

RESEARCH ARTICLE

## AMERICAN THREE-TOED WOODPECKER RESPONSE TO BURN SEVERITY AND PREY AVAILABILITY AT MULTIPLE SPATIAL SCALES

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### ABSTRACT

We evaluated American three-toed woodpecker (*Picoides dorsalis*) response to spatial heterogeneity of burn severity and prey availability over multiple scales at the 56 000 ha Hayman Fire (2002) located in the Colorado Front Range. In 2003 and 2004, we quantified the response of three-toed woodpeckers to burn severity, beetle occurrence, and tree size at three levels: home-range scale (36 ha), foraging patches (~1 ha), and trees within foraging patches. We used the differenced normalized burn ratio (dNBR) to quantify burn severity at the home range scale. Woodpecker response to burn severity was strongly scale dependent. Three-toed woodpeckers generally established territories in moderately burned areas containing patches of live and dead trees, and were less common in unburned forests and in large severely burned areas lacking live trees. Woodpeckers disproportionately foraged in patches with a higher proportion of severely burned trees than were available in moderately burned areas, but rarely foraged in severely burned patches within severely burned areas. Burn severity was similar among trees within foraging patches and was not useful for predicting woodpecker use at this scale. Three-toed woodpecker response to beetle occurrence and tree size also varied across scales. Tree size and beetle occurrence were both greater in foraging patches compared to available trees. At the largest scale (home range), burn severity best accounted for three-toed woodpecker use, whereas tree size and beetle occurrence played a stronger role at the smallest scale (individual trees). At the intermediate scale (foraging patches), all factors were important in explaining woodpecker use. Our results indicate that the scaling of burn severity patterns can affect the woodpecker's use of burned forests and demonstrate the importance of evaluating burn severity across multiple spatial scales. The prevalence of breeding three-toed woodpeckers in mixed-severity areas with both lightly and severely burned trees highlights the importance of mixed-severity regimes to such fire-dependent species and the need for fire management that includes a range of fire behaviors, including high-severity fires.

**Keywords:** American three-toed woodpecker, Colorado Front Range, foraging, mixed-severity fire regime, montane forest, *Picoides dorsalis*, spatial scales, wood-boring beetles

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## INTRODUCTION

Fire is a dominant process affecting landscape structure and dynamics in many systems. Post-fire heterogeneity results from complex interactions among climate, vegetation, fuel, and topography. The relative importance of climate and fuels in dictating fire behavior is a primary determinant of fire regimes (Schoennagel *et al.* 2004). In montane forests of the Rocky Mountains, scientists characterize forests of mixed ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) as having mixed-severity fire regimes because both low- and high-severity fires commonly occur (also called variable severity; Schoennagel *et al.* 2004; Sherriff and Veblen 2006, 2007; Baker *et al.* 2007). In this regime, the relative importance of weather and fuels varies within and among burns (Schoennagel *et al.* 2004) resulting in complex spatial patterning, which can vary across multiple spatial scales. Fire size and time since fire can also contribute to highly variable stand densities and landscape structure (Turner *et al.* 1997, Ehle and Baker 2003).

Spatial heterogeneity in burn severity may affect the response of birds and other wildlife to fire. Initially, most studies of the responses of bird communities to fire in the Rocky Mountains classified burns as either high- or low-severity, and compared the effects of burns to nearby unburned areas (see Finch *et al.* 1997, Kotliar *et al.* 2002, Saab *et al.* 2005 for reviews). Early studies demonstrated the close association that many species have with severely burned forests, including cavity-nesting species such as the American three-toed woodpecker (*Picoides dorsalis*; Koplin 1969, 1972). High-intensity surface or crown fires result in numerous dead trees, which provide nest sites

for three-toed woodpeckers (Hutto 1995). In addition, forests with a preponderance of recently killed and dying trees attract high densities of bark beetles (Scolytinae) and wood-boring beetles (Cerambycidae and Buprestidae; Amman and Ryan 1991), the primary prey of three-toed woodpeckers in early post-fire forests (Murphy and Lehnhausen 1998). The association of these beetle taxa with severely burned trees is well established (McCambridge and Knight 1972, Amman and Ryan 1991, Ryan and Amman 1996, Parker *et al.* 2006, Hood and Bentz 2007).

Although many species have a strong association with severely burned forests, little is known about how burn-severity patterns can affect the responses of these species to burns. Recent studies have quantified the effects of burn severity on avifaunal communities (Dwyer 2000, Smucker *et al.* 2005, Covert-Bratland *et al.* 2006, Kirkpatrick *et al.* 2006, Vierling and Lentile 2006, Koivula and Schmiegelow 2007, Kotliar *et al.* 2007), but burn severity classes and sampling scales often vary among studies (Kotliar *et al.* 2007). The observed differences in the response of species to burn severity could result from variation among burns in post-fire spatial patterns, as well as different methods or scales used to quantify burn severity (Kotliar *et al.* 2007). Currently, our understanding of the scale-dependent nature of burn severity and how it affects resource distribution and species' response patterns remains rudimentary.

Habitat selection and foraging behavior by three-toed woodpeckers within post-fire landscapes may be inextricably linked to the spatial patterns of burn severity. Because burn severity influences resource distribution (e.g., nest sites, food availability) at multiple scales, it is critical to link information between differ-

ent scales (Wiens 1989, Kotliar and Wiens 1990, Levin 1992). Decisions at a particular scale (e.g., where to forage) may be constrained by decisions related to patterns of burn severity at finer (e.g., selection of individual trees within patches) and larger spatial scales (decisions about where to establish a territory). In addition, beetle availability can vary dramatically over very short time frames (e.g., <5 yr post-fire; Hutto 1995, Murphy and Lehnhausen 1998, Covert-Bratland *et al.* 2006). Consequently, tracking prey availability within a post-fire landscape requires three-toed woodpeckers to integrate information across spatial and temporal scales.

Our overall objective was to evaluate the response of American three-toed woodpeckers to patterns of burn severity and prey availability across multiple spatial scales at the 56 000 ha Hayman Fire (Figure 1). The Hayman Fire was at least an order of magnitude larger than recent large fires in the Colorado Front Range, although comparably sized fires occurred in this region within the last several centuries (Romme *et al.* 2003). Variation in the scaling of burn-severity patterns included extensive areas (e.g., >1000 ha) dominated by severely burned forests, as well as more heterogeneous burn-severity patterns (e.g., severely burned areas <100 ha).

Because of their known association with severely burned forests, we expected that burn severity would influence three-toed woodpeckers across a range of spatial scales. However, it was not clear how the spatial patterning of burn severity would affect their use of the burned landscape, in part because of our limited understanding of how burn-severity patterns affect beetle abundance. In addition, tree size can influence foraging decisions of woodpeckers (Murphy and Lehnhausen 1998). To quantify the response of three-toed woodpeckers to burn severity and prey availability at multiple scales, we evaluated scales corresponding to home range size (reported as ranging from 30

ha to 300 ha; Leonard 2001), foraging patches within home ranges, and trees within patches. At each of these scales, we evaluated the relative importance of burn severity, beetle occurrence, and tree size in predicting the settlement patterns and foraging behavior of three-toed woodpeckers. We use the scaling of burn severity patterns at the Hayman Fire, and the woodpecker's response to these patterns, to illustrate the importance of scale in evaluating burn severity in studies of fire effects. Because of the importance of burned forests to three-toed woodpeckers, we also discuss the implications of our results for fire management in forested systems characterized by a mixed-severity fire regime.

