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RESEARCH ARTICLE

Apparent foraging success reflects habitat quality in an irruptive species, the Black-backed Woodpecker

Christopher T. Rota,[1]* Mark A. Rumble,[2] Chad P. Lehman,[3] Dylan C. Kesler,[1] and Joshua J. Millspaugh[1]

[1] Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, Missouri, USA
[2] Forest and Grasslands Research Laboratory, Rocky Mountain Research Station, Rapid City, South Dakota, USA
[3] South Dakota Department of Game, Fish and Parks, Custer State Park, Custer, South Dakota, USA
* Corresponding author: rotact@missouri.edu

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ABSTRACT

Dramatic fluctuations in food resources are a key feature of many habitats, and many species have evolved a movement strategy to exploit food resources that are unpredictable in space and time. The availability of food resources may be a particularly strong determinant of habitat quality for irruptive bird species. We studied the apparent foraging success of Black-backed Woodpeckers (*Picoides arcticus*), an irruptive species that responds opportunistically to pulsed food resources in burned forests and mountain pine beetle (MPB) infestations. Prior investigations revealed that the highest population growth rates of Black-backed Woodpeckers occurred in habitat created by summer wildfire, with intermediate population growth rates in MPB infestations, and the lowest population growth rates in habitats created by prescribed fire in fall. We tested whether apparent foraging success was associated with known habitat quality in order to assess the potential for food availability to regulate population growth. We counted the number of successfully captured wood-boring beetle larvae and "small" prey on each tree that a Black-backed Woodpecker used for foraging and modeled these counts as a function of habitat, tree diameter, number of years postfire, and tree disturbance category. Total apparent foraging success (the sum of observed captures of wood-boring beetle larvae and small prey per tree) did not vary across habitats, but woodpeckers foraging in habitats created by summer wildfire were expected to capture 2.2 and 2.0 times more wood-boring beetles than woodpeckers foraging in habitats created by fall prescribed fire and MPB infestations, respectively. These results suggest that the availability of food resources may contribute to population regulation in this irruptive species. Furthermore, population growth in irruptive species may be highly sensitive to the availability of preferred food resources. Forests recently burned by summer wildfires provide relatively abundant food resources for Black-backed Woodpeckers and represent high-quality habitat for this species of conservation concern.

Keywords: bark beetles, disturbance, ephemeral habitat, foraging, wood-boring beetles

Le succès de recherche alimentaire apparent reflète la qualité de l'habitat chez une espèce irruptive, *Picoides arcticus*

RÉSUMÉ

Une fluctuation dramatique des ressources alimentaires est une caractéristique importante de nombreux habitats et plusieurs espèces ont développé une stratégie de mouvement pour exploiter les ressources alimentaires qui sont imprévisibles dans l'espace et le temps. La disponibilité des ressources alimentaires peut être un déterminant particulièrement fort de la qualité de l'habitat chez les espèces aviaires irruptives. Nous avons étudié le succès de recherche alimentaire chez *Picoides arcticus*, une espèce irruptive qui répond de façon opportuniste aux ressources alimentaires pulsées dans les forêts brûlées et les infestations de dendroctone du pin ponderosa (DPP). Des études antérieures ont révélé les plus hauts taux de croissance des populations de *P. arcticus* dans les habitats créés par des feux de friches estivaux, des taux de croissance des populations intermédiaires dans les infestations de DPP et les plus faibles taux de croissance des populations dans les habitats créés par les feux dirigés automnaux. Nous nous sommes demandés si le succès de recherche alimentaire apparent était associé à la qualité de l'habitat afin d'évaluer le potentiel de la disponibilité de la nourriture à réguler la croissance des populations. Nous avons compté le nombre de larves de scolytes capturées avec succès et de « petites » proies sur chaque arbre utilisé par *P. arcticus* pour s'alimenter et nous avons modélisé ces décomptes comme une fonction de l'habitat, du diamètre de l'arbre, du nombre d'années après le feu et de la catégorie de perturbation de l'arbre. Le succès de recherche alimentaire apparent total (défini comme étant la somme des larves de scolytes et des petites proies par arbre) n'a pas varié entre les habitats mais on s'attendait à ce que les pics s'alimentant dans les habitats créés par les feux de friches estivaux capturent 2,2 et 2,0 fois plus de buprestidés par rapport aux habitats créés par les feux dirigés automnaux et les infestations de DPP, respectivement. Ces résultats suggèrent que la disponibilité des ressources alimentaires peut contribuer à la régulation des populations de cette espèce irruptive. Par ailleurs, la croissance des populations chez les espèces irruptives peut être très sensible à la disponibilité de leurs ressources alimentaires préférées. Les forêts récemment brûlées par les feux de friches estivaux fournissent des ressources alimentaires relativement abondantes pour *P. arcticus* et représentent un habitat de grande qualité pour cette espèce dont la conservation est préoccupante.

Mots-clés: scolytes, perturbation, habitat éphémère, recherche alimentaire, buprestidés

INTRODUCTION

Dramatic fluctuations in food resources are a key feature of many ecosystems. For example, many tree species exhibit marked variation in seed production among years (Koenig and Knops 2000), which can lead to highly variable resources for birds that depend on seeds for food. As a consequence, many bird species have evolved movement strategies that allow them to track food resources that are unpredictable in space and time (Newton 2006a). Such movements may occur over hundreds or thousands of kilometers in response to spatial fluctuations in food resources, for example, Red Crossbills (*Loxia curvirostra*) moving in response to variation in spruce cone crops (Newton 2006b) or Snowy Owls (*Bubo scandiacus*) moving in response to local rodent outbreaks (Kerlinger and Lein 1988). Many ecological processes can lead to pulses in food resources, such as mast seeding by numerous tree species (Koenig and Knops 2000), insect outbreaks (Drever et al. 2009, Edworthy et al. 2011), and disturbance events such as wildfire (Powell 2000, Saint-Germain et al. 2004).

Food availability can be a major determinant of habitat quality (Arcese and Smith 1988, Lyons 2005, Johnson 2007). Differences in food availability among habitats may affect reproduction and survival, which in turn may have an impact on population growth rates and fitness (Siikamäki 1998, Strong and Sherry 2000, Norris and Martin 2014). Food resources may be a particularly strong determinant of habitat quality for irruptive bird species, whose life history is shaped around finding food resources that are unpredictable in space and time. Indeed, large-scale irruptions of many bird species are often driven by spatiotemporal fluctuations in food availability (Koenig and Knops 2001, Koenig et al. 2011, Lindén et al. 2011), suggesting that populations of irruptive species may be regulated by pulses of food resources.

