturbance dependent species that rely on ephemeral habitats created by fire and mountain pine beetle (MPB) infestations. Understanding movement dynamics of Black-backed Woodpeckers will answer two key questions important to understanding population dynamics of this sensitive species: what are the factors associated with dispersing away from a disturbed forest patch, and what are the probabilities of transitioning among disturbance types. We studied movement dynamics of Black-backed Woodpeckers by attaching VHF radio-transmitters to adult birds and tracking long-distance movements with aerial telemetry. We modeled movement dynamics with Bayesian multi-state models that allowed for movements among and between burned forest and MPB infestations. We collected movement data between April 2008 and August 2011 from 122 adult Black-backed Woodpeckers that collectively totaled 771 months of observations. We observed a total of 18 dispersal events ranging from 4 – 60 km. We found that the probability of dispersing during a single time step (1 month) was associated with nest failure the previous time step and increased with increasing time post-fire, regardless of nest fate. We also found that dispersing Black-backed Woodpeckers were most likely to move to a burned forest relative to the amount of burned forest available. Black-backed Woodpeckers appear to rely on cues associated

with decreasing fitness, such as nest failure or potentially decreasing food resources though time, when dispersing from ephemeral habitats. The high relative probability of moving to burned forest when dispersing suggests a preference for this disturbance type, which is consistent with other studies that conclude Black-backed Woodpeckers are an early post-fire specialist.

Introduction

Understanding how individuals move among ephemeral habitats is essential for understanding the dynamics of species that rely on such habitats. An ephemeral habitat is a patch that is suitable to an organism for only a short period relative to that organism's lifespan, such as a forest canopy gap or a temporary pool. Often, the occurrence of ephemeral habitat is unpredictable in space and time. A major consequence of residing in such habitats is the need to track constantly shifting resources. Species that rely on ephemeral habitats are thus predicted to evolve high dispersal rates and movements among habitats is an important component of the dynamics of these species (Denno et al. 1996, Travis and Dytham 1999).

Movement among habitat patches is considered essential for species persistence (Hanski 1994). Two components of the movement process that may be particularly important for species occupying ephemeral habitats are dispersal away from a particular patch and transitioning to another suitable patch of habitat (Keymer et al. 2000). Here, we define dispersal as the movement from one home range to another home range (Greenwood 1980, Johnson and Gaines 1990). We define transition probability as the probability, conditional on dispersing away from a home range, that an organism will

establish a new home range in a particular habitat patch. The process of dispersing away from a particular patch is important for species occupying ephemeral habitats because failure to disperse may leave an individual occupying unsuitable habitat, while dispersing too frequently may expose individuals to unnecessary dispersal costs. The process of transitioning to a new suitable habitat patch is important for species occupying ephemeral habitats because its occurrence is unpredictable in space and time, with many individuals potentially unable to find suitable habitat if transition probabilities are too low.

Understanding dispersal and transition probabilities are thus critical for understanding the population dynamics of species that rely on ephemeral habitats.

Black-backed Woodpeckers are a disturbance-dependent species that rely on ephemeral habitats. Black-backed Woodpeckers are most strongly associated with recently burned forest (Hutto 1995, Murphy and Lehnhausen 1998, Dudley and Saab 2007, Nappi and Drapeau 2009, Dudley et al. 2012), particularly forests that burned at moderate to high severity (Hanson and North 2008, Hutto 2008). Despite this burn-centric association, Black-backed Woodpeckers also use mountain pine beetle infestations (Goggans et al. 1989, Bonnot et al. 2008, 2009), particularly in areas where recently burned forests may not be readily available. Black-backed Woodpeckers are attracted burned forests and MPB infestations because they contain high concentrations of beetle larvae. Recently burned forests attract abundant populations of wood-boring beetle larvae (family Cerambycidae and Buprestidae), which feed on the phloem of trees injured or killed by fire (Saint-Germain et al. 2004, Costello et al. 2011). Similarly, MPB infestations harbor abundant populations of bark beetles (Scolytinae, Arnett et al. 2002). These disturbed forests are only of value to Black-backed Woodpeckers as long as there

is an abundant prey base. However, wood-boring beetle larvae typically emerge as adults by 2-years post-fire (Murphy and Lehnhausen 1998) and mountain pine beetles only spend 1 year in host trees before exiting and infesting new trees. Recently disturbed forests thus represent ephemeral habitat for Black-backed Woodpeckers.

Although Black-backed Woodpeckers are strongly associated with burned forests and MPB infestations, these disturbances carry considerable economic cost. As a consequence, fire suppression, salvage logging, and sanitation logging are often used to reduce the economic impacts of these natural disturbances, which may lead to habitat loss for Black-backed Woodpeckers. As a consequence of potential habitat loss and potentially low abundance throughout portions of their range, Black-backed Woodpeckers are considered a sensitive species in Region 2 of the US Forest Service and have recently been petitioned for protection under the Endangered Species Act (Hanson et al. 2012).

An evaluation of the movement dynamics of Black-backed Woodpeckers can provide insight into two processes important to the management of this sensitive species; how long disturbed habitats may be available and how woodpeckers move among disturbed habitats. There is considerable uncertainty regarding how long disturbed forest remains suitable for Black-backed Woodpeckers. For example, Murphy and Lehnhausen (1998) failed to detect Black-backed Woodpeckers 3 years post-fire, while Bock and Lynch (1970) and Dudley et al. (2012) found Black-backed Woodpeckers occupying 8 year post-fire forest. Furthermore, no studies have addressed how long Black-backed Woodpeckers are likely to inhabit MPB infestations. These studies have primarily determined how long burned forest is suitable for Black-backed Woodpeckers by

observing (or failing to observe) woodpeckers in burned forest of various ages. Much of the uncertainty regarding how long disturbed forests are available thus stems from a lack of understanding of factors that may contribute to deteriorating habitat quality through time for Black-backed Woodpeckers. Understanding the proximate factors that contribute to a woodpecker dispersing away from a disturbed forest may provide insight into factors that contribute to deteriorating habitat quality and also improve our ability to predict how long disturbed forests may remain suitable.

Although Black-backed Woodpeckers are known to use both burned forests and MPB infestations, there is considerable uncertainty regarding the relative value of these habitats to Black-backed Woodpeckers. Black-backed Woodpeckers readily use MPB infestation in the eastern Cascades of Oregon and in the Black Hills of South Dakota (Goggans et al. 1989, Bonnot et al. 2008, 2009). Furthermore, Bonnot et al.'s (2008) research suggests that reproductive success of Black-backed Woodpeckers in MPB infestations may be adequate to maintain viable populations. However, Black-backed Woodpeckers are rarely detected in MPB infestations other portions of their range, such as the northern Rocky Mountains or British Columbia (Cilimburg et al. 2006, Edworthy et al. 2011). Furthermore, the results of *Chapter 1* suggest that population growth rates in MPB infestations in the Black Hills may be negative in most years. A major factor contributing to the probability of Black-backed Woodpeckers using MPB infestations in certain portions of their range may be the relative availability of this habitat across the landscape. Thus, understanding the probability a Black-backed Woodpecker will use burned forests or MPB infestations relative to the amount of disturbed forests will likely

provide insight into the apparent differences in propensity for Black-backed Woodpeckers to use MPB infestations across their range.

We evaluated movement dynamics of Black-backed Woodpeckers occupying disturbance-killed forests in the Black Hills, South Dakota. We studied factors that contributed to woodpeckers dispersing away from a home range and the probabilities of a dispersing woodpecker transitioning to burned forest or MPB infestations. The Black Hills represents an ideal location to study the movement dynamics of Black-backed Woodpeckers because it represents an island of forest bounded by a sea of prairie. Thus, movements of Black-backed Woodpeckers were likely bounded by the limits of the Black Hills and were tractable.