## METHODS

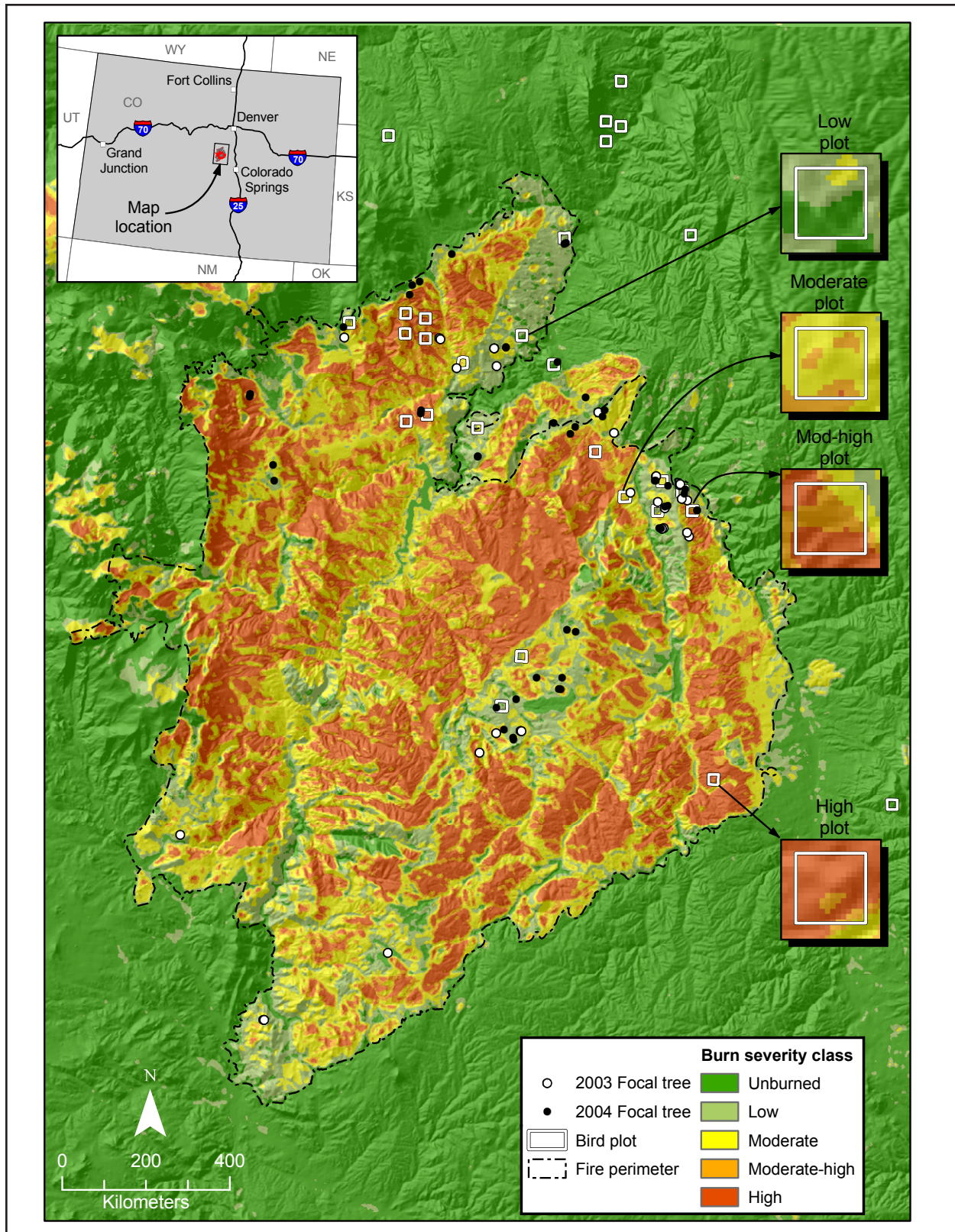
### *Study Area*

The Hayman Fire occurred 50 km southwest of Denver, Colorado, USA (Figure 1). Fifty-six percent of the fire occurred between 2200 m to 2550 m elevation, which generally corresponds to a mixed-severity fire regime in this region (Sheriff and Veblen 2006, Baker *et al.* 2007); 11 % between 2000 m and 2200 m, where frequent low-severity fires are more common; and 33 % between 2550 m and 2600 m, where infrequent high-severity fires predominate. Ponderosa pine and Douglas-fir are the dominant species, encompassing 53 % and 36 % of the burn, respectively (Romme *et al.* 2003). Engleman spruce (*Picea englemanii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) are also present.

### *Study Design*

*Plot descriptions.* To survey three-toed woodpeckers and beetles and to quantify tree characteristics and burn severity, we established 36 ha survey plots, which corresponds



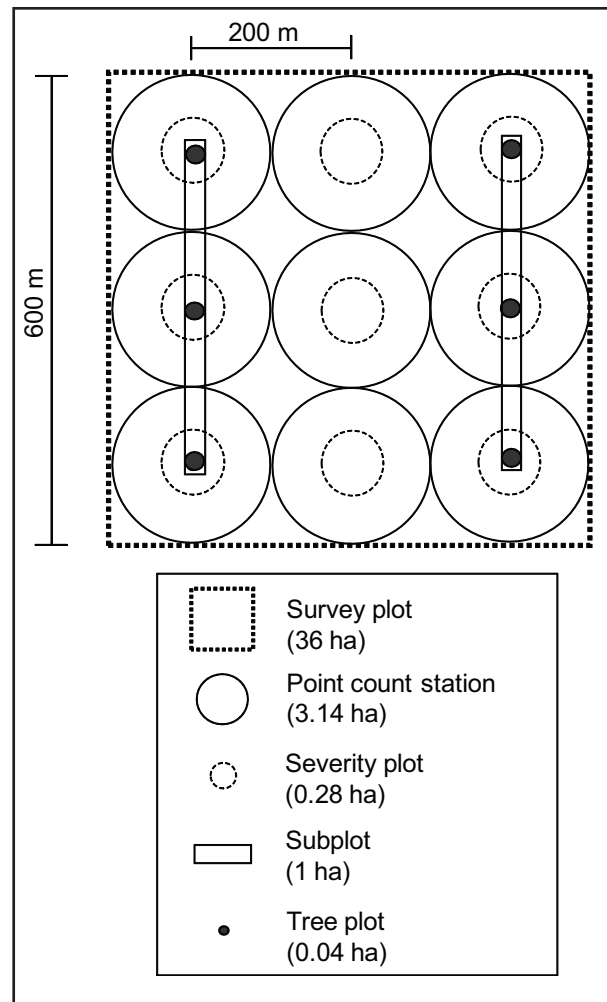


**Figure 1.** Hayman Fire (2002) severity map with the location of survey plots and American three-toed woodpecker foraging patches (2003 to 2004), Colorado, USA. Focal trees indicate the location of foraging three-toed woodpeckers. Burn severity was determined from differenced normalized burn ratio (dNBR) calculated from a 100 m radius moving window. Insert panels provide examples of survey plots for each burn severity class. See Table 1 for dNBR scores in each burn severity class.

to the minimum reported territory size of three-toed woodpeckers (Leonard 2001). We restricted sampling to areas dominated by ponderosa pine and Douglas-fir and avoided areas with extremely steep slopes or limited accessibility. We randomly selected the start point for all survey plots.