The Black-backed Woodpecker (*Picoides arcticus*) is a disturbance-dependent species that responds opportunistically to pulses in prey resources, particularly wood-boring beetles and bark beetles in recently killed trees. In general, the Black-backed Woodpecker is considered to be an irruptive species that exploits various kinds of insect outbreaks throughout its range (Yunick 1985, Dixon and Saab 2000). In particular, Black-backed Woodpeckers are strongly associated with early postwildfire habitat, because of high concentrations of wood-boring beetles (Cerambycidae and Buprestidae) that are attracted to recently burned forests (Hutto 1995, Murphy and Lehnhausen 1998, Tingley et al. 2014), and mountain pine beetle (*Dendroctonus ponderosae*; hereafter MPB) infestations (Goggans et al. 1989, Bonnot et al. 2008, 2009), because of high abundances of bark and wood-boring beetles. Additionally, Black-backed Woodpeckers are known to occupy habitat created by prescribed fire (Russell et al. 2009). Despite apparent preferences for each of these disturbed habitats, Rota et al. (2014a) demonstrated that Black-backed Woodpeckers in the Black Hills of South Dakota, USA, had positive population growth rates only in habitats created by recent wildfire, and had negative growth rates in habitats created by prescribed fire and by MPB infestations, suggesting differences in the relative quality of each of these habitats.

The differences in habitat-specific Black-backed Woodpecker population growth rates observed by Rota et al. (2014a) may have arisen from differences in food availability and foraging success among habitats. Within the Black Hills, several mechanisms may produce differences in food availability among habitats created by wildfire, prescribed fire, and MPB infestations. Differences in food availability between habitats created by wildfire and by MPB infestations may be related to differences in the primary prey item between these two habitats. Wood-boring beetles of the families Cerambycidae and Buprestidae are attracted to early postwildfire habitat (Costello et al. 2011) and feed on the moist phloem of recently killed or dying trees (Saint-Germain et al. 2004). Mountain pine beetles are primarily responsible for the current beetle infestation in the Black Hills (Negrón et al. 2008), although wood-boring beetles and other bark beetles (*Ips* spp.) also occur in MPB infestations. We hereafter assume that wood-boring beetle larvae provide greater food resources relative to bark beetle larvae and other small prey because wood-boring beetles are much larger than bark beetles (Arnett et al. 2002), Black-backed Woodpeckers have adaptations for extracting wood-boring beetle larvae (Spring 1965), and Black-backed Woodpeckers preferentially forage on wood-boring beetle larvae (Beal 1911, Murphy and Lehnhausen 1998). Differences in food availability between habitats created by wildfire and prescribed fire may arise due to the seasonality of these fires. Wildfires are most likely to occur in dry summer months, while forests are often treated with prescribed fire during months

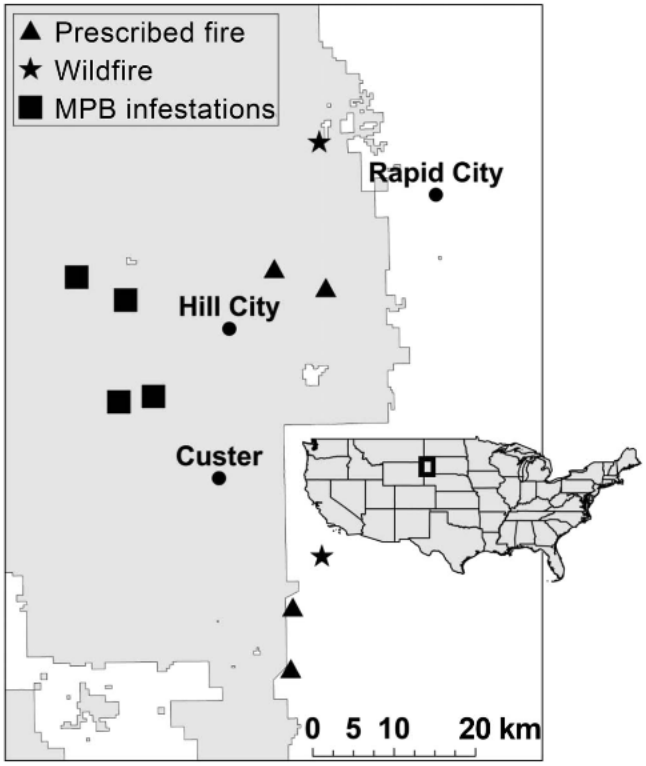

FIGURE 1. Map of study sites for evaluating the apparent foraging success of Black-backed Woodpeckers in habitats created by wildfire, prescribed fire, and mountain pine beetle (MPB) infestations in the Black Hills National Forest (shaded in gray) and surrounding areas, South Dakota, USA, 2008–2012.

when fire is easiest to control, such as spring or autumn (Knapp et al. 2009). Treating forests with prescribed fire during autumn months may prevent wood-boring beetles from immediately colonizing treated forests (M. A. Rumble personal observation), resulting in reduced abundance of wood-boring beetles in habitats created by prescribed fire relative to habitats created by wildfire.

Here we evaluate the potential for food resources to regulate the population dynamics of Black-backed Woodpeckers relying on spatially and temporally varying food resources. We quantify the foraging success of Black-backed Woodpeckers occupying three habitats subject to food pulses—wildfire, prescribed fire, and MPB infestations—that are known to differ in relative quality (Rota et al. 2014a). We indirectly evaluate the potential for food resources to regulate population dynamics by asking whether apparent foraging success is associated with known differences in habitat quality. We address this question by first comparing total apparent foraging success for all prey across habitats created by wildfire, prescribed fire, and MPB infestations. While such an analysis will give a broad overview of differences in foraging success across habitats, it may mask differences in foraging success due to different prey bases (e.g., it may mask the fact that woodpeckers in MPB infestations may compensate for low abundance of wood-boring beetles by capturing more bark beetles). We therefore also compare foraging success for wood-boring beetle larvae and small prey between habitats created by wildfire and by prescribed fire, and between habitats created by wildfire and by MPB infestations. If food resources have the potential to regulate population dynamics, we predict that: (1) total apparent foraging success will be greatest in habitat created by wildfire, or (2) total apparent foraging success will be equivalent across habitats and apparent foraging success for wood-boring beetles will be higher in habitat created by wildfire relative to habitats created by prescribed fire and by MPB infestations.

METHODS

Study Sites

This study occurred between 2008 and 2012 in the Black Hills, South Dakota, USA, at 10 study sites representing habitat created by wildfire, prescribed fire, and MPB infestations (Figure 1, Table 1). Two study sites represented habitat created by wildfire, which burned during June or July (hereafter, we use wildfire synonymously with summer wildfire); 4 study sites represented habitat created by prescribed fires, which were ignited during September or October (hereafter, we use prescribed fire synonymously with fall prescribed fire); and 4 study sites represented habitat created by MPB infestations. 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 in each severity category varied by study site. All MPB infestation study sites contained a mix of trees that had been infested for <1 yr, trees that had been infested for 1–2 yr, and trees that had been infested for >2 yr. Further, although each study site was predominantly composed of one disturbance type (wildfire, prescribed fire, or MPB infestation), most study sites had components of both fire and MPB infestations; most wildfire and prescribed fire study sites had small MPB infestations close to the burn periphery, and several MPB infestation 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).