Methods

Study Sites

This study occurred throughout the Black Hills, located in southwest South Dakota and northeast Wyoming. The Black Hills consists of approximately 467,111 hectares of primarily ponderosa pine (*Pinus ponderosa*) forest (USDA 2009a), which strongly contrasts with the surrounding prairie landscape. Within the Black Hills, we established numerous study sites in habitats created by summer wildfire, fall prescribed fire, and MPB infestations (Table 4.1). All established study sites were composed primarily of monotypic ponderosa pine forest (*Pinus ponderosa*) forest, with quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*) occurring less frequently (Hoffman and Alexander 1987). Field work began in April 2008 and continued year-round through August 2011.

Capture and Radio-telemetry

We recorded Black-backed Woodpecker movements by fitting VHF radio-transmitters to adult birds. We targeted Black-backed Woodpeckers for capture by playing audio recordings of territorial calls at potential study sites. Once found, we captured woodpeckers using mist nets, hoop nets, and netguns. We used mist nets only during the 2009 and 2010 breeding seasons and quickly abandoned them in favor of the more efficient hoop net and netgun capture approach (Lehman et al. 2011). Hoop nets were an efficient capture method only during the breeding season when woodpeckers were actively attending cavities. Alternatively, the netgun allowed capture away from nest cavities and outside the breeding season. Once captured, we weighed all birds and attached a small (3.0 – 3.3 g) transmitter (Rappole and Tipton 1991). 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 (Fair et al. 2010). Additionally, we fit all birds with a unique combination of colored leg bands, including a uniquely numbered U.S. Fish & Wildlife Service aluminum leg band. As VHF radio-transmitters died, we attempted to recapture previously marked individuals and replace transmitters. We supplemented recaptured birds with unmarked birds that were captured opportunistically during trapping events. We attempted to locate adult woodpeckers with active transmitters at least once per month, though most woodpeckers were relocated more frequently (mean number of telemetry locations per month = 6).

Whenever we were unable to locate at least 3 birds with potentially active transmitters, we conducted aerial telemetry with a fixed-wing aircraft. Aerial telemetry flights were largely limited to the Hell Canyon, Mystic, and Northern Hills Districts of

the Black Hills National Forest (i.e., we did not conduct aerial telemetry in the Bearlodge District, Fig. 4.1). We conducted aerial telemetry flights on approximate north-south transects over forested portions of the Black Hills. We found that transmitters had a reliable line-of-sight range of approximately 3 km, so we spaced aerial telemetry transects by approximately 5 km. Additionally, we flew concentric circles around field sites where birds were last detected. We searched for birds either until we found all missing birds or until we searched an area bounded approximately by Mt. Rushmore to the east, Spearfish Canyon to the west, and forested portions of the Black Hills to the north and south. We recorded approximate GPS coordinates of all birds detected via aerial telemetry and attempted to locate birds on the ground within 24 hours of locating them from the air. Once located on the ground, we attempted to relocate birds that had dispersed away from field sites every other week.

Estimating Movement Probabilities

We modeled Black-backed Woodpecker movement dynamics with a Bayesian multi-state mark-recapture model (Williams et al. 2002, Kéry and Schaub 2012). We considered a 4 state model where Black-backed Woodpeckers could occupy burned forest (state 1), burned forest' (read 'burned forest prime', state 2), MPB infestation (state 3) or MPB infestation' (state 4). The 'prime' designation denotes a bird dispersing between two discrete units of the same disturbance type. For example, a Black-backed Woodpecker occupying the 4-Mile wildfire study site in time step 1 and the Box Elder wildfire study site in time step 2 would transition from burned forest to burned forest' (state 1 to state 2). Note that birds occupying either habitat created by wildfire or

prescribed fire were assumed to occupy a burned forest state. We assumed the following state-transition matrix:

		State at time step t			
		1	2	3	4
State at time step $t - 1$	1	ϕ_{it}	$(1 - \phi_{it}) \gamma$	0	$(1 - \phi_{it}) (1 - \gamma)$
	2	$(1 - \phi_{it}) \gamma$	ϕ_{it}	0	$(1 - \phi_{it}) (1 - \gamma)$
	3	0	$(1 - \phi_{it}) \gamma$	ϕ_{it}	$(1 - \phi_{it}) (1 - \gamma)$
	4	0	$(1 - \phi_{it}) \gamma$	$(1 - \phi_{it}) (1 - \gamma)$	ϕ_{it}

where woodpecker i transitions from the state along the row (the state at time $t - 1$) to the state along the column (the state at time t) with the associated cell probability. We thus modeled a woodpecker's state at time t as a multinomial random variable:

$$state_t \sim multinomial(\mathbf{M}_{t-1}, 1)$$

where \mathbf{M}_{t-1} is the row of the state transition matrix associated with a woodpecker's state at time $t - 1$. We denote the probability of woodpecker i not dispersing between the end of time step $t - 1$ and the end of time step t as ϕ_{it} . Conditional on a bird dispersing, we denote the probability of a bird transitioning to a burned forest as γ . We further modeled the probability of woodpecker i not dispersing between the end of time step $t - 1$ and the end of time step t as a function of disturbance type, sex, number of years post-fire, and whether a nest failed the previous time step:

$$\begin{aligned} \logit(\phi_{it}) = & \beta_0 + \beta_1 wildfire_{i,t-1} + \beta_2 rx_{i,t-1} + \beta_3 sex_i + \beta_4 year_{i,t-1} \times (wildfire_{i,t-1} + rx_{i,t-1}) + \\ & \beta_5 fail_{i,t-1} \end{aligned}$$

where $wildfire_{i,t-1}$ and $rx_{i,t-1}$ are a dummy variables = 1 if woodpecker i is occupying habitat created by wildfire or prescribed fire, respectively, in time step $t - 1$, sex_i is a dummy variable = 1 if woodpecker i is a male, 0 otherwise, $year_{i,t-1}$ is the number of years post-fire in either habitat created by wildfire and prescribed fire, $fail_{i,t-1}$ is a dummy variable = 1 if the nest of woodpecker i failed the previous time step, and β_0, \dots, β_5 are model parameters. We assumed monthly time steps to reflect the maximum time between relocation of birds with active transmitters.

We only included birds in the analysis that were detected for at least two consecutive time steps. We started detection histories the first time step a woodpecker was captured and only modeled detection histories until the final time step a woodpecker was observed. Many detection histories were punctuated by at least 1 period of non-detection, such as when a transmitter failed and a bird was only intermittently detected. We censored portions of detection histories punctuated by periods of non-detection because we did not observe covariates during these time steps and thus could not calculate the probability a bird would be in a particular state. Whenever detection histories were censored, we retained the most recent series of observations where a bird had an active transmitter and was detected in at least two successive time steps.

Birds were assigned a state corresponding to the habitat they occupied at the end of a time step. We coded a bird as having transitioned from a state at time step $t - 1$ to a new state at time step t if the bird left one discrete disturbance for another discrete disturbance, and was not observed again in the previous disturbance. For example, a woodpecker was considered to have transitioned from state 1 to state 2 (or equivalently from state 2 to state 1) if it occupied one discrete prescribed fire site in time step $t - 1$ and

occupied another discrete prescribed fire site in time step t . We only considered birds to have transitioned to a new state if we obtained at least 2 successive locations that were within 4 km. This 4 km rule is based on the approximate diameter of the largest home range reported in *Chapter 2* (based on $n = 74$ estimated home ranges). A bird was not considered to have transitioned to a new state if we only obtained a single detection > 4 km from prior or subsequent detections because such detections may represent part of a dispersal path. Birds are likely to encounter many habitats while dispersing, but this does not mean they transition to that habitat. If first or last observations were > 4 km from successive locations, we begin or end detection histories during the time step when at least 2 observations were collected within 4 km.