We stratified our survey plots by four fire severity classes: unburned, understory fire, mixed-severity fire, and crown fire. We used these qualitative fire severity classes only to stratify survey plots and not in subsequent analyses. Unburned areas were outside the burn perimeter, had not experienced crown fires in >70 yrs, and were generally similar in structure and composition to pre-fire conditions of the burn. Most trees in areas burned by understory fires had bole or partial crown scorch. Mixed-severity areas experienced both understory and crown fire. Most trees in the areas burned by crown fire had complete crown consumption. Using our preliminary burn-severity map, we established four plots of each fire severity class ( $n = 16$ ) in areas of the Hayman Fire that had consistent severity patterns at the scale of our survey plots (see Figure 1 for an updated burn severity map described below). To ensure that some survey plots had consistent fire patterns at greater spatial extents, we identified three ~400 ha areas in the following severities: (1) unburned, (2) mixed-severity fire, and (3) crown fire (understory fire was too fine grained to sample at the 400 ha scale). We established an additional four 36 ha survey plots ( $n = 12$ ) in each 400 ha area.

**Bird surveys.** We surveyed three-toed woodpeckers the first two years post-fire (2003 and 2004) using both point counts and area searches. We used point counts to determine the presence of three-toed woodpeckers on survey plots. Within each survey plot, we established a  $3 \times 3$  array of nine 100 m radius point count stations (Figure 2). Twice each breeding season, we surveyed each station for



**Figure 2.** Schematic of three-toed woodpecker survey plot design.

10 min; the first sampling period occurred between 22 May and 15 June, and the second period was from 15 June to 3 July.

To locate foraging three-toed woodpeckers, we conducted area searches in 19 additional accessible areas distributed across the entire burn. All search areas contained the full range of burn severities and ranged from ~50 ha to 2000 ha, for a total of ~10 000 ha searched. Within these areas, two observers simultaneously walked along transects of variable length, spaced 100 m apart. Once an observer located a foraging woodpecker, we waited 10 s (Hejl and Verner 1990, Block 1991) before recording up to 10 foraging trees per



bird or until the bird was out of view. To minimize the probability of including more than one foraging bout per individual, we only included birds that were at least 500 m from previously encountered three-toed woodpeckers of the same sex (i.e.,  $\geq 20$  ha sighting area around each bird; Block 1991). We also included birds that were within 500 m of another individual but associated with different nest cavities.

We marked the location of each tree using a global positioning system (GPS) and recorded residency time of foraging birds. We refer to each series of foraging trees as a foraging patch and define the focal tree of each foraging patch as the tree with the longest woodpecker residency time. We paired each foraging tree with a randomly selected tree (paired tree) within 10 m, regardless of species, that was  $>8$  cm diameter at breast height (dbh) and that the woodpecker did not use during that foraging series.

*Tree characteristics.* For all foraging and paired trees, we sampled beetle presence and quantified burn severity and dbh. We examined trees for internal evidence of beetles using a cordless hand-held drill and hole saw bit to remove a 102 cm<sup>2</sup> bark sample, 1.4 m above ground level, from the north and south sides of each sampled tree. By examining the bark sample and exposed cambial layer of the tree, we determined the presence of bark or wood-boring beetles (Pulley *et al.* 1977, Powell *et al.* 2002). We identified bark beetles by their distinctive gallery systems, and we used either the presence of larva, wood-borer galleries, or holes in the cambial zone to identify wood-borers (Powell *et al.* 2002).

To quantify burn severity of individual trees, we estimated the percent of the crown that was: (1) live, (2) scorched by fire heat, or (3) consumed by fire (Fowler and Sieg 2004). We combined the three scores into a single index of burn severity for each tree, the “tree-crown burn index” (TBI) defined as:

$$TBI = [(\% \text{ live crown} \times 0) + (\% \text{ scorched crown} \times 1) + (\% \text{ consumed crown} \times 2)] \times 200^{-1}$$

We scaled TBI from zero to one; where 0 corresponds to a tree with 100 % live crown, 0.5 corresponds to a tree with 100 % crown scorch, and 1 corresponds to a tree with 100 % needle consumption.

In 2003 and 2004, we also quantified tree characteristics in survey plots by sampling two 1 ha subplots located at opposite ends of the survey plots (Figure 2). These subplots roughly corresponded to the size of foraging patches. Within each subplot, we centered three 11.3 m radius tree plots within point count stations (Figure 2). Within tree plots, we quantified burn severity (TBI), tree size (dbh), and evidence of beetles in trees  $>12$  cm dbh. In 2003, we sampled four randomly selected trees per tree plot. We based the presence of beetles on external evidence of wood-boring and bark beetles including frass, exit holes, or exposed galleries. We sampled all burned subplots, but only eight unburned subplots in 2003. To obtain internal evidence of beetles, we surveyed all mixed-severity and crown fire survey plots again in 2004. We sampled two trees nearest each tree plot center for internal evidence of beetles. We did not survey understory or unburned survey plots in 2004 because of concern that removing bark samples could increase opportunities for beetle attack in these areas (J. Negron, U.S. Forest Service, personal communication).

For each sample unit (subplot, foraging patch, and series of paired trees), we calculated mean dbh and mean TBI. We also determined the proportion of trees per sample unit with evidence of beetles (beetle occurrence). To compare the different beetle survey methods on subplots in the two different years (2003 vs. 2004), we evaluated pilot data collected at subplots ( $n = 16$ ) in 2003 to determine if external and internal evidence of beetles were correlated (Pearson correlation = 0.594). Although we

did not combine different beetle sampling techniques in a single analysis, these results indicate that beetle occurrence patterns were generally similar for internal and external evidence of beetles. We eliminated all foraging patches, and associated paired trees, with fewer than three trees from these calculations.

*Hayman landscape burn severity.* To quantify burn severity across the entire burn, we used the differenced normalized burn ratio (dNBR) map (National Burn Severity Mapping Project 2002). The dNBR is an index of burn severity and is derived from comparisons of pre- and post-fire Thematic Mapper imagery with a 30 m resolution (Kotliar et al. 2003, Key and Benson 2006). We calculated the mean dNBR within 100 m buffers (dNBR<sub>100</sub>) at each survey plot. We also evaluated burn severity in the field based on the condition of overstory trees in a 30 m radius area (severity plot) centered at each point count station (Figure 2). We used the following six field severity ranks: unburned (no evidence of needle or bole scorch), low (bole scorch only), low-moderate (<33 % crown scorch), moderate (33 % to 67 % crown scorch), moderate-high (>67 % crown scorch), and high (100 % needle consumption). We selected these field severity ranks to represent a continuum of dominant structural changes to forests immediately fol-

lowing a fire that may be relevant to woodpeckers and beetles.

To classify dNBR<sub>100</sub>, we divided the dNBR gradient into six intervals of 100, which we compared to the field severity ranks in each severity plot (Table 1). Negative dNBR values corresponded to unburned areas; however, we truncated dNBR at zero. Unburned and high-severity field ranks had good correspondence to dNBR<sub>100</sub> (Table 1). We pooled low and low-moderate (hereafter low severity) field ranks because of considerable overlap in dNBR<sub>100</sub>. Moderate-severity field ranks corresponded to dNBR<sub>100</sub> = 201 to 400. Only 34 % of moderate-high severity plots were correctly classified based on dNBR<sub>100</sub> = 401 to 500, with 38 % misclassified as moderate-severity and 25 % misclassified as high-severity (Table 1). Overall, the five burn-severity classes had a 68.7 % overall classification accuracy. Using mean dNBR derived from a 100 m radius moving window, we created a burn-severity map based on the five burn-severity classes (Figure 1).