TABLE 1. Study sites used to evaluate the 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
Box Elder	Wildfire	44°08′N, 103°26′W	129	July 2007	2008–2010
4-Mile	Wildfire	43°41′N, 103°27′W	955	June 2007	2008–2011
Bullock	Prescribed fire	44°00′N, 103°30′W	486	September 2008	2010–2012
Bitter	Prescribed fire	43°58′N, 103°26′W	304	October 2010	2011–2012
Headquarters West	Prescribed fire	43°34′N, 103°30′W	255	September 2009	2010, 2011
American Elk	Prescribed fire	43°37′N, 103°29′W	1,376	October 2010	2012
Bear Mountain	MPB infestation	43°51′N, 103°46′W	>48 [c]	Before 1995	2008, 2010, 2011
East Slate Creek	MPB infestation	43°58′N, 103°43′W	>1,303 [d]	Before 1995	2008–2011
Deerfield Lake	MPB infestation	44°00′N, 103°49′W	>169 [c]	Before 1995	2008–2011
Medicine Mountain	MPB infestation	43°52′N, 103°42′W	>1,748 [d]	Before 1995	2009–2011

[a] Size of mountain pine beetle (MPB) infestations calculated from Forest Health Protection (FHP) Aerial Detection Surveys (http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3_041629). This is an estimate of the minimum total area affected by MPBs in each study site in a given year.
[b] The first year that MPB infestations were detected in FHP Aerial Detection Surveys. Note that there is no aerial detection data prior to 1995.
[c] Calculated from the 2008 FHP Aerial Detection Survey.
[d] Calculated from the 2010 FHP Aerial Detection Survey.

Capture and Radio-Telemetry

We studied the apparent foraging success of Black-backed Woodpeckers by observing radio-tagged birds. We captured woodpeckers using mist nets, hoop nets, and net guns. We captured birds with mist nets by luring them into nets with woodpecker decoys and recordings of territorial vocalizations or by placing nets along known flight paths. Mist nets were used with limited success during only the 2009 and 2010 breeding seasons, and were quickly abandoned in favor of the more efficient hoop net and net gun capture methods (Lehman et al. 2011). We captured birds with hoop nets by waiting for a bird to enter a nest cavity and then placing the net over the cavity entrance. Hoop nets were an efficient capture method during the breeding season, but were effective only when woodpeckers were actively attending cavities. Finally, we used the net gun to capture woodpeckers by luring them in with territorial recordings or by stalking foraging woodpeckers. The net gun allowed capture away from nest cavities and outside the breeding season.

Once captured, all birds were weighed and a (3.0–3.3 g, <5% of average adult body mass) transmitter was attached (Rappole and Tipton 1991, Fair et al. 2010). Additionally, we banded each bird with a unique combination of colored leg bands and a U.S. Fish & Wildlife Service aluminum leg band. We attempted to recapture previously marked individuals to replace transmitters as batteries expired, and captured additional unmarked birds opportunistically during trapping events.

Foraging Observations

Observers conducted 10-min foraging observations of radio-tagged woodpeckers when birds were located. The relocation schedule varied from once every 4 hr to once per month (Rota et al. 2014a, 2014b). Foraging observations were conducted year-round. During foraging observations, observers with binoculars counted the number of apparent "large" and "small" prey items that a woodpecker extracted from each tree that it used for foraging. We defined "large" prey as items that were approximately the length of a woodpecker's bill and "small" prey as items that were <½ bill length. We defined apparent foraging success as the count of successfully captured prey from each tree used for foraging. We assumed that large prey items were wood-boring beetle larvae, since wood-boring beetle larvae (e.g., Cerambycidae) are typically ≥15 mm in length (Arnett et al. 2002, p. 568). There is a large size discrepancy between wood-boring beetle larvae and the "small" prey that the woodpeckers captured. For example, bark beetle larvae (e.g., Scolytinae) are typically 1–3 mm in length (Arnett et al. 2002, p. 793). We did not attempt to further classify small prey items, since small prey could be a variety of species (e.g., MPB, *Ips* spp., small wood-boring beetle larvae, or wasp larvae). Observers almost certainly underestimated the number of prey successfully captured. However, we believe it is reasonable to assume that the detection rates of all prey were constant across habitats so that differences in apparent foraging success reflect differences in absolute foraging success. 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 assumed that foraging behavior was not biased by proximity of observers. Occasionally, observers were unable to complete 10 min of observation, although this occurred during <5% of all observations. When foraging observations were truncated, counts of successfully extracted prey from the trees used by a woodpecker for foraging were still included in the analysis (because counts were recorded per tree).

Observers recorded several variables to characterize each tree that a woodpecker used for foraging. Burn severity was 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" (infestation <1 yr old) if boles exhibited fresh pitch tubes, indicating attack by MPBs, and green needles; "red hits" (infestation 1–2 yr old) if pitch tubes were present but the needles were red; and "gray hits" (infestation >2 yr old) if pitch tubes were present and there were few or no needles. Trees were further classified as "Burn/MPB" if they were both burned and infested with MPBs and "undisturbed" if they were neither burned nor infested with MPBs. There were not enough observations of birds foraging on trees both burned and infested with MPBs to simultaneously classify each tree 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 that a woodpecker used for foraging. Observers additionally measured the DBH of the final tree included in foraging observations for self-calibration and to ensure that 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 that estimated DBH was a reasonable representation of tree diameter. We classified the number of years postfire based on a 12 mo period starting on April 1 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 yr postfire (4-Mile burned in June 2007). We began 12-mo periods 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 postfire reflects the number of breeding seasons postfire.

Statistical Methods

Total apparent foraging success. We modeled counts of apparent foraging success as a Poisson random variable:

$$y_{ijk} \sim Poisson(\lambda_{ijk}),$$

where y_{ijk} is the count of successfully captured prey that observer i made of woodpecker j foraging on tree k. We first evaluated how total apparent foraging success, defined as the sum of all wood-boring beetle larvae and small prey captured at each tree used for foraging, varied across habitats. Although we were primarily interested in how total apparent foraging success varied across habitats, we also modeled total apparent foraging success as a function of tree condition, years postfire in habitats created by wildfire and prescribed fire, and estimated tree DBH to account for additional sources of variation. We assumed a log-linear model for the expected count of total apparent foraging success:

$$\log(\lambda_{ijk}) = \mathbf{x}'_k \boldsymbol{\beta}_j + \text{Obs}_i + \varepsilon_{ijk},$$

where $\mathbf{x}'_k$ is a vector of variables associated with tree k and $\boldsymbol{\beta}_j$ is a conformable vector of slope parameters associated with woodpecker j. We assumed a random intercept associated with each observer to account for systematic differences in counts of apparent foraging success:

$$\text{Obs} \sim \text{Normal}(\beta_0, \sigma^2_{obs}),$$

where β_0 is the mean intercept and σ^2_{obs} is the variance of the random observer effect. We also assumed random slopes for regression coefficients associated with each woodpecker:

$$\boldsymbol{\beta} \sim \text{Normal}(\boldsymbol{\mu}, \boldsymbol{\Sigma}),$$

where $\boldsymbol{\mu}$ is a vector of mean population-level regression coefficients and $\boldsymbol{\Sigma}$ is a diagonal covariance matrix (i.e. we assumed independent normal random slopes). For all models, 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 included a random error term to account for extra-Poisson variation in counts (Kéry 2010):

$$\varepsilon \sim \text{Normal}(0, \sigma^2).$$

Finally, we assumed the following prior distributions:

$$\beta_0 \sim \text{Normal}(0, 100),$$

$$\sigma_{obs} \sim \text{Uniform}(0, 100),$$

$$\boldsymbol{\mu} \sim \text{Normal}(\mathbf{0}, 100\mathbf{I}),$$

$$\sqrt{\boldsymbol{\Sigma}_{ll}} \sim \text{Uniform}(0, 100),$$

and

$$\sigma \sim \text{Uniform}(0, 100).$$

Wildfire vs. prescribed fire. We modeled apparent foraging success for wood-boring beetle larvae and small prey on burned trees in habitats created by wildfire and prescribed fire with two separate submodels; one model used counts of successfully captured wood-boring beetle

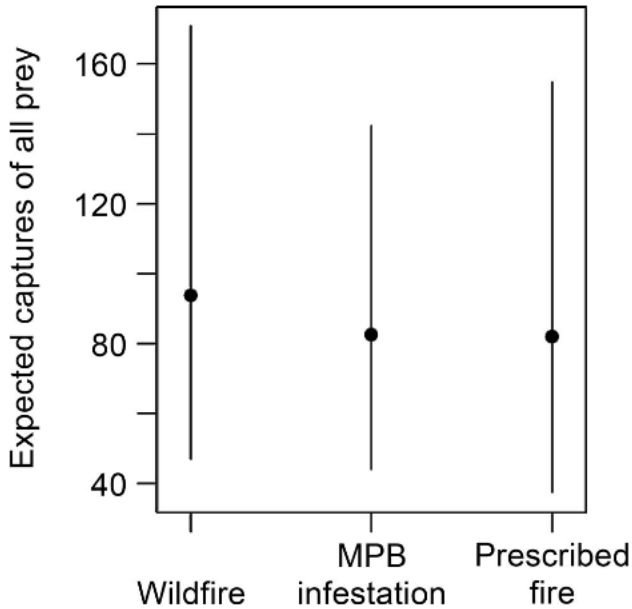

FIGURE 2. Expected counts (dots) and 95% credible intervals (vertical lines) of Black-backed Woodpecker total apparent foraging success per 1,000 24-cm DBH trees in habitat created by wildfire, mountain pine beetle (MPB) infestations, and prescribed fire in South Dakota, USA, 2008–2012.

larvae as the response variable, and the other model used counts of successfully captured small prey as the response variable. Although we were primarily interested in how apparent foraging success varied between habitats created by wildfire and by prescribed fire, we also modeled apparent foraging success as a function of burn severity, number of years postfire, and estimated tree DBH to account for additional sources of variation. We assumed a log-linear model for the expected count of apparent foraging success, and assumed random slopes, random intercepts, random error, and prior distributions as above.

Wildfire vs. MPB infestations. We modeled apparent foraging success for wood-boring beetle larvae and small prey in wildfire and MPB infestations with two separate submodels; one model used counts of successfully captured wood-boring beetle larvae as the response variable, and the other model used counts of successfully captured small prey as the response variable. Although we were primarily interested in how apparent foraging success varied between habitats created by wildfire and by MPB infestations, we also modeled apparent foraging success as a function of tree condition, years postfire in habitat created by wildfire, and estimated tree DBH to account for additional sources of variation. We assumed a log-linear model for the expected count of apparent foraging success, and assumed random slopes, random intercepts, random error, and prior distributions as above.

Goodness-of-fit and computation. We determined model adequacy by conducting posterior predictive checks (Kéry 2010, Gelman et al. 2014). Posterior predictive checks involve comparing a test statistic calculated from observed data with a test statistic calculated from predictions simulated from the fitted model. We calculated the sum of squared Pearson residuals for our test statistic:

$$tst_{dat} = \sum_{ijk} \frac{(y_{ijk} - \lambda_{ijk})^2}{\lambda_{ijk}}$$

$$tst_{pred} = \sum_{ikj} \frac{(Y_{ijk} - \lambda_{ijk})^2}{\lambda_{ijk}},$$

where tst_{dat} is the test statistic calculated from observed data, tst_{pred} is the test statistic calculated from simulated predictions, and Y_{ijk} is a predicted observation simulated from a fitted model. We then calculated Bayesian p-values as $Pr(tst_{dat} > tst_{pred})$; Bayesian p-values close to 0.5 indicate adequate goodness-of-fit, while values of p close to 0 or 1 indicate poor goodness-of-fit (Kéry 2010, Gelman et al. 2014). We interpreted Bayesian p-values between 0.10 and 0.90 as adequate goodness-of-fit.

We fitted all 3 models in WinBUGS version 1.4.3 (Gilks et al. 1994) via the R2WinBUGS interface (Sturtz et al. 2005) in program R version 3.1.0 (R Development Core Team 2014). For each model, we simulated marginal posterior distributions of parameters from 3 Markov chains, saving 1,000 draws from each chain, for a total of 3,000 random draws from the marginal posterior distribution of each parameter. We discarded the first 1,000 iterations from each Markov chain as burn-in. Additionally, most Markov chains exhibited some degree of autocorrelation. We thus thinned chains at a rate such that the Gelman-Rubin convergence diagnostic (Gelman and Rubin 1992) indicated adequate convergence for all monitored parameters ($\hat{R} \approx 1$) when 1,000 draws were saved from each of 3 chains.

RESULTS

Total Apparent Foraging Success

We modeled total apparent foraging success from 4,444 observations of woodpeckers foraging in habitat created by wildfire (n = 2,120 trees), MPB infestations (n = 1,414 trees), and prescribed fire (n = 910 trees). We observed a total of 1,261 successful captures of prey, including 581, 473, and 207 captures in habitats created by wildfire, MPB infestations, and prescribed fire, respectively. This dataset included observations of 99 different woodpeckers collected by 15 different observers. Posterior predictive checks indicated adequate goodness-of-fit (Bayesian p-value = 0.44).