We fit multi-state models in WinBUGS (Gilks et al. 1994) via the R2WinBUGS interface (Sturtz et al. 2005). We assumed vague $N(\mu = 0, \sigma^2 = 100)$ prior distributions for the β_0, \dots, β_5 parameters and we assumed a uniform(0, 1) prior distribution for the γ parameter. We simulated posterior distributions of all parameters from 3 Markov chains, each of which ran for 150,000 iterations, with the first 50,000 iterations discarded as burn-in. We kept every 100th sample to minimize correlation between successive draws. Estimates of posterior distributions are thus based on 1,000 draws from each Markov chain for a total of 3,000 random samples from the posterior distribution of each parameter. The Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998) indicated adequate convergence ($\hat{R}=1$) for all parameters.

Results

We estimated dispersal and transition probabilities from 122 Black-backed Woodpeckers. Detection histories of approximately 24% of individuals included at least 1 time step when an individual was not detected. After censoring, the dataset consisted of 276, 150, and 345 cumulative months in habitat created by wildfire, prescribed fire, and MPB infestations, respectively. Our analysis included a total of 18 transitions with a mean dispersal distance of 18 km (range = 4 – 60 km, Fig. 4.2).

The probability of dispersal during a single time step was associated with nest failure the previous time step and the number of years post fire. For example, a female occupying 2-year post-wildfire habitat dispersed with probability 0.24 (95% CI = [0.06, 0.53]) if a nest failed the previous time step, but dispersed with probability 0.02 (95% CI = [0.00, 0.04]) if a nest did not fail the previous time step (Fig. 4.3). The probability of dispersal was also positively associated with the number of years post fire. For example, a female whose nest did not fail the previous time step dispersed with probability 0.01 (95% CI = [0.00, 0.03]) from a 1-year post-wildfire habitat and dispersed with probability 0.09 (95% CI = [0.02, 0.22]) from a 4-year post-wildfire habitat (Fig. 4.4). The probability of dispersal during a single time step was not strongly associated with sex. For example, a male that occupied 1-year post-fire habitat and whose nest did not fail the previous time step dispersed with probability 0.01 (95% CI = [0.00, 0.03]), which is nearly identical (within rounding error) to the female in the same habitat described above.

Habitat-specific dispersal probabilities during a single time step differed primarily as a function of the number of years post-fire. The probability of dispersing from MPB infestations, 1-year post-wildfire and 1-year post-prescribed fire habitat during a single

time step was similar. For example, a female whose nest did not fail the previous time step dispersed with probability 0.003 (95% CI = [0.000, 0.010]) from an MPB infestation, dispersed with probability 0.007 (95% CI = [0.001, 0.025]) from 1-year post-wildfire habitat, and dispersed with probability 0.006 (95% CI = [0.001, 0.020]) from 1-year post-prescribed fire habitat (note that birds were rarely observed in 1-year post-prescribed fire habitat, *Chapter 2*). Subsequent changes in dispersal probabilities were attributed to the number of years post-fire rather than habitat-specific differences (Fig. 4.5).

Dispersing Black-backed Woodpeckers transitioned to burned forest and MPB infestations with a greater probability relative to the availability of these habitats in the Black Hills. Dispersing birds transitioned to burned forest with probability 0.45 (95% CI = [0.24, 0.67]) and to an MPB infestation with probability 0.55 (95% CI = [0.33, 0.76]). Over the period 2008 – 2011, there was an average of approximately 4,545 ha of 1-5 year post-fire forest in the Black Hills (Unpublished data, Black Hills National Forest, Custer, SD), approximately 1.0% of the forested area of the Black Hills (USDA 2009a). Over the same period, there was an average of approximately 17,957 ha of MPB infested forest in the Black Hills (USDA 2008, USDA 2009b, USDA 2010, USDA 2011b), approximately 3.8% of the forested area of the Black Hills (USDA 2009a). Black-backed Woodpeckers were thus 46 (95% CI = [25, 69]) times more likely to transition to burned forest relative to mean availability, while Black-backed Woodpeckers were 14 (95% CI = [9, 20]) times more likely to transition to MPB infested forest relative to mean availability (Fig. 4.6). Even though Black-backed Woodpeckers demonstrated an

apparently greater probability of transitioning to MPB infestations, they transitioned to burned forest with greater probability relative to the available habitat.

Discussion

We found that the probability of dispersal during a single time step was strongly associated with factors that influence fitness. The probability of dispersal during a single time step was most strongly associated with nest failure during the previous time step, a clear determinant of fitness. We also found dispersal probability increased with the number of years post-fire. The results of *Chapter 1* suggest decreasing adult and juvenile survival as the number of years post-fire increased, suggesting that fitness in general may decline with increasing years post-fire. Several factors may contribute to decreasing fitness with increasing time post-fire. Wood-boring beetle larvae are a primary food source of Black-backed Woodpeckers in recently burned forests, but most wood-boring beetle larvae pupate by 2-years post-fire (Murphy and Lehnhausen 1998). Furthermore, the results of *Chapter 3* suggest Black-backed Woodpeckers had the lowest apparent foraging success for wood-boring beetles in 3-year post-fire habitat. Food resources are likely a strong determinant of fitness (Siikamäki 1998, Strong and Sherry 2000) and Black-backed Woodpeckers may use declining food resources as a proximate cue to disperse from aging forest burns.

We also found the probability of a Black-backed Woodpecker transitioning to either a burned forest or an MPB infestation was high relative to the availability of these habitats across the Black Hills. However, the likelihood of transitioning to a burned forest, relative to availability, was several times greater than the probability of

transitioning to an MPB infestation. This suggests Black-backed Woodpeckers may prefer burned forests over MPB infestations when recently burned forests are available, and is consistent with suggestions that Black-backed Woodpeckers are a post-fire specialist (Hutto 1995, 2008). Furthermore, an apparent preference for burned forests relative to MPB infestations is consistent with positive population growth rates estimated in post-wildfire forest and negative population growth rates estimated in MPB infestations (*Chapter 1*). The apparent preference for burned forest relative to MPB infestations may explain a failure to observe Black-backed Woodpeckers in MPB infested habitats in portions of their range with readily available burned forests (Cilimburg et al. 2006, Edworthy et al. 2011). Although there is not likely a linear relationship between the area of burned forest available and the probability of transitioning to a burned forest, a preference for burned forest relative to MPB infestations may result in woodpeckers rarely settling in MPB infestations if there is an adequate area of recently burned forest (*sensu* Fretwell and Lucas 1970). Despite this apparent preference for burned forests, Black-backed Woodpeckers were still more likely to transition to MPB infestations relative to availability, suggesting MPB infestations may hold greater value to Black-backed Woodpeckers than undisturbed forest.

Although Black-backed Woodpeckers exhibited an apparent preference for burned forest relative to MPB infestations, they were least likely to disperse away from MPB infestations in a single time step relative to burned forest, particularly compared to 4-year post-fire habitat. This may be because MPB infestations represent relatively stable habitat compared to post-wildfire habitat. Wildfires and prescribed fires occur as discrete disturbances. In contrast, MPB infestations occur over a much longer time

period and a new cohort of trees are infested with MPBs every summer. Thus, food resources for Black-backed Woodpeckers in active MPB infestations may not diminish through time. Additionally, Black-backed Woodpecker density can be up to 4 times greater in recently burned forests (*Chapter 2*) relative to MPB infestations, and we rarely observed adjacent Black-backed Woodpecker territories in MPB infestations. There may thus be less competition for space in MPB infestations relative to post-fire habitat, leading to lower overall dispersal probabilities (Greenwood 1980).

We found that Black-backed Woodpecker movements were most strongly associated with nest failure in the previous time step. This may represent a bet-hedging life history strategy for Black-backed Woodpeckers, since bet hedgers typically have high annual survival but variable reproductive success among years (Sæther et al. 1996). Nest failure is commonly associated with breeding dispersal (Catlin and Rosenberg 2008, Schaub and von Hirschheydt 2009) and may be a strong proximate cue associated with habitat quality. Nest failure may thus be an easily accessed indicator of habitat quality for Black-backed Woodpeckers, since population growth rates are largely insensitive to variation in this demographic rate (*Chapter 1*). Indeed, species that rely on ephemeral habitats in general may need to rely on ‘cheap’ but reliable cues of habitat quality in order to know the appropriate time to disperse.