To quantify burn severity for each survey plot, we calculated mean dNBR (dNBR<sub>p</sub>). We also calculated mean dNBR at the home range scale in 339 m buffers (36 ha) around focal trees and subplot centers (dNBR<sub>h</sub>). To retain the burn severity gradient and avoid breakpoints between severity classes and classification errors, we used mean dNBR<sub>p</sub> or dNBR<sub>h</sub> for

**Table 1.** Relationship between burn severity class and the differenced normalized burn ratio (dNBR) at the Hayman Fire (2003), Colorado, USA. Burn severity classes were derived from comparisons of six field severity ranks to dNBR<sub>100</sub> at severity plots ( $n = 252$ ). The overall classification accuracy was 68.7 %.

	Burn severity class				
	Unburned	Low	Moderate	Moderate-high	High
Field severity rank	0 % tree scorch	<33 % crown scorch <sup>a</sup>	33 % to 67 % crown scorch	>67 % crown scorch	>50 % crown consumed
dNBR <sub>100</sub> <sup>b</sup>	≤100	101 to 200	201 to 400	401 to 500	>500
Classification accuracy <sup>c</sup>	95.1 %	66.7 %	50.0 %	34.4 %	58.8 %

<sup>a</sup> Field severity ranks (bole scorch and <33 % crown scorch) were pooled because of substantial overlap in dNBR<sub>100</sub>.

<sup>b</sup> dNBR<sub>100</sub> is the mean dNBR score in 100 m buffers surrounding severity plot centers.

<sup>c</sup> % Classification Accuracy = (number correctly predicted samples in burn severity class) ÷ (total number samples in class).

all analyses. We used the burn severity classes only for interpretation and display of results.

### Data Analyses

**Hierarchical levels of analysis.** We evaluated the response of three-toed woodpeckers to burn severity, beetle occurrence, and tree size at three levels: home-range, foraging patches, and trees within foraging patches. At the largest scale, corresponding to home-range size, the dependent variable was the presence or absence of three-toed woodpeckers in survey plots. To evaluate use vs. availability at the foraging-patch scale, we compared foraging patches to subplots. Within patches, we evaluated the characteristics of used vs. unused trees by comparing foraging and paired trees. Each hierarchical level was analyzed separately.

**Home range level.** We compared the presence and absence of three-toed woodpeckers (woodpecker occurrence) in survey plots by burn-severity ( $dNBR_p$ ), beetle occurrence (external evidence), and tree size. Although we had insufficient detections ( $n = 34$ ) to evaluate whether detection rates varied with burn severity, 87 % of three-toed woodpecker detections were auditory, which is less likely than visual detections to be affected by canopy consumption. Previous studies of burn severity con-

cluded that detection rates did not differ across the burn severity gradient for most species including a congeneric species (hairy woodpecker [*Picoides villosus*]; Smucker et al. 2005, Kotliar et al. 2007). Because of low detections on survey plots in 2003 ( $n = 9$ ), we pooled detections of three-toed woodpeckers on each survey plot across years and defined presence at a plot if we detected three-toed woodpeckers there in at least one year. We summarized the mean beetle occurrence and tree size by survey plot.

We used logistic regression to model the presence of three-toed woodpeckers in relation to burn severity, beetle occurrence, and tree size (Table 2). To evaluate nonlinear patterns, we used a quadratic term for burn severity. Because beetle occurrence was correlated with burn severity at the home range scale (Pearson correlation = 0.80), a quadratic term for beetle occurrence in the model would not account for much additional variation. We only tested for a linear relationship between woodpecker and beetle occurrence because we assumed a nonlinear relationship between woodpeckers and beetles was primarily a response to burn severity at this scale. We used  $dNBR_p$  to assign each survey plot to a burn severity class (Table 1) and present the results using these five burn severity classes.

**Table 2.** Model selection results based on logistic regression of factors influencing the occurrence<sup>a</sup> of American three-toed woodpeckers in survey plots at the Hayman burn (2003 to 2004), Colorado, USA. Logit models are listed beginning with the best-fitting model and sorted by  $\Delta AIC_c$ .  $AIC_c$  weights ( $w_i$ ), indicate the relative likelihood of each model.

Model ( $n = 28$ )	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
$dNBR_p + (dNBR_p)^2 + \text{Beetles}^b$	4	33.64	0.00	0.45
Beetles	2	35.37	1.73	0.19
$dNBR_p + (dNBR_p)^2 + \text{Beetles} + \text{dbh}$	4	36.48	2.84	0.11
$dNBR_p + (dNBR_p)^2 + \text{dbh}$	5	36.55	2.91	0.10
$dNBR_p + (dNBR_p)^2$	4	37.29	3.65	0.07
dbh	3	37.70	4.07	0.06
Constant	2	40.38	6.75	0.02
$dNBR_p$	1	42.24	8.60	0.00

<sup>a</sup> Presence/absence of woodpeckers.

<sup>b</sup> Beetle occurrence (proportion of trees with external evidence of beetles).



*Foraging patch level.* We used logistic regression to evaluate the potential factors (tree size, TBI, and beetle occurrence) influencing woodpecker use of patches within home ranges compared to subplots. We retained  $dNBR_h$  in all models to control for the effects of burn severity at the home range scale on TBI and beetle occurrence within patches (Table 3). Because we did not collect the full set of variables in both years, we analyzed years separately. In 2003, we lacked internal evidence of beetles on the subplots and, therefore, we did not include this parameter in the model set. We included  $(dNBR_h)^2$  in each 2003 model because occurrence of three-toed woodpeckers was highest in moderately burned areas at the home range scale (Figure 3). In 2004, we did not sample the full range of burn severity at the home range scale by subplots ( $dNBR_h > 200$  for 94 % of subplots), thus we did not include  $(dNBR_h)^2$  in this model set.

*Within foraging patches.* We used logistic regression to evaluate the potential factors (tree size, beetle occurrence, and TBI) influencing the selection of trees within patches (Table 4). We compared foraging patches ( $n = 48$ ) to the series of paired trees ( $n = 48$ ). Because we sampled an unknown number of woodpeckers in both years, we retained year in each model to control for this potential source of variation.