We found no strong evidence that total apparent foraging success varied among habitats (Figure 2). On average, observers were expected to record woodpeckers capturing 1.17 times (95% CI = 0.66, 1.96) more prey in habitat created by wildfire relative to habitat created by MPB infestations and 1.03 times (95% CI = 0.54, 1.86) more prey in habitat created by prescribed fire relative to habitat created by MPB infestations. Across all habitats, the average observer was expected to record woodpeckers capturing 94 prey items (95% CI = 47, 171) from every 1,000 24-cm DBH trees in habitat created by wildfire, 83 prey items (95% CI = 44, 142) from every 1,000 24-cm DBH trees in habitat created by MPB infestations, and 82 prey items (95% CI = 38, 155) from every 1,000 24-cm DBH trees in habitat created by prescribed fire (Figure 2). Total apparent foraging success did not vary appreciably as a function of tree condition, time since fire, or tree diameter (i.e. 95% CI of population-level regression coefficients associated with tree condition, time since fire, and tree diameter variables all overlapped 0).

Wildfire vs. Prescribed Fire

We modeled apparent foraging success for wood-boring beetle larvae and small prey from 2,625 observations of woodpeckers foraging on burned trees in habitat created by wildfire (n = 1,817 trees) and prescribed fire (n = 808 trees). With this subset of the data, we observed a total of 242 and 477 successful captures of wood-boring beetle larvae and small prey, respectively, including 201 and 326 successful captures of wood-boring beetle larvae and small prey, respectively, in habitat created by wildfire, and 41 and 151 successful captures of wood-boring beetle larvae and small prey, respectively, in habitat created by prescribed fire. This subset of the data included observations of 61 different woodpeckers collected by 14 different observers. Posterior predictive checks indicated adequate goodness-of-fit for both the model with counts of wood-boring beetle larvae (Bayesian p-value = 0.60) and the model with small prey (Bayesian p-value = 0.50) as the response variable.

We found evidence that apparent foraging success for wood-boring beetle larvae was greater in habitat created by wildfire relative to prescribed fire. On average, observers were expected to record woodpeckers capturing 2.23 times (95% CI = 0.90, 4.74) more wood-boring beetle larvae in habitat created by wildfire relative to habitat created by prescribed fire, with >95% of the posterior density of the population-level regression coefficient associated with trees in habitat created by wildfire > 0 (Figure 3A). For example, the average observer was expected to record woodpeckers capturing 40 (95% CI = 14, 82) wood-boring beetle larvae from every 1,000 24-cm DBH severely burned trees in 1-yr postwildfire habitat, compared with 20 (95% CI = 6, 45) wood-boring beetle larvae on identical trees in 1-yr post–prescribed fire habitat, suggesting that more wood-boring beetle larvae were captured in habitat created by wildfire than in habitat created by prescribed fire (Figure 3B).

Apparent foraging success for wood-boring beetle larvae in trees burned by wildfire and prescribed fire 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 diameter (i.e. the 95% CI of the population-level regression coefficient associated with tree DBH did not overlap 0) and was lowest 3 yr postfire. Apparent foraging success for wood-boring beetle larvae did not vary appreciably as a function of burn severity (i.e. the 95% CI of the population-level regression coefficients associated with tree condition overlapped 0; Figures 4A, 4B, 4C).

We found little evidence that apparent foraging success for small prey differed between habitats created by wildfire vs. prescribed fire. On average, observers were expected to record woodpeckers capturing 0.88 times (95% CI = 0.41, 1.70) fewer small prey in habitat created by wildfire relative to habitat created by prescribed fire, with 68% of the posterior density of the population-level regression coefficient associated with trees in habitat created by wildfire < 0 (Figure 3C). For example, the average observer was expected to record woodpeckers capturing 40 (95% CI = 12, 93) small prey from every 1,000 24-cm DBH severely burned trees in 1-yr postwildfire habitat compared with 46 (95% CI = 15, 105) small prey on identical trees in habitat created by prescribed fire, suggesting no strong differences in apparent foraging success for small prey between habitats created by wildfire and by prescribed fire (Figure 3D). Apparent foraging success for small prey did not vary appreciably as a function of burn severity, time since fire, or tree DBH (Figures 4C, 4D, 4E).

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 (n = 2,120 trees) and by MPB infestations (n = 1,414 trees). With this subset of the data, we observed a total of 281 and 773 successful captures of wood-boring beetle larvae and small prey, respectively, including 218 and 363 successful captures of wood-boring beetle and small prey, respectively, in habitat created by wildfire and 63 and 410 successful captures of wood-boring beetles and small prey, respectively, in habitat created by MPB infestations. This subset of the data included observations of 73 different woodpeckers collected by 12 different observers. Posterior predictive checks indicated adequate goodness-of fit-for both the model with counts of wood-boring beetle larvae