Dispersal and transition probabilities are an essential component of the population dynamics of species relying on ephemeral habitats. Individual habitat patches are dynamic in time and space, and it is thus critical to understand how long habitat patches are available to a species and how likely individuals are to move among patches. Black-backed Woodpeckers have recently been proposed for listing under the Endangered

Species Act (Hanson et al. 2012) and knowledge of the population dynamics of this sensitive species will be essential in the listing and recovery process. An understanding of movement dynamics, coupled with demographic data (*Chapter 1*), can thus be used to more fully understand population dynamics and to evaluate the relative outcomes of different potential management plans.

Our study of the movement dynamics of Black-backed Woodpeckers provides important insights into this ephemeral habitat specialist. Our evaluation of the factors associated with dispersal probabilities improves our understanding of how long particular disturbed patches may be available to Black-backed Woodpeckers. Additionally, our evaluation of transition probabilities may help explain apparently high use of MPB infestations in the Black Hills, which is likely a function of greater availability relative to recently burned forest, rather than a preference for this disturbance type. Finally, we expect estimates of movement probabilities will inform population viability analyses that can be used to model landscape-level population dynamics of this sensitive species. In general, we expect evaluation of such movement dynamics may improve our ability to understand the dynamics of species that rely on ephemeral habitats.

Table 4.1: Study sites used to evaluate movement of Black-backed Woodpeckers in the Black Hills, South Dakota, USA.

Site	Habitat	Coordinates	Size (Ha) ^a	Month / Year Disturbed ^b	Years Included in Study ^a
Ricco	Wildfire	44°13'N, 103°25'W	1,602	July 2005	2008, 2010
Box Elder	Wildfire	44°9'N, 103°24'W	129	July 2007	2008, 2009
4-Mile	Wildfire	43°41'N, 103°26'W	955	June 2007	2008 - 2011
Bullock	Rx Fire	44°0'N, 103°30'W	486	Sept. 2008	2010 – 2012
Bitter	Rx Fire	43°58'N, 103°26'W	304	Oct. 2010	2012
Headquarters West	Rx Fire	43°34'N, 103°30'W	255	Sept. 2009	2011
American Elk	Rx Fire	43°61'N, 103°49'W	1376	Oct. 2010	2012
Norbeck	MPB	43°50'N, 103°30'W	> 213 ^c	1998	2008
Bear Mountain	MPB	43°51'N, 103°45'W	> 48 ^c	Before 1995	2008 – 2011
East Slate Creek	MPB	43°58'N, 103°44'W	> 1,303 ^d	Before 1995	2008 - 2011
Deerfield Lake	MPB	44°00'N, 103°49'W	> 169 ^c	Before 1995	2008
Medicine Mountain	MPB	43°52'N, 103°42'W	> 1,748 ^d	Before 1995	2009 - 2011

- ^a Size of MPB infestations Calculated from FHP Aerial Detection Surveys, available at <http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3_041629> (accessed Feb. 13, 2013). This is an estimate of the minimum total area impacted by MPBs in each study site in a given year.
- ^b The first year MPB infestations were detected in FHP Aerial Detection Surveys. Note there is no aerial detection data prior to 1995.
- ^c calculated from 2008 FHP Aerial Detection Survey
- ^d calculated from 2010 FHP Aerial Detection Survey

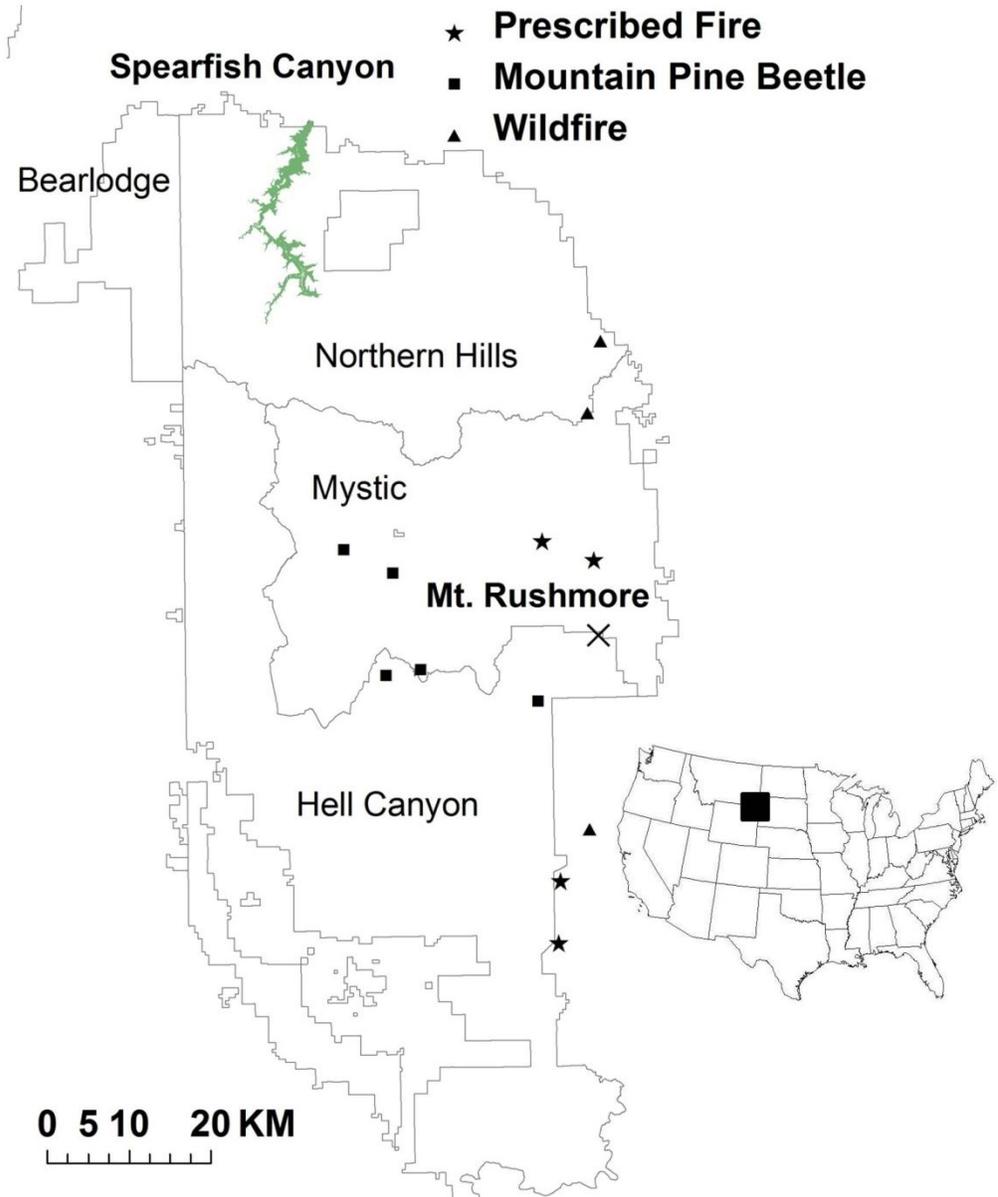


Figure 4.1: Administrative units within the Black Hills National Forest. Aerial telemetry flights for Black-backed Woodpeckers with potentially active transmitters were conducted over forested portions of the Hell Canyon, Mystic, and Northern Hills Ranger Districts. North-south aerial telemetry transects were spaced approximately 5 km apart and were approximately bounded on the east by Mt. Rushmore, on the west by Spearfish Canyon, and on the north and south by forested portions of the Black Hills (which corresponds with northern and southern limits of the Black Hills National Forest). The locations of wildfire, prescribed fire, and mountain pine beetle infested study sites are indicated on the map.