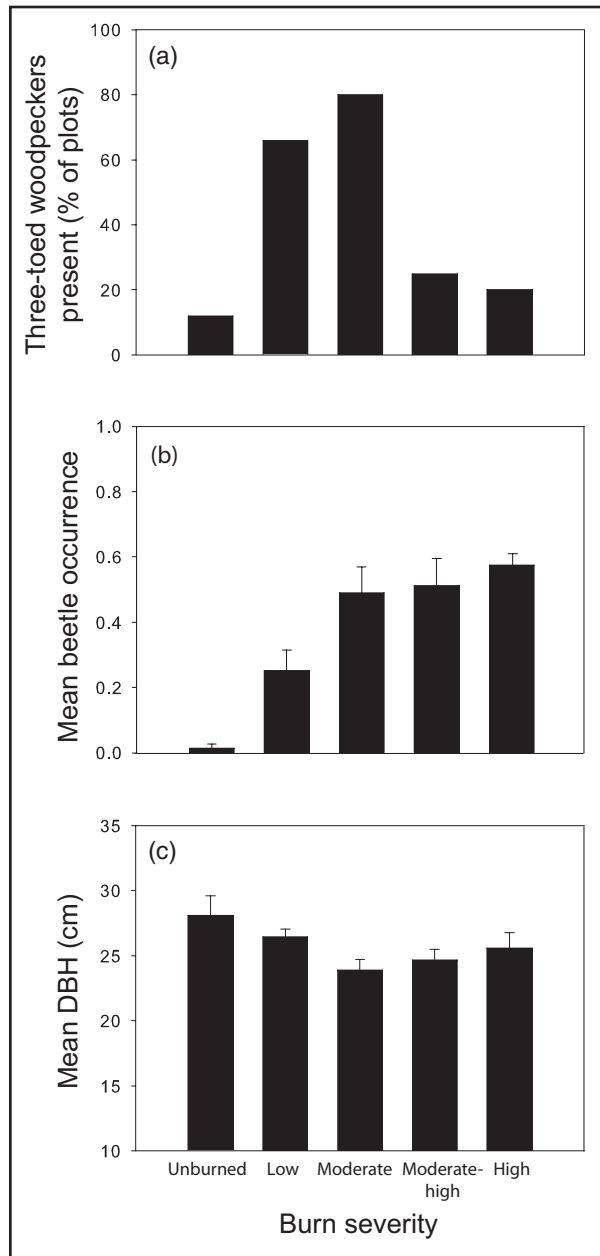
We used SYSTAT 12.02 (SPSS, Inc., Chicago, Illinois) for all statistical tests. We rescaled mean  $dNBR$  by dividing by 100. For logistic regressions, we used Akaike's information criterion (AIC), and corrected for small samples sizes ( $AIC_c$ ; Akaike 1973, Burnham and Anderson 2002). We used  $\Delta AIC < 2$  as an indicator of models with substantial support (Burnham and Anderson 2002). For all models with  $\Delta AIC < 2$ , regression coefficients ( $\beta$ ) with 95 % confidence intervals that broadly spanned zero indicated variables that had weak contributions to models. The AIC weight is an indicator of how any one model performed

compared to the others we tested; where the higher the weight, the better the fit (Burnham and Anderson 2002). We provide means and  $\pm$  standard deviations in the text and standard errors in the figures.

## RESULTS

### Home Range Level

At the scale corresponding to home range size, three-toed woodpecker presence in survey plots best corresponded to burn severity and external evidence of beetles. We most commonly detected woodpeckers in moderate- and low-severity plots, and rarely in unburned, moderate-high, and high-severity areas at this scale (Figure 3a). This nonlinear pattern is demonstrated by inclusion of the quadratic term  $[(dNBR_p)^2]$  in the best-fitting model and a negative slope for the parameter  $(dNBR_p)$ :  $\beta = 4.32$ , 95 % CI =  $-0.03, 8.5$ ;  $(dNBR_p)^2$ :  $\beta = -0.65$ , 95 % CI =  $-1.24, -0.05$ ; Table 2). Beetle occurrence only weakly contributed to the top model, as indicated by a 95 % confidence interval that broadly spanned zero ( $\beta = -7.371$ , 95 % CI =  $-16.91, 2.17$ ; Table 2). Although beetle occurrence was high in plots that burned at moderate and high severities, beetle occurrence was much lower in low-severity plots, where woodpecker occurrence was high (Figure 3b). In addition, woodpecker occurrence was low in high-severity plots, where beetle occurrence was consistently the highest (Figure 3b). However, the top two models ( $\Delta AIC_c < 2$ ) had combined AIC weights of 0.64 (Table 2), indicating model uncertainty. None of the top models included tree size and tree size did not correspond to woodpecker occurrence. Trees were slightly larger in unburned and low-severity plots compared to moderate- and high-severity plots (Figure 3c). Thus, three-toed woodpecker occurrence was most strongly related to burn severity at the scale of home ranges.



**Figure 3.** Variables used to predict the occurrence of American three-toed woodpeckers in survey plots (unburned:  $n = 8$ , low:  $n = 6$ , moderate:  $n = 5$ , moderate-high:  $n = 4$ , high:  $n = 5$ ): (a) percent of plots with three-toed woodpeckers present; (b) mean  $\pm$  SE beetle occurrence (proportion of trees with external evidence of beetles); (c) mean  $\pm$  SE tree size (dbh).

#### Foraging Patch Level

In 2003, tree size and burn severity best predicted the use of foraging patches compared

to that available in the burn, and the top logit model included both factors (AIC weight = 0.81; Table 3a). Diameter at breast height (dbh) was greater in foraging patches ( $28.9 \text{ cm} \pm 6.31 \text{ cm}$ ) compared to subplots ( $25.8 \text{ cm} \pm 3.5 \text{ cm}$ ;  $\beta = 0.18$ , 95 % CI = 0.01, 0.36). As we observed at the home range level (Figure 3a), foraging patches most commonly occurred within larger areas that had intermediate burn severities (Figure 4:  $\text{dNBR}_h = 201$  to 400;  $\text{dNBR}_h$ :  $\beta = 0.29$ , 95 % CI =  $-0.04$ , 5.86;  $(\text{dNBR}_h)^2$ :  $\beta = -0.71$ , 95 % CI =  $-1.20$ ,  $-0.22$ ). Tree-crown burn index (TBI) of foraging patches ( $0.61 \pm 0.23$ ) was only slightly higher than subplots ( $0.53 \pm 0.40$ ) and there was considerable overlap in TBI (Figure 4). However, when we compare two scales of burn severity (home range and foraging patch; Figure 4), the contribution of TBI in predicting woodpecker use ( $\beta = 5.20$ , 95 % CI = 1.15, 9.26) is apparent. The majority of foraging patches (68.2 %) included trees with  $\text{TBI} \geq 0.5$  (corresponding to 100 % crown scorch and partial to complete crown consumption) within home ranges that had intermediate burn severities (Figure 4). Woodpecker use of severely burned patches within moderately burned areas was much greater than available in subplots (14.6 %). For  $\text{TBI} < 0.5$  (partially scorched and unburned patches), use (27.3 %) was lower than that available (50 %). Three-toed woodpeckers rarely foraged in severely burned patches ( $\text{TBI} \geq 0.5$ ) within larger areas that were also more severely burned ( $\text{dNBR}_h > 400$ ), and use of severely burned areas (4.5 %) was much less than that available (35.4 %). Burn severity at both the foraging patch and home range scales, as well as tree size, were all necessary to characterize foraging patches used by three-toed woodpeckers in 2003.

In 2004, tree size, beetle occurrence, and TBI were all useful in characterizing patches used by foraging three-toed woodpeckers. However, there was considerable model uncertainty, and three models had  $\Delta\text{AIC}_c < 2$  (Table

**Table 3.** Model selection results based on logistic regression of factors influencing the use of foraging patches by American three-toed woodpeckers compared to subplots at the Hayman Fire (2003 to 2004), Colorado, USA. Logit models are listed with the best-fitting model first and sorted by  $\Delta AIC_c$ . The  $AIC_c$  weights ( $w_i$ ), indicate the relative likelihood of each model.