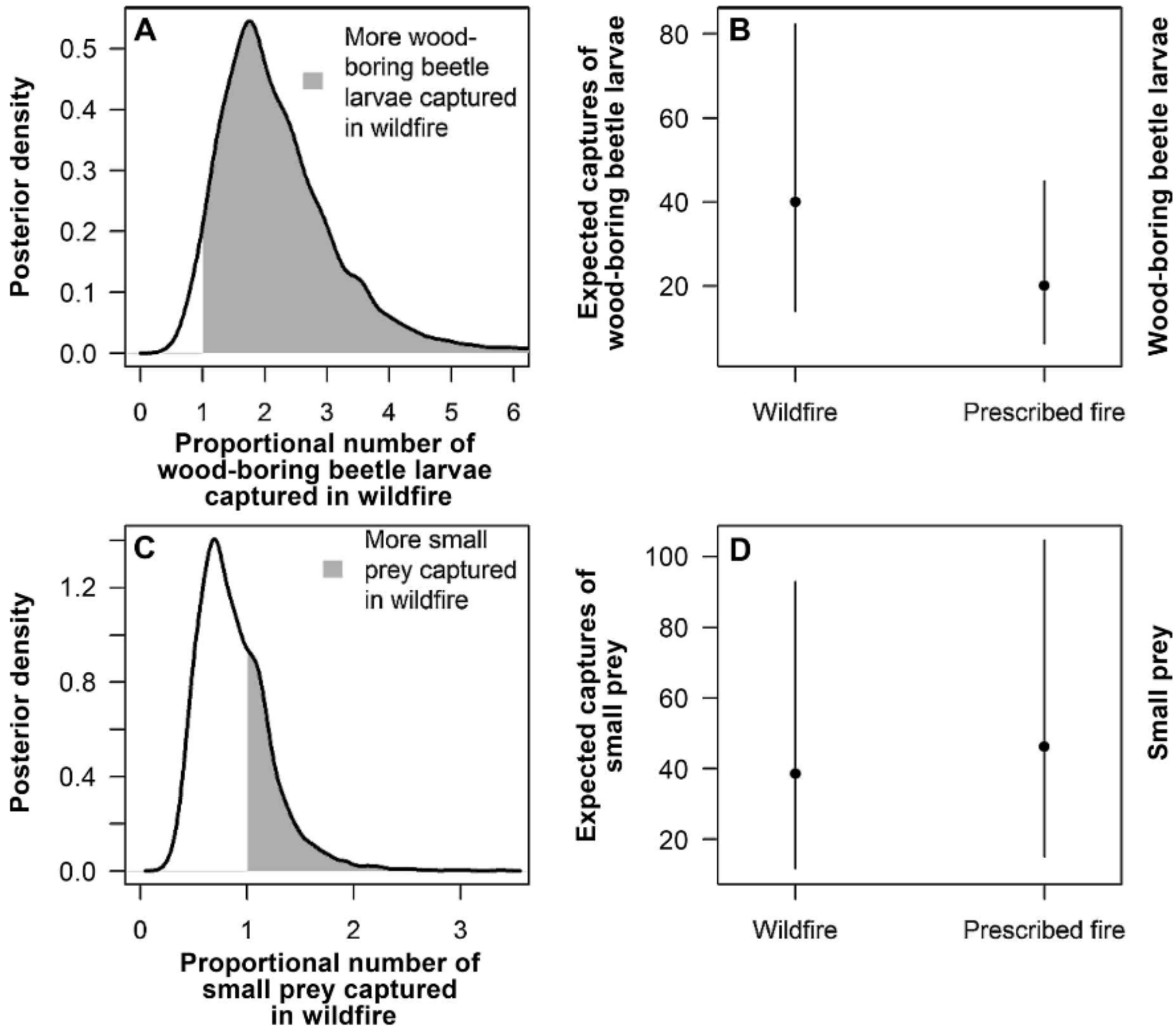

FIGURE 3. Apparent foraging success of Black-backed Woodpeckers for wood-boring beetle larvae and small prey in habitat created by wildfire and prescribed fire in South Dakota, USA, 2008–2012. (**A**) Posterior density of the proportional count of successfully captured wood-boring beetle larvae in habitat created by wildfire relative to habitat created by prescribed fire (e.g., a value of 2 indicates 2× more wood-boring beetles captured in habitat created by wildfire relative to habitat created by prescribed fire). Values > 1, indicated by the shaded area, mean that more wood-boring beetle larvae are expected to be captured in habitat created by wildfire relative to habitat created by prescribed fire. (**B**) Expected counts (dots) and 95% credible intervals (vertical lines) of successfully captured wood-boring beetle larvae per 1,000 trees in habitat created by wildfire and prescribed fire. Woodpeckers are assumed to be foraging on 24-cm DBH severely burned trees. (**C**) Posterior density of the proportional count of successfully captured small prey in habitat created by wildfire relative to habitat created by prescribed fire. (**D**) Expected counts and 95% credible intervals of successfully captured small prey per 1,000 trees in habitat created by wildfire and prescribed fire. Woodpeckers are assumed to be foraging on 24-cm DBH severely burned trees.

(Bayesian p-value $= 0.64$) and the model with small prey (Bayesian p-value $= 0.46$) as the response variable.

We found weak evidence that apparent foraging success for wood-boring beetle larvae was greater in habitat created by wildfire relative to habitat created by MPB infestations. On average, observers were expected to record woodpeckers capturing 1.98 times (95% CI $= 0.72$, 4.25) more wood-boring beetle larvae in habitat created by wildfire relative to habitat created by MPB infestations, with >89% of the posterior density of the population-level regression coefficient associated with trees in habitat created by wildfire > 0 (Figure 5A). For example, the average observer was expected to record woodpeckers capturing 21 (95% CI $= 3$, 64) wood-boring beetle larvae from every 1,000 24-cm DBH red-hit trees in postwildfire habitat compared with 10 (95% CI $= 2$, 27) wood-boring beetle larvae on identical trees in MPB infestations (Figure 5B).

Apparent foraging success for wood-boring beetle larvae in wildfire vs. MPB infestations also varied as a function of