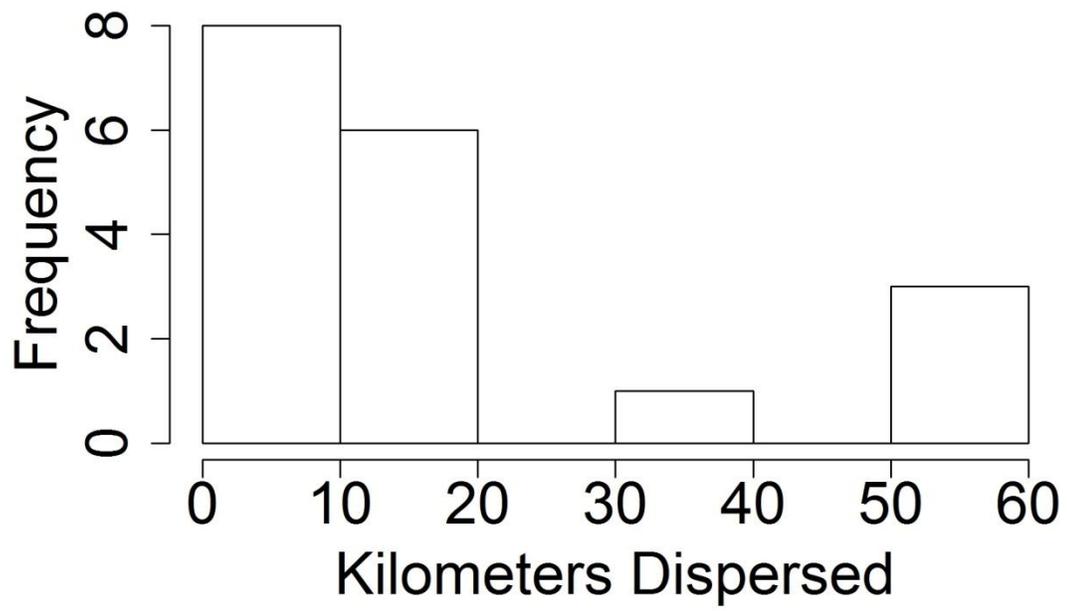


Figure 4.2: Histogram of observed dispersal distances of Black-backed Woodpeckers in the Black Hills, South Dakota.

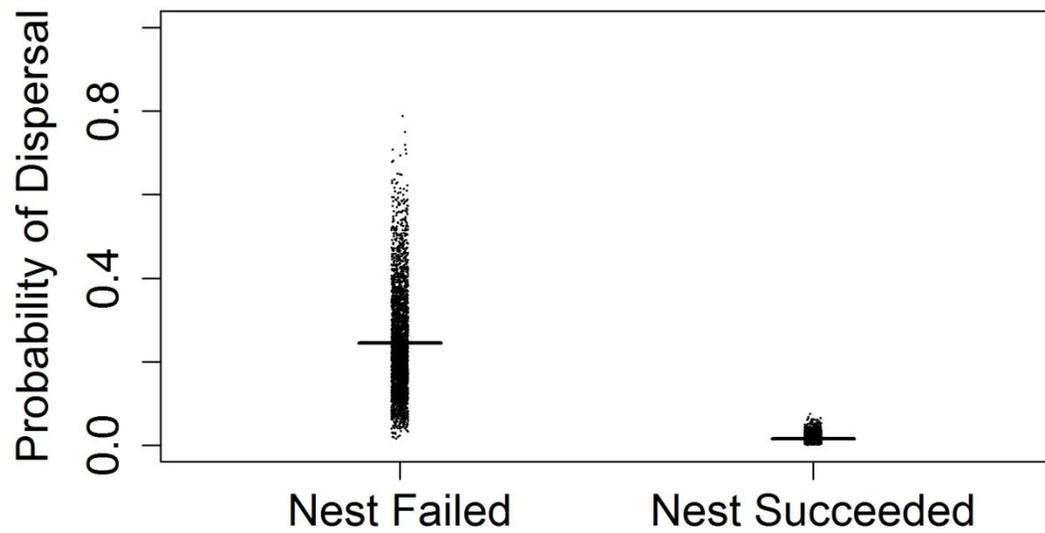


Figure 4.3: Realized results from the posterior distributions of the probability a female Black-backed Woodpecker disperses from a 2-year post-wildfire forest in a single time step (1 month) as a function of whether a nest succeeded or failed the previous month. The dots represent a random draw from each posterior distribution and horizontal lines represent means of each posterior distribution.

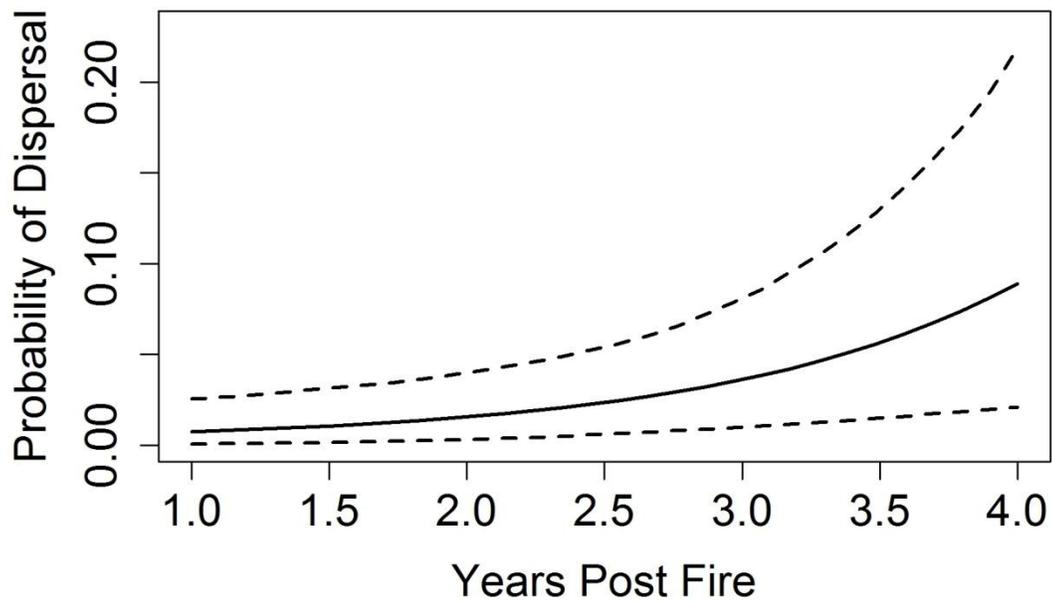


Figure 4.4: The probability of a female Black-backed Woodpecker whose nest did not fail dispersing from a post-wildfire forest during a single time step (1 month) as a function of the number of years post-fire. The solid line represents the mean probability of dispersing and the dashed line represents 95% credible intervals.