**a.** Foraging patch vs. subplots 2003.

Model ( $n = 70$ ) <sup>a</sup>	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
$dNBR_h + (dNBR_h)^2 + dbh + TBI$	5	61.85	0.00	0.81
$dNBR_h + (dNBR_h)^2 + TBI$	4	65.55	3.70	0.13
$dNBR_h + (dNBR_h)^2 + dbh$	4	67.36	5.51	0.05
$dNBR_h + (dNBR_h)^2$	3	70.35	8.50	0.01
Constant	1	89.20	27.35	0.00

**b.** Foraging patch vs. subplots 2004.

Model ( $n = 58$ ) <sup>a</sup>	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
$dNBR_h + dbh$	3	49.05	0.00	0.41
$dNBR_h + dbh + Beetles^b + TBI$	5	50.22	1.17	0.23
$dNBR_h + dbh + Beetles$	4	50.28	1.23	0.22
$dNBR_h + dbh + TBI$	4	51.32	2.27	0.13
$dNBR_h + TBI + Beetles$	4	65.10	16.05	0.00
$dNBR_h + Beetles$	3	67.15	18.10	0.00
$dNBR_h$	2	70.02	20.97	0.00
$dNBR_h + TBI$	3	72.12	23.07	0.00
Constant	1	81.85	32.80	0.00

<sup>a</sup>  $dNBR_h$  represents burn severity at the home range scale (36 ha); dbh and TBI were evaluated within foraging patches or subplots.

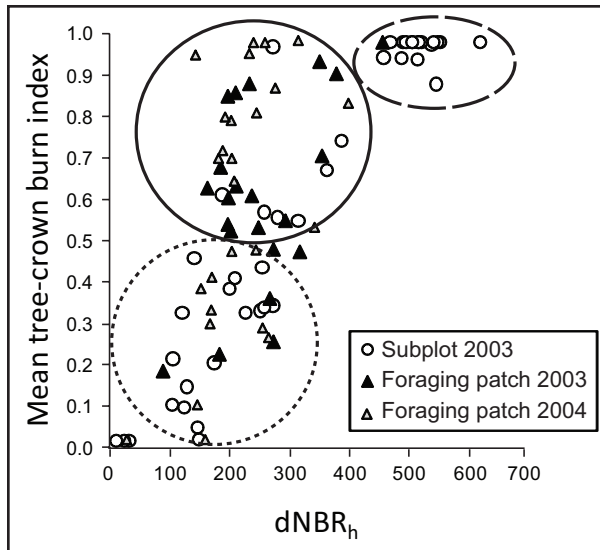
<sup>b</sup> Beetle occurrence (proportion of trees with internal evidence of beetles) within foraging patches or subplots.

**Table 4.** Model selection results based on logistic regression of factors influencing American three-toed woodpecker use of trees within foraging patches compared to paired trees at the Hayman Fire (2003 to 2004), Colorado, USA. Year was included in all logit models. Models are listed with the best-fitting model first and sorted by  $\Delta AIC_c$ .  $AIC_c$  weights ( $w_i$ ), indicate the relative likelihood of each model.

Model ( $n = 96$ )	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
Year + dbh	3	115.50	0.00	0.34
Year + dbh + Beetles	4	115.67	0.16	0.32
Year + dbh + Beetles <sup>a</sup> + TBI	5	116.36	0.86	0.22
Year + dbh + TBI	4	117.66	2.16	0.12
Constant	1	135.12	19.62	0.00
Year + Beetles + TBI	4	136.37	20.87	0.00
Year + Beetles	3	137.12	21.61	0.00
Year	2	137.21	21.70	0.00
Year + TBI	3	138.95	23.44	0.00

<sup>a</sup> Beetle occurrence (proportion of trees with internal evidence of beetles).





**Figure 4.** Burn severity at the home range ( $dNBR_h$ ) and foraging patch [tree-crown burn index (TBI)] levels of areas used by foraging American three-toed woodpeckers compared to subplots (i.e., available conditions). The solid circle includes points that represent burn severity patterns where use is much greater than availability, the dotted circle includes points where use is less than availability, and the dashed circle includes points that represent use much less than availability.

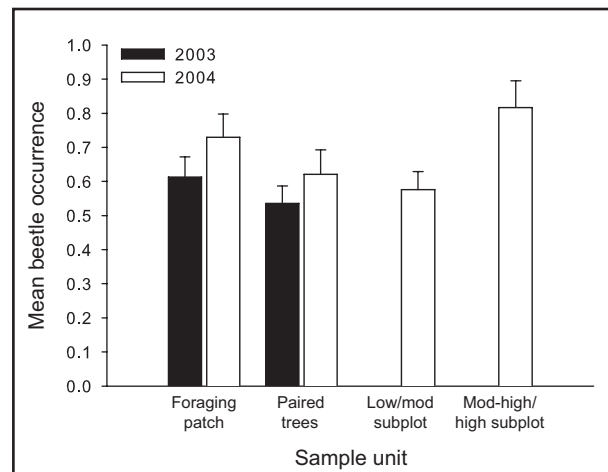
3b). Again, dbh was greater in foraging patches ( $34.9 \text{ cm} \pm 8.82 \text{ cm}$ ) than in subplots ( $25.2 \text{ cm} \pm 4.5 \text{ cm}$ ) and was included in all top models. The second best logit model ( $\Delta AIC_c = 1.17$ ; Table 3b) included all parameters in the model set;  $dNBR_h$  ( $\beta = -1.03$ , 95 % CI =  $-1.91, -0.15$ ), dbh ( $\beta = 0.29$ , 95 % CI =  $0.09, 0.49$ ), beetle occurrence ( $\beta = 4.18$ , 95 % CI =  $-0.59, 8.94$ ), and TBI ( $\beta = -3.64$ , 95 % CI =  $-8.52, 1.26$ ). The relatively weak contribution of TBI to the model reflects the same relationship between TBI and  $dNBR_h$  observed in 2003 (Figure 4); both scales of burn severity (home range and foraging patch) were necessary to predict woodpecker patch use. Beetle occurrence in foraging patches was higher than in low/moderate-severity subplots, and slightly lower than in more severely burned subplots (Figure 5). Tree size was not correlated with beetle occurrence or TBI (Pearson correlation  $< 0.17$ ). However, beetle occurrence was cor-

related with TBI (Pearson correlation = 0.70) and the full logit model ( $AIC_c = 50.22$ ) was only slightly better than the logit model without TBI ( $AIC_c = 50.28$ ; Table 3b), contributing to model uncertainty.

Because the models sets differed between years, we were unable to simultaneously evaluate all three variables (beetle occurrence, TBI, and tree size) at the foraging patch level across the full range of burn severities ( $dNBR_h$ ). The inclusion of all variables in the top logit models in both years indicated that all three variables contributed to the differences between foraging patches and subplots.