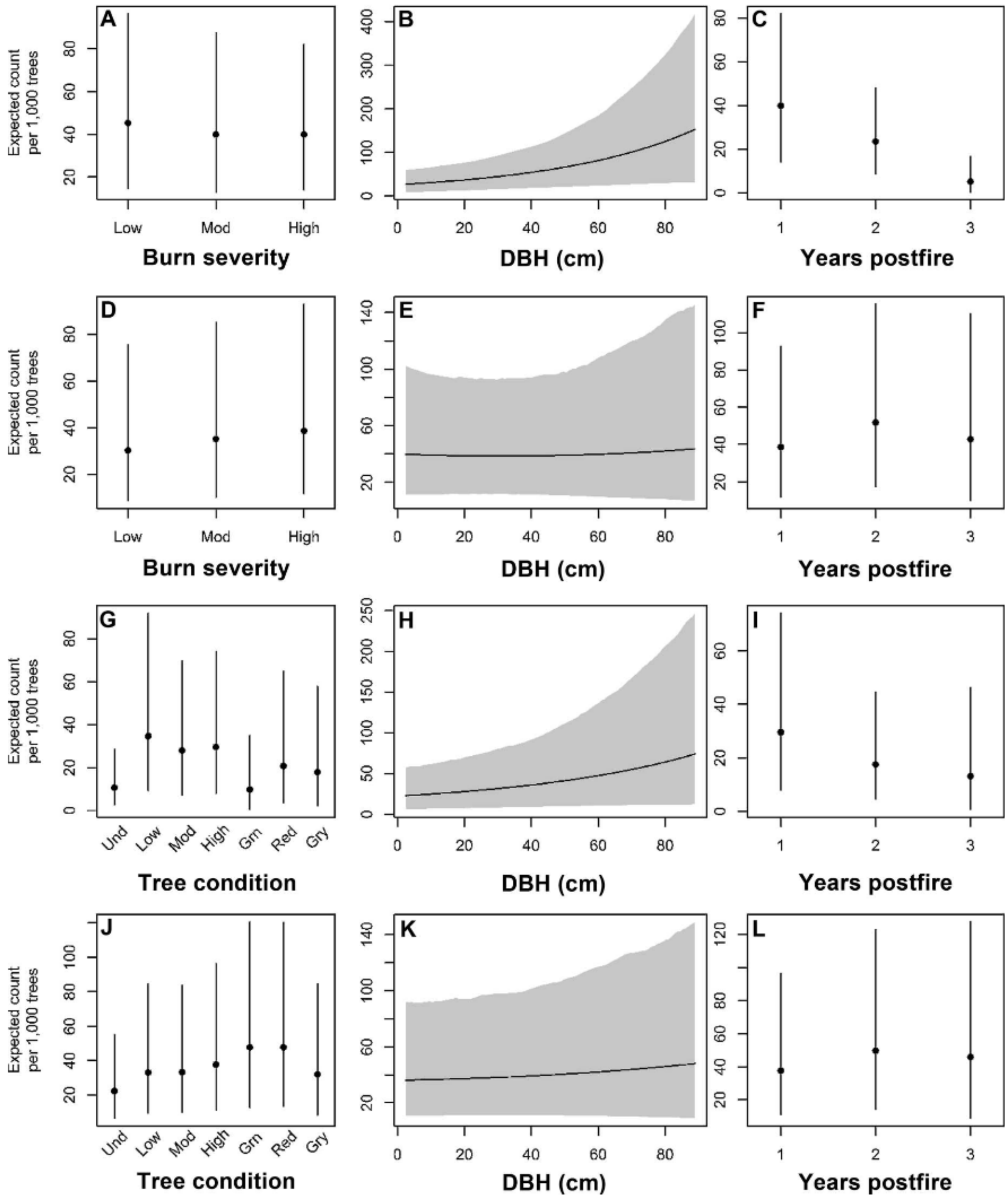

FIGURE 4. Apparent foraging success of Black-backed Woodpeckers in South Dakota, USA, 2008–2012, foraging for wood-boring beetle larvae and small prey in burned forests and mountain pine beetle (MPB) infestations as a function of tree condition (low-, moderate- [Mod], or high-severity burn, green [grn; MPB infestation <1 yr old], red [MPB infestation 1–2 yr old], or gray [gry; MPB infestation >2 yr old] hit trees, and trees neither burned nor infested with MPBs [Und]), estimated tree diameter, and number of years postfire in burned forests. Apparent foraging success for (**A**, **B**, **C**) wood-boring beetle larvae in habitat created by wildfire vs. prescribed fire, (**D**, **E**, **F**) small prey in habitat created by wildfire vs. prescribed fire, (**G**, **H**, **I**) wood-boring beetle larvae in habitat created by wildfire vs. MPB infestation, and (**J**, **K**, **L**) small prey in habitat created by wildfire vs. MPB infestation.

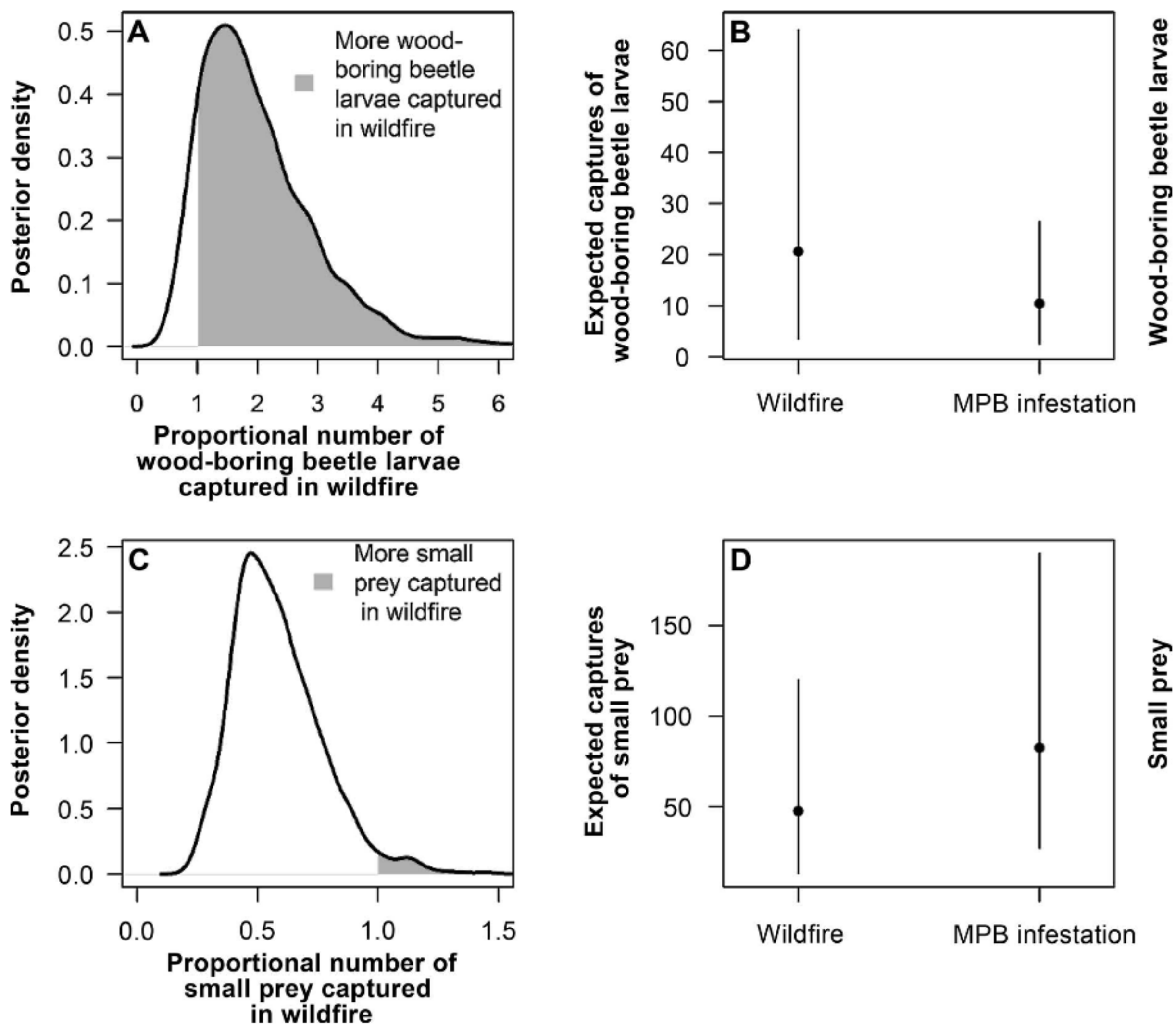

FIGURE 5. Apparent foraging success of Black-backed Woodpeckers for wood-boring beetle larvae and small prey in habitat created by wildfire and mountain pine beetle (MPB) infestations in South Dakota, USA, 2008–2012. (**A**) Posterior density of the proportional count of successfully captured wood-boring beetle larvae in habitat created by wildfire relative to habitat created by MPB infestations (e.g., a value of 2 indicates 2× more wood-boring beetles captured in habitat created by wildfire relative to habitat created by MPB infestations). Values $>$ 1, indicated by the shaded area, mean that more wood-boring beetle larvae are expected to be captured in habitat created by wildfire relative to habitat created by MPB infestations. (**B**) Expected counts (dots) and 95% credible intervals (vertical lines) of successfully captured wood-boring beetle larvae per 1,000 trees in habitat created by wildfire and MPB infestations. Woodpeckers are assumed to be foraging on 24-cm DBH red-hit (MPB infestation 1–2 yr old) trees. (**C**) Posterior density of the proportional count of successfully captured small prey in habitat created by wildfire relative to habitat created by MPB infestations. (**D**) Expected counts and 95% credible intervals of successfully captured small prey per 1,000 trees in habitat created by wildfire and MPB infestations. Woodpeckers are assumed to be foraging on 24-cm DBH red-hit trees.

tree condition. Apparent foraging success for wood-boring beetle larvae was greater in trees that burned at low severity, moderate severity, and high severity relative to undisturbed trees. Apparent foraging success for wood-boring beetle larvae in wildfire vs. MPB infestations did not vary appreciably as a function of time since fire or tree diameter (Figures 4G, 4H, 4I).