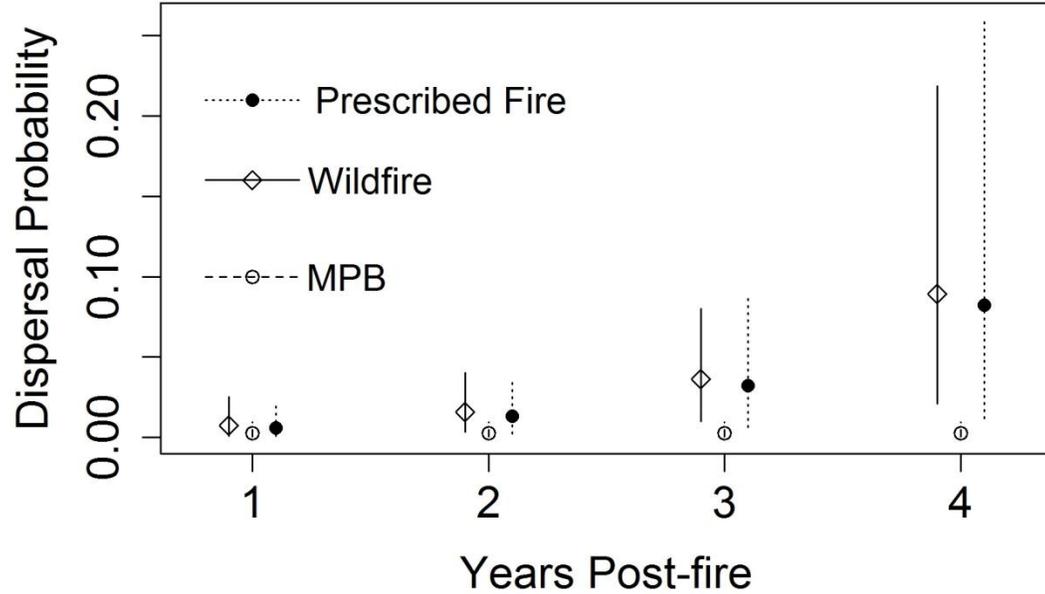


Figure 4.5: The probability of a female Black-backed Woodpecker whose nest did not fail the previous time step dispersing during a single time step (1 month) as a function of habitat (wildfire, prescribed fire, and mountain pine beetle infestation (MPB)) and the number of years post-fire. Points represent mean dispersal probabilities and vertical lines represent 95% credible intervals.

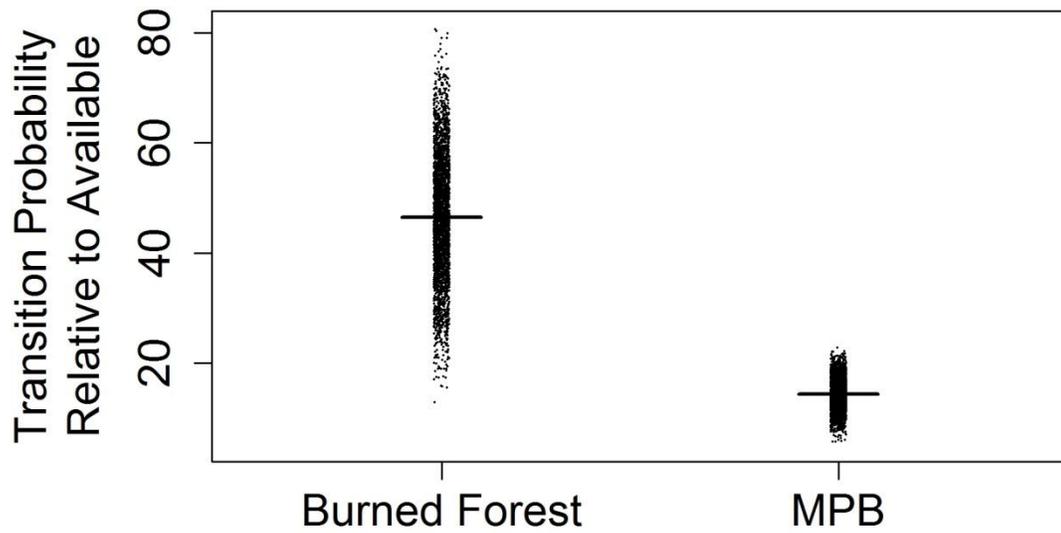


Figure 4.6: The relative probability (estimated probability of transitioning to a burned forest or mountain pine beetle (MPB) infestation divided by the proportion of that disturbance type in the Black Hills) of a dispersing Black-backed Woodpecker transitioning to a burned forest or MPB infestation. Points represent random realizations from the posterior distributions of relative probabilities, and horizontal lines represent the mean of each distribution.

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APPENDIX 1: STATISTICAL METHODS FOR MODELING DEMOGRAPHIC RATES OF BLACK-BACKED WOODPECKERS

Detection Probability

We modeled detection probability as a function of whether woodpecker i had an active transmitter during timestep t :

$$\text{logit}(p_{it}) = \alpha_0 + \alpha_1 \tau_{it}$$

where $\tau_{it} = 1$ if woodpecker i has an active transmitter during timestep t , 0 otherwise, and α_0 and α_1 are regression coefficients. Because we do not know exactly how long transmitters lasted if we failed to observe woodpeckers, we assumed adult transmitters were active for 5 time steps (5 months) and juvenile transmitters were active for 7 time steps (14 weeks), unless we observed otherwise (e.g., observed a woodpecker with an inactive transmitter prior to the assumed fail time or observed a woodpecker with an active transmitter beyond the assumed fail time). If transmitters were active beyond the assumed fail time, we assumed the transmitter failed the time step immediately following the last observation with an active transmitter.

Adult Survival Probability

We modeled monthly adult survival probability as a function of sex, season, habitat, and number of years post-fire:

$$\begin{aligned} \text{logit}(\phi_{it}^{ad}) = & \beta_0^{ad} + \beta_1^{ad} \zeta_i + \beta_2^{ad} \gamma_{it} + \beta_3^{ad} \omega_{it}^{ad} + \beta_4^{ad} x_{it}^{ad} \\ & + \beta_5^{ad} \eta_{it}^{ad} (\omega_{it}^{ad} + x_{it}^{ad}) \end{aligned} \quad \text{Eqn. A1.1}$$

where $\zeta_i = 1$ if adult woodpecker i is male, 0 if female, $\gamma_{it} = 1$ if the observation of adult woodpecker i is made during the breeding season (April –September), 0 if made during the non-breeding season, $\omega_{it}^{ad} = 1$ if adult woodpecker i is occupying habitat created by

wildfire at the end of time step t , 0 otherwise, $x_{it}^{ad} = 1$ if adult woodpecker i is occupying habitat created by prescribed fire at the end of time step t , 0 otherwise, η_{it}^{ad} is the age (in years) of habitat created by wildfire or prescribed fire adult woodpecker i occupied at the end of time step t ($\eta_{it}^{ad} \in [0, 1, 2, 3, 4, 5]$), and $\beta_0^{ad}, \dots, \beta_5^{ad}$ are regression coefficients. Note that the time since fire term applies only to woodpeckers occupying habitat created by wildfire or prescribed fire, since $\omega_{it}^{ad} + x_{it}^{ad} = 0$ if adult woodpecker i is occupying habitat created by MPB infestations at the end of time step t .

Juvenile Survival Probability

We modeled juvenile bi-weekly survival probability as a function of habitat (wildfire, MPB, and prescribed fire), the number of years post-fire, and the number of two-week time intervals since fledging:

$$\begin{aligned} \text{logit}(\phi_{it}^{juv}) = & \beta_0^{juv} + \beta_1^{juv} \omega_{it}^{juv} + \beta_2^{juv} x_{it}^{juv} \\ & + \beta_3^{juv} \eta_{it}^{juv} (\omega_{it}^{juv} + x_{it}^{juv}) + \beta_4^{juv} \log(\delta_{it}) \end{aligned} \quad \text{Eqn. A1.2}$$

where $\omega_{it}^{juv} = 1$ if juvenile i occupied habitat created by wildfire at the end of time step t , 0 otherwise, $x_{it}^{juv} = 1$ if juvenile i occupied habitat created by prescribed fire at the end of time step t , 0 otherwise, η_{it}^{juv} is the age (in years) of habitat created by wildfire or prescribed fire juvenile i occupied at the end of time step t ($\eta_{it}^{juv} \in [0, 1, 2, 3, 4, 5]$), δ_{it} is the number of time steps juvenile i has been fledged from the nest at the end of time step t ($\delta_{it} \in [1, 2, \dots, 21]$), and $\beta_0^{juv}, \dots, \beta_4^{juv}$ are regression coefficients. Modeling juvenile survival probability as a function of the \log_e number of time steps fledged allowed survival probability to change in a non-linear manner.