### Within Foraging Patches

Tree size best explained woodpecker use of trees within foraging patches, as indicated by its inclusion in all three best-fitting models (Table 4). There was considerable model uncertainty, however, and three models had  $\Delta AIC_c < 2$  (Table 4). The second best logit model ( $\Delta AIC_c = 0.16$ ; Table 4) included tree



**Figure 5.** Beetle occurrence (the proportion of trees with internal evidence of beetles) in patches used by foraging woodpeckers compared to available conditions. Subplots represent prey availability at the foraging patch scale, whereas paired trees represent prey availability within foraging patches. Internal evidence of beetles was measured in subplots in 2004 only and all subplots sampled in 2004 burned at  $dNBR_h > 200$ . Means  $\pm$  SE are provided.

size and beetle occurrence, and both variables were higher in foraging patches compared to paired trees (dbh:  $\beta = 0.16$ , 95 % CI = 0.08, 0.24; beetles:  $\beta = 1.09$ , 95 % CI = -0.43, 2.60; Figure 5). Year effects were weak in all models ( $\beta = -0.38$ , 95 % CI = -1.31, 0.54 in the top model). TBI was similar in foraging patches ( $0.61 \pm 0.28$ ) and paired trees ( $0.63 \pm 0.29$ ) and only weakly contributed to the third best logit model ( $\beta = -1.33$ , 95 % CI = -3.49, 0.82). Indeed, TBI was highly correlated between foraging patches and the associated paired trees (Pearson correlation = 0.85), indicating that burn severity was similar among trees within patches. Tree size was not correlated with beetle occurrence (Pearson correlation = 0.11). Thus, within patches, three-toed woodpeckers were more likely to forage on large trees that had a high probability of beetle occurrence.

### *Beetle Families*

Cerambycidae and Buprestidae (wood-boring beetles) were the two most abundant beetle families we found in trees at the Hayman Fire. We only detected bark beetles (Scolytinae) in <1 % of all trees sampled. In 2004, internal beetle occurrence increased, on average, by 0.14 in foraging patches (Figure 5), and by 0.17 in subplots (based on internal beetle occurrence in 12 subplots sampled in both years).

## **DISCUSSION**

### *Woodpecker Response Patterns*

Our results at the Hayman Fire demonstrated that burn severity patterns, prey availability, and tree size affected three-toed woodpecker habitat selection at multiple scales. The relative importance of these factors in predicting woodpecker occurrence and foraging patterns depended on the scale of analysis. Furthermore, the response of three-toed wood-

peckers to these factors was not consistent across scales.

The response to burn severity was strongly scale-dependent. Three-toed woodpeckers generally established territories in moderately burned areas, which were heterogeneous and included the full spectrum of burn severities. At the foraging-patch level, it was necessary to evaluate burn severity at two scales (foraging patches, home range) in order to characterize use of severely burned foraging patches; within home ranges, woodpeckers disproportionately foraged in patches of trees that had complete crown scorch or canopy consumption compared to that available. However, they rarely used severely burned patches within larger severely burned areas (Figure 4). Within foraging patches, burn severity was not useful in predicting foraging patterns because burn severity was relatively homogeneous at this scale. These scale-dependent patterns indicate that the spatial heterogeneity of post-fire forests may affect use by three-toed woodpeckers. The woodpeckers rarely established territories in severely burned areas that did not contain live trees (Figure 3a), but readily foraged in severely burned patches within home ranges of intermediate burn severities (Figure 4). Consequently, the scaling of burn-severity patterns may affect how three-toed woodpeckers respond to burn severity.

As with burn severity, three-toed woodpecker responses to prey availability varied across spatial scales. At the home-range scale, the woodpeckers used areas with intermediate beetle occurrence levels (Figure 3b). In contrast, beetle occurrence was almost as high in foraging patches as in the highest severity areas ( $\text{dNBR}_h > 400$ ), and was higher than available in intermediate-severity areas ( $\text{dNBR}_h = 201$  to 400) and in paired trees (Figure 5). These results suggest that preferential foraging in severely burned patches with high beetle occurrence within low and moderately burned home ranges can increase prey availability to levels similar to that observed in more severely

burned areas. Overall, beetle occurrence was more useful for explaining use of foraging patches, and trees within patches, than it was in accounting for woodpecker settlement patterns at the home range scale.

The relative importance of burn severity, beetle occurrence, and tree size in predicting three-toed woodpecker use varied among spatial scales (Table 5). Tree size and beetle occurrence were the strongest predictors of woodpecker use at the smallest scale (Figure 5), whereas burn severity played a stronger role at the largest scale (Figure 3). At intermediate scales, all factors were important in predicting woodpecker use (Figure 4, Figure 5). Because the likelihood of finding beetles was

not correlated with tree size, the proportionally greater use of larger trees than were available may simply reflect greater beetle abundance due to larger surface area.

Burn severity and beetle occurrence can be strongly correlated (Hood and Bentz 2007), making it difficult to tease apart the relative importance of these factors to three-toed woodpeckers. It is unclear whether the woodpeckers are responding primarily to beetle availability, burn severity, or a combination of both. Foraging woodpeckers may use burn severity, as well as other external visual and auditory cues of beetle occurrence, to increase their success at locating beetle larvae.

**Table 5.** Summary of factors contributing to differences in areas used by foraging American three-toed woodpeckers in comparison to available areas at several hierarchical levels at the Hayman Fire (2003 to 2004), Colorado, USA. Cells in bold indicate factors that best account for woodpecker occurrence and use at that scale.

Level (scale)	Reference areas	Response variable	Factors		
			Burn severity	Beetle occurrence	Tree size
Home Range (36 ha)	Survey plots	Woodpecker occurrence <sup>a</sup>	<b>Highest in low and moderate severity areas<sup>b</sup></b>	Highest at intermediate beetle levels <sup>c</sup>	No pattern
Foraging patches <sup>d</sup> (~1 ha)	Subplots (in low/moderate severity areas) <sup>e</sup>	Use vs. available	<b>Use &gt; availability in severely burned patches<sup>f</sup></b>	<b>Foraging patches higher<sup>g</sup></b>	<b>Larger in foraging patches (all severities)</b>
			Use < availability in lightly burned patches <sup>h</sup>		
	(in moderate-high/high severity areas) <sup>i</sup>		<b>Use &lt; availability in severely burned patches<sup>f</sup></b>	<b>Foraging patches lower<sup>g</sup></b>	
Trees within foraging patches (~1 ha)	Paired trees	Use vs. available	Similar	<b>Foraging trees higher<sup>g</sup></b>	<b>Foraging trees larger</b>

<sup>a</sup> Presence or absence of three-toed woodpeckers.

<sup>b</sup> dNBR<sub>p</sub> = 201 to 400.

<sup>c</sup> External beetle occurrence.

<sup>d</sup> Most foraging patches were in 36 ha areas that burned at moderate severities (dNBR<sub>h</sub> = 201 to 400).

<sup>e</sup> dNBR<sub>h</sub> = 201 to 400

<sup>f</sup> Complete crown scorch or canopy consumption (TBI ≥ 0.5).

<sup>g</sup> Internal beetle occurrence.

<sup>h</sup> Partial crown scorch or unburned (TBI < 0.5).

<sup>i</sup> dNBR<sub>h</sub> > 400.



Nevertheless, if woodpeckers were responding solely to beetle occurrence at the home range scale, we would expect peak woodpecker occurrence in high-severity areas where beetle occurrence was highest, in contrast to what we observed at the Hayman Fire. Accordingly, patterns of beetle occurrence at home-range scales were not sufficient to predict the settlement patterns of three-toed woodpeckers within the burn, suggesting other features of moderately burned areas (e.g., presence of live trees or congeneric species) played an important role at this scale. Within foraging patches, however, beetle occurrence was more important than burn severity in predicting tree use. Such variation among scales indicates that both beetle occurrence and burn severity may influence three-toed woodpeckers. Linkages between scales may also affect how three-toed woodpeckers respond to post-fire conditions (Figure 4). Decisions about where to establish a territory may be influenced by prey availability. The establishment of territories subsequently constrains prey availability for nesting woodpeckers. Consequently, analyses at a particular scale reflect factors that may be necessary, but not sufficient, to understand woodpecker decisions at that scale.