We found evidence that apparent foraging success for small prey was lower in habitat created by wildfire than in habitat created by MPB infestations. On average, observers were expected to record woodpeckers capturing 0.58 times (95% CI = 0.29, 1.03) fewer small prey in habitat created by wildfire relative to habitat created by MPB infestations, with >97% of the posterior density of the population-level regression coefficient associated with trees in habitat created by wildfire $<$ 0 (Figure 5C). For example, the average observer was expected to record woodpeckers capturing 48 (95% CI = 14, 120) small prey from every 1,000 24-cm DBH red-hit trees in postwildfire habitat compared with 82 (95% CI = 27, 190) small prey on identical trees in MPB infestations, suggesting that more small prey were captured in habitat created by MPB infestations than in habitat created by wildfire (Figure 5D).

Apparent foraging success for small prey also varied as a function of tree condition. Expected counts of successfully captured small prey items were greater on green hit trees and red hit trees relative to undisturbed trees. Apparent foraging success for small prey did not vary appreciably as a function of time since fire or tree diameter (Figures 4J, 4K, 4L).

DISCUSSION

Apparent foraging success for wood-boring beetle larvae closely tracked patterns of known habitat quality for Black-backed Woodpeckers, suggesting the potential for food resources to regulate populations of this irruptive species. Rota et al. (2014a) demonstrated that population growth rates of Black-backed Woodpeckers were lowest in habitat created by fall prescribed fire, intermediate in MPB infestations, and greatest in habitat created by summer wildfire. While we found no strong differences in total apparent foraging success among habitats, woodpeckers in this study captured more wood-boring beetle larvae when foraging in habitat created by summer wildfire relative to habitats created by fall prescribed fire and MPB infestations. This suggests that woodpeckers consume proportionally more wood-boring beetle larvae in habitat created by summer wildfire, which may contribute to the higher population growth rates in this habitat.

Previous studies have demonstrated that movements of irruptive species, including Black-backed Woodpeckers, are associated with pulsed food resources (Yunick 1985, Koenig and Knops 2001, Newton 2006a, Lindén et al. 2011). This study complements and builds upon those studies by demonstrating that apparent variation in foraging success in habitats subjected to resource pulses is associated with known habitat quality. Our results further suggest that populations of irruptive species may be particularly sensitive to the local abundance of preferred food resources. For example, even though MPB infestations contained abundant bark beetle larvae, Black-backed Woodpeckers may have been unable to efficiently exploit this abundant food resource because of specializations for foraging on wood-boring beetle larvae (Spring 1965). Many irruptive bird species have evolved specializations to forage on particular food resources that are unpredictable in space and time (e.g., Red Crossbills; Newton 2006b), which may make population growth for these species sensitive to the availability of preferred food resources. Understanding how natural and anthropogenic processes may influence the abundance and distribution of such food resources will thus be important for the management and conservation of irruptive species.

Postdisturbance conditions in habitats created by wildfire, prescribed fire, and MPB infestations arise through different processes, which leads to differences in prey bases and the availability of preferred food resources among these habitats, and ultimately may contribute to differences in habitat quality. Wildfire and MPB infestations host different communities of potential prey species: Wood-boring beetles occur in greater abundance in fire-killed trees relative to MPB-killed trees in the Black Hills, while many species of bark beetle are only found in MPB-killed trees (Costello et al. 2013). Woodpeckers occupying habitat created by wildfire may forage less for small than for large prey because of greater marginal gains when foraging for wood-boring beetle larvae and due to adaptations that make foraging for burrowing prey such as wood-boring beetles more efficient (Spring 1965). Conversely, woodpeckers occupying MPB infestations likely compensated for low relative abundance of wood-boring beetle larvae by capturing more MPB larvae and other small prey. Such reliance on a smaller primary prey item may impose costs not incurred in habitats created by wildfire, such as searching for prey over a larger spatial extent (Rota et al. 2014b). Although habitats created by wildfire and prescribed fire both occur as a result of burning, differences in timing may lead to differences in relative abundance of prey. The wildfire study sites burned during the months of June and July, while the prescribed fire study sites were treated during the months of September and October. These differences in timing may influence apparent foraging success for wood-boring beetle larvae if wood-boring beetles are unable to immediately colonize late-season burns.

We also found that variation in apparent foraging success through time matched temporal changes in habitat quality. Apparent foraging success for wood-boring beetles on burned trees in habitat created by wildfire and prescribed fire was lowest 3 yr postfire, which is consistent with many studies reporting declining habitat quality as time since fire increases. For example, Rota et al. (2014a) report declining population growth rates in habitats created by wildfire and prescribed fire as time since fire increases. Additionally, Rota et al. (2014b) report 4-fold increases in home range size in habitat 3–4 yr postfire relative to habitat 1–2 yr postfire, Nappi and Drapeau (2009) report declines in nest success 3 yr postfire, and Murphy and Lehnhausen (1998) report declines in densities of Black-backed Woodpeckers in habitat 3 yr postfire. These consistent changes in apparent foraging success, home range size, nest success, and density that occur 3 yr postfire may reflect life-history patterns of wood-boring beetle larvae, which typically emerge from host trees 2–3 yr after eggs are initially deposited (Murphy and Lehnhausen 1998).

Our study provides insight into the vegetation characteristics important for the Black-backed Woodpecker, a species of conservation concern that has recently been petitioned for listing as threatened or endangered under the Endangered Species Act (Federal Register 2013). We found that apparent foraging success for wood-boring beetle larvae was positively associated with the diameter of burned trees in habitats created by wildfire and prescribed fire, suggesting that relatively large-diameter burned trees may be an important foraging resource for Black-backed Woodpeckers. This result is consistent with that of Nappi et al. (2003) and Saint-Germain et al. (2004), who found that wood-boring beetle abundance was positively associated with tree diameter, and with the studies of Nappi and Drapeau (2011), Dudley et al. (2012), and Rota et al. (2014b), who found that Black-backed Woodpeckers selected relatively large-diameter trees within their home range. Overall, in our study, Black-backed Woodpeckers were predicted to capture the most wood-boring beetles on relatively large-diameter trees in 1–2 yr post–summer wildfire habitat, suggesting that recent summer wildfires produce high-quality habitat. This result is consistent with numerous other studies that have concluded that recently burned forests provide high-quality habitat (Hutto 1995, Murphy and Lehnhausen 1998, Hobson and Schieck 1999, Hoyt and Hannon 2002, Nappi and Drapeau 2009, Rota et al. 2014a, 2014b) and further highlights the importance of recently burned forest for this species of conservation concern.

Our study is the first 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 summer wildfire compared with habitat created by fall prescribed fire or MPB infestations may help to explain why population growth rates were consistently positive only in wildfire habitat in the Black Hills (Rota et al. 2014a). Black-backed Woodpecker preference for recently burned forests may thus be fundamentally driven by a superabundant food resource in the form of wood-boring beetle larvae, which may be a strong determinant of habitat quality for this irruptive species.

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