We fit adult and juvenile MSMR models in WinBUGS (Gilks et al. 1994) via the R2WinBUGS interface (Sturtz et al. 2005). We assumed vague $N(\mu = 0, \sigma^2 = 1,000)$ prior distributions on all regression coefficients. We simulated posterior distributions of all regression coefficients from 3 Markov chains, each of which ran for 5.5 million iterations and discarding the first 500,000 iterations as burn-in. There was evidence of correlation within Markov chains so we kept every 50th iteration to reduce correlation between successive draws. Estimates of posterior distributions are thus based on 100,000 draws from each Markov chain for a total of 300,000 random draws from the posterior distribution of each regression coefficient. The Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998) indicated adequate convergence ($\hat{R}=1$) for all regression coefficients.

Daily Nest Survival Probability

We assume survival ($y_{it} = 1$) or failure ($y_{it} = 0$) of nest i during day t is a Bernoulli random variable:

$$y_{it} \sim \text{Bernoulli}(\psi_{it})$$

where ψ_{it} is the probability nest i survives day t . We further modeled daily survival probability as a function of habitat and time since fire:

$$\begin{aligned} \text{logit}(\psi_{it}) = & \theta_0 + \theta_1 \omega_i^{nest} + \theta_2 x_i^{nest} \\ & + \theta_3 \eta_i^{nest} (\omega_i^{nest} + x_i^{nest}) \end{aligned} \tag{Eqn. A1.3}$$

where $\omega_i^{nest} = 1$ if nest i is located in habitat created by wildfire, 0 otherwise, $x_i^{nest} = 1$ if nest i is located in habitat created by prescribed fire, 0 otherwise, η_i^{nest} is the age (in years) of habitat created by wildfire or prescribed where nest i was located ($\eta_i^{nest} \in [0, 1, 2, 3, 4, 5]$), and $\theta_0, \dots, \theta_3$ are regression coefficients.

We fit nest survival models in WinBUGS via the R2WinBUGS interface. We assumed vague $N(\mu = 0, \sigma^2 = 1,000)$ prior distributions on all regression coefficients. We simulated posterior distributions of all regression coefficients from 3 Markov chains, each of which ran for 110,000 iterations, with the first 10,000 iterations discarded as burn-in. Estimates of posterior distributions are thus based on 100,000 draws from each Markov chain for a total of 300,000 random draws from the posterior distribution of each regression coefficient. The Brooks-Gelman-Rubin convergence diagnostic indicated adequate convergence ($\hat{R}=1$) for all regression coefficients.

Expected Number of Young Fledged

We modeled the number of young fledged (z_i) from successful nest i using a zero-truncated Poisson model:

$$z_i \sim \text{truncated Poisson}(\rho_i)$$

where $k_i = \rho_i / (1 - e^{-\rho_i})$ is the expected number of young fledged from nest i (David and Johnson 1952). We modeled the number of young fledged as a function of habitat:

$$\log(\rho_i) = \pi_0 + \pi_1 \omega_i^{nest} + \pi_2 x_i^{nest} \quad \text{Eqn. A1.4}$$

where π_0 , π_1 , and π_2 are regression coefficients.

A zero-truncated Poisson distribution is not among the distributions offered in the WinBUGS package. We therefore wrote a Metropolis-Hastings algorithm to sample from the posterior distributions of model parameters. We tuned the Metropolis-Hastings algorithm to have an acceptance probability of approximately 20% (King et al. 2010, p. 131). We assumed vague $N(\mu = 0, \sigma^2 = 1,000)$ prior distributions on all regression coefficients. We simulated posterior distributions of all regression coefficients from 3 Markov chains, each of which ran for 5.1 million iterations with the first 100,000

iterations discarded as burn-in. To minimize correlation within chains due to the accept / reject step in the Metropolis-Hastings algorithm, we kept every 50th iteration. Estimates of posterior distributions are thus based on 100,000 draws from each Markov chain for a total of 300,000 random draws from the posterior distribution of each regression coefficient. The Brooks-Gelman-Rubin convergence diagnostic indicated adequate convergence ($\hat{R} \approx 1$) for all regression coefficients.

Scaling Demographic Rates

We calculated habitat specific fecundity (m_h) as a function of habitat specific nest success and number of young fledged per successful nest:

$$m_h = \varepsilon_h(\kappa_h/2)$$

where ε_h is habitat specific nest success, defined as the probability a nest in habitat h successfully fledges young. We divided the expected number of young fledged per nest, κ_h , by 2 because we assume a 50:50 fledgling sex ratio. We estimated habitat-specific growth rates by calculating the dominant eigenvalue of projection matrix A_h .

We calculated habitat specific fecundity, annual adult survival probability, and the probability a juvenile survives to the adult stage class as a function of the regression coefficients estimated from demographic analyses above and habitat-specific covariates.

We calculated habitat-specific annual female adult survival as:

$$\text{logit}(P_h^{ad}) = [\hat{\beta}_0^{ad} + \hat{\beta}_2^{ad}\gamma + \hat{\beta}_3^{ad}I_{wild} + \hat{\beta}_4^{ad}I_{Rx} + \hat{\beta}_5^{ad}\eta(I_{wild} + I_{Rx})]^6 \times$$

$$[\hat{\beta}_0^{ad} + \hat{\beta}_3^{ad}I_{wild} + \hat{\beta}_4^{ad}I_{Rx} + \hat{\beta}_5^{ad}\eta(I_{wild} + I_{Rx})]^6$$

where I_{wild} and I_{Rx} are indicator variables = 1 if habitat h is wildfire or prescribed fire, respectively, 0 otherwise, and $\hat{\beta}_0^{ad}, \dots, \hat{\beta}_5^{ad}$ represent random samples from the posterior distributions of regression coefficients defined in Eqn. A1.1. Equations are raised to the

6th power because adult survival probability was modeled on monthly time steps. Note the term $\hat{\beta}_2^{ad}\gamma$ represents the regression coefficient for season-specific adult survival probability, which is why the term is excluded from the equation for 6 months. We calculated the habitat-specific probability a juvenile will survive to an adult as:

$$\text{logit}(P_h^{Juv}) = \prod_{j=1}^{21} [\hat{\beta}_0^{juv} + \hat{\beta}_1^{juv} I_{wild} + \hat{\beta}_2^{juv} I_{Rx} + \hat{\beta}_3^{juv} \eta(I_{wild} + I_{Rx}) + \hat{\beta}_4^{juv} \log(j)]$$

where $\hat{\beta}_0^{juv}, \dots, \hat{\beta}_4^{juv}$ represent random samples from the posterior distributions of regression coefficients defined in Eqn. A1.2. Note that the estimate of the probability a juvenile survives to the adult stage class incorporates a different survival probability for each time step fledged. By multiplying this term over 21 time steps, we assume a fledge date of approximately 24 June and that juveniles transition to the adult stage by approximately 1 April the following year. We calculate habitat-specific nest success as:

$$\text{logit}(\varepsilon_h) = [\hat{\theta}_0 + \hat{\theta}_1 I_{wild} + \hat{\theta}_2 I_{Rx} + \hat{\theta}_3 \eta(I_{wild} + I_{Rx})]^{36}$$

where $\hat{\theta}_0, \dots, \hat{\theta}_3$ represent random samples from the posterior distributions of regression coefficients defined in Eqn. A1.3. Our calculation of habitat-specific nest success assumes a 36 day nesting period (incubation period = 13 days, nestling period = 23 days), which was based on observed length of nesting periods and closely corresponds with the published literature (Dixon and Saab 2000, Bonnot et al. 2008). Our nesting period was three days longer than Bonnot et al. (2008) because we assumed the nest was at risk of failure the day the first egg was laid. Finally, we calculated the expected number of young fledged in habitat h as:

$$k_h = \frac{\rho_h}{(1 - e^{-\rho_h})}$$

where

$$\log(\rho_h) = \hat{\pi}_0 + \hat{\pi}_1 I_{wild} + \hat{\pi}_2 I_{Rx}$$

and $\hat{\pi}_0, \dots, \hat{\pi}_2$ represent random samples from the posterior distributions of regression coefficients defined in Eqn. A1.4.