Other studies of three-toed woodpeckers use of burns found somewhat different patterns (Murphy and Lehnhausen 1998, Koivula and Schmiegelow 2007), but the studies differed in sampling scales, among other factors. Neither study provided information on available burn-severity patterns, but instead focused on comparisons with other species of woodpeckers. Murphy and Lehnhausen (1998) studied a single 67 ha plot along the edge of a 3500 ha high-severity burn in a spruce/fir forest near Fairbanks, Alaska, USA, that had been mostly salvage logged. They compared three-toed woodpeckers with black-backed woodpeckers (*Picoides arcticus*) and hairy woodpeckers and found that three-toed woodpeckers used

more lightly burned trees compared to the other two woodpecker species (Murphy and Lehnhausen 1998). Koivula and Schmiegelow (2007) compared seven woodpecker species (including three-toed woodpeckers) in a 267 000 ha burn that occurred in a mixed-conifer forest in northeastern Alberta, Canada. They sampled 24 transects, covering 97 ha each, which varied in degree of salvage logging; they averaged burn severity across each 4.5 km triangular transect. At this scale, they found that burn severity was not significantly related to three-toed woodpecker abundance. It is difficult to resolve differences in results observed at the Hayman Fire with those of other burns because so many factors varied across studies, including burn severity, prey availability, salvage logging, forest type, and the presence of black-backed woodpeckers, which do not occur in Colorado.

Our results at the Hayman Fire demonstrate that response patterns can vary among studies simply as a result of differences in sampling scale and the scaling of burn severity patterns. Even within the same forest type and fire regime, the spatial patterning of burn severity can vary. Consider, for example, several recent fires that occurred on the Pike National Forest near the Hayman Fire. In 2000, the 4422 ha Hi Meadow Fire had relatively small crown fire patches (<500 ha) compared to the Hayman Fire. In 1996, the 3059 ha Buffalo Creek Fire was dominated by a wind-driven crown fire, but because of its elongated shape, the center of the crown fire area generally did not exceed 500 m from live trees. In contrast, the size of the crown fire areas at the Hayman Fire greatly exceeded the total size of these smaller burns, and portions of the crown fire areas were as much as 1000 m from live trees. Our results indicate that the spatial scaling of high-severity burns at the Hi Meadow Fire and Buffalo Creek Fire created potentially suitable habitat for three-toed woodpeckers. Likewise, heterogeneity in burn severity across much of

the Hayman Fire provides suitable habitat for three-toed woodpeckers, but the center of the high-severity areas at the Hayman Fire may be too far from live trees to be readily used by three-toed woodpeckers. Remnant patches of live trees within high-severity patches may increase the likelihood that three-toed woodpeckers would use such areas.

Such variation among burns underscores the importance of measuring burn severity in used and available areas across a range of scales. Because of spatial heterogeneity within burns, an area classified as moderate severity at one scale can change to low or high severity when evaluated at smaller or larger scales, thus, quantification of burn severity should be scale explicit. As we have demonstrated here, quantification of burn severity at more than one scale may be necessary to evaluate the response of species to post-fire conditions across a severity gradient. In addition, differences in burn severity classifications among studies can be avoided by using continuous measures of burn severity such as dNBR (Kotliar *et al.* 2007). These recommendations will help to facilitate comparisons among studies.

Differences in prey availability may also contribute to variation among studies. In particular, the effects of burn severity on beetle occurrence can vary among tree species, which may be related to the effect of bark thickness on water loss during burning (Saint-Germain *et al.* 2004). In a burn in Quebec, Canada, severely burned black spruce (*Picea mariana*), which has relatively thin bark, had low densities of bark and wood-boring beetles (Saint-Germaine *et al.* 2004). In contrast, severely burned ponderosa pine and Douglas-fir, which have relatively thick bark, had high densities of wood-boring beetles at the Hayman Fire. Previous studies in unburned (Imbeau and Desrochers 2002) and burned (Murphy and Lehnhausen 1998) forests concluded that three-toed woodpeckers disproportionately consumed bark beetle larvae. However, our

results suggest that three-toed woodpeckers may opportunistically consume the most numerically dominant prey species, which in our system was the much larger wood-boring beetle larvae. Thus, information on prey availability, in addition to burn severity, is necessary to compare woodpecker studies. The presence of congeners may also affect prey use by three-toed woodpeckers (Murphy and Lehnhausen 1998).

Time since fire can greatly affect prey availability. Beetle abundance typically peaks within the first year or two post-fire because beetles most readily attack dying or recently dead trees (Ryan and Amman 1996). In areas of complete crown consumption, most trees die within the first year post-fire. Mortality can be more protracted in moderate-severity areas because some partially burned trees may take several years to succumb to the stress of fire and beetle attack. As a result, beetle abundance may remain elevated longer in moderately burned areas than in high-severity areas (McHugh and Kolb 2003). Because three-toed woodpeckers have high nest site fidelity (Cramp 1985), selection for areas with mixed-severity burns may result in greater average prey availability than in more severely burned areas over longer time frames than evaluated here. Consequently, both spatial and temporal variation in resources may affect burn use by three-toed woodpeckers.

### *Management Implications*

At the Hayman Fire, wind-driven crown fire that burned ~25 000 ha in a single day created an extensive area of dead trees (Graham 2003). Yet, the fire created considerable heterogeneity by leaving remnant patches of live trees within and along the edges of this large severely burned area, where we often found three-toed woodpeckers (Figure 1). They also occurred in areas with finer-scale heterogeneity in burn severity created by more moderate

fire behavior (Figure 1). The strong association of three-toed woodpeckers with burned forests containing large areas of moderately and severely burned trees demonstrates the importance of the mixed-severity fire regime to this species. It is becoming increasingly clear that severe fires played a greater role in historic fire regimes in ponderosa pine and Douglas-fir forests of the Colorado Front Range than generally acknowledged (Sheriff and Veblen 2006, 2007). Because the fire regime of most of the area burned by the Hayman Fire is either mixed- or high-severity, fire suppression (and its effect on fuels) may have played a lesser role in the severity of this fire than climate variation and past legacies of severe fires (Sheriff and Veblen 2006, 2007). Yet, fire management programs typically emphasize the use of understory fires and forest thinning to

prevent severe fires. This could negatively affect three-toed woodpeckers by destroying existing snags while potentially reducing the opportunities for creating large areas of snags that provide critical foraging and nesting sites (Horton and Mannan 1988, Hutto and Gallo 2006). Post-fire salvage logging, which often targets larger trees, further compounds this problem by reducing the suitability of post-fire forests for this species (Hutto 1995, Kotliar *et al.* 2002), in part by reducing prey availability (Hutto 2006, Hutto and Gallo 2006). Thus, inclusion of high-intensity fires in management prescriptions and judicious use of salvage logging is essential for fire-dependent species like three-toed woodpeckers (Hutto 1995, Kotliar *et al.* 2002, Hutto 2006, Hutto and Gallo 2006).

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