We estimated the posterior distribution of habitat specific fecundity, annual adult survival probability, and the probability a juvenile survives to the adult stage class by repeatedly sampling from the posterior distributions of component regression coefficients. This repeated sampling allowed us to propagate uncertainty in estimated regression coefficients throughout the modeling process. We repeated this process 300,000 times for each habitat-specific demographic rate. Finally, we estimated the posterior distribution of habitat-specific growth rates by constructing 300,000 random projection matrices for each habitat, with each cell element comprising a random draw from the posterior distribution of habitat-specific adult survival, juvenile survival, and fecundity.

APPENDIX 2: DERIVATION OF RELATIVE FOOD RESOURCE EQUATION

Motivation for Relative Food Resource Equation

Let $a = 1$ wood-boring beetle larva captured from a tree in *MPB habitat*. We let $a = 1$ wood-boring beetle larva because the rest of the variables are calculated relative to a .

Let $b =$ the expected number of *small prey* captured from a tree in *MPB habitat* for every 1 wood-boring beetle larva captured from a tree in *MPB habitat*.

Let $c =$ the expected number of *wood-boring* beetle larvae captured from a tree in *wildfire habitat* for every 1 wood-boring beetle larva captured from a tree in *MPB habitat*.

Let $d =$ the expected number of *small prey* captured from a tree in *wildfire habitat* for every 1 wood-boring beetle larva captured from a tree in *wildfire habitat*.

By standardizing relative to 1 wood-boring beetle larva in *MPB habitat*, we get relative counts for both prey in both habitats. For example, a is directly comparable to c in terms of counts of wood-boring beetle larvae between *wildfire* and *MPB infestations*.

The motivation for equation 3.1 is simple. How many extra units of food resources, denoted x , does a wood-boring beetle larva need to provide relative to small prey for total food resources per tree in *MPB* and *wildfire habitat* to be equal? The equation below assumes equal food resources in each habitat:

$$ax + b = cx + cd.$$

The left hand side of this equation is food resources in *MPB infestations*, and the right hand side is food resources in *wildfire habitat*. Here, x can be interpreted as the

ratio of wood-boring beetle larvae food resources to food resources provided by small prey. It can also be thought of as the amount of ‘extra’ food wood-boring beetle larvae need to provide relative to a small prey for food resources between habitats to be equal.

Notice that we multiply d by c so that we standardize by a . For example, assume we get 2 wood-boring beetle larvae in wildfire habitat for every 1 wood boring beetle larva in MPB habitat. Further assume we get 2 small prey in wildfire habitat for every 1 wood-boring beetle larva in wildfire habitat. We then get 4 small prey in wildfire habitat for every 1 wood-boring beetle larva in MPB habitat.

Substituting Model Parameters

Recall that $\hat{\beta}_0^{wb}$ is the intercept parameter in the wood-boring beetle model. This intercept parameter represents trees in MPB infestations. Thus, the expected number of wood-boring beetle larvae successfully captured from a tree in an MPB infestation is $e^{\hat{\beta}_0^{wb}}$ (because I used a log link with the negative binomial GLMM). Recall also that $\hat{\beta}_0^{sm}$ is the intercept parameter in the small prey model. Thus, the expected number of small prey captured from a tree in an MPB infestation is $e^{\hat{\beta}_0^{sm}}$.

To calculate the expected number of *small beetles* captured from a tree in *MPB habitat* for every 1 wood-boring beetle larva captured from a tree in MPB habitat, we calculate the ratio $e^{\hat{\beta}_0^{sm}}/e^{\hat{\beta}_0^{wb}}$. Notice that this ratio is denoted δ_{mpb} . Also notice that, by definition, $b = e^{\hat{\beta}_0^{sm}}/e^{\hat{\beta}_0^{wb}}$.

Notice that the expected number of wood-boring beetle larvae pulled from a tree in wildfire habitat is $e^{\hat{\beta}_0^{wb} + \hat{\beta}_{wild}^{wb}}$ and that the expected number of small prey pulled from a tree in wildfire habitat is $e^{\hat{\beta}_0^{sm} + \hat{\beta}_{wild}^{sm}}$. This is because the wildfire regression coefficients, $\hat{\beta}_{wild}^{wb}$ and $\hat{\beta}_{wild}^{sm}$, describe the change in expected count of wood-boring beetle larvae and

small prey, respectively, in post-wildfire habitat relative to MPB habitat. To calculate the expected number of *wood-boring* beetle larvae captured in *wildfire habitat* for every 1 wood-boring beetle larva captured in MPB habitat, we calculate the ratio $e^{\widehat{\beta}_0^{wb} + \widehat{\beta}_{wild}^{wb}} / e^{\widehat{\beta}_0^{wb}} = e^{\widehat{\beta}_{wild}^{wb}}$. Notice that, by definition, $c = e^{\widehat{\beta}_{wild}^{wb}}$.

Finally, to calculate the expected number of *small prey* captured in *wildfire* habitat for every 1 wood-boring beetle larva captured in wildfire habitat, we calculate the ratio $e^{\widehat{\beta}_0^{sm} + \widehat{\beta}_{wild}^{sm}} / e^{\widehat{\beta}_0^{wb} + \widehat{\beta}_{wild}^{wb}}$. Notice that, by definition, $d = e^{\widehat{\beta}_0^{bb} + \widehat{\beta}_{wild}^{bb}} / e^{\widehat{\beta}_0^{wb} + \widehat{\beta}_{wild}^{wb}}$. Notice also that this ratio is denoted δ_{wild} .

Recall the basic motivating equation:

$$ax + b = cx + cd.$$

Substituting for a , b , c , and d yields:

$$1 \times x + \frac{e^{\widehat{\beta}_0^{sm}}}{e^{\widehat{\beta}_0^{wb}}} = e^{\widehat{\beta}_{wild}^{wb}} x + e^{\widehat{\beta}_{wild}^{wb}} \frac{e^{\widehat{\beta}_0^{sm} + \widehat{\beta}_{wild}^{sm}}}{e^{\widehat{\beta}_0^{wb} + \widehat{\beta}_{wild}^{wb}}}.$$

Factoring common terms and substituting $\delta_{wild} = \frac{e^{\widehat{\beta}_0^{sm} + \widehat{\beta}_{wild}^{sm}}}{e^{\widehat{\beta}_0^{wb} + \widehat{\beta}_{wild}^{wb}}}$ and $\delta_{mpb} = \frac{e^{\widehat{\beta}_0^{sm}}}{e^{\widehat{\beta}_0^{wb}}}$ yields:

$$x + \delta_{mpb} = e^{\widehat{\beta}_{wild}^{wb}} (x + \delta_{wild}).$$

Finally, solving for x yields:

$$x = \frac{\delta_{mpb} - e^{\widehat{\beta}_{wild}^{wb}} \delta_{wild}}{e^{\widehat{\beta}_{wild}^{wb}} - 1}$$

which is equation 3.1.

VITA

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Christopher first attended graduate school at the University of Florida, where he earned a Master's of Science degree in Wildlife Ecology and Conservation in 2009. Under the advisement of Dr. Robert J. Fletcher, Jr., Christopher studied the problem of imperfect detection when modeling the geographic distribution of landbird species. By spring 2013, Christopher was first author on 3 peer-reviewed publications and contributing author on 2 peer-reviewed publications. Additionally, Christopher was a contributing author on 4 book chapters.