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RESEARCH ARTICLE

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Age-dependent habitat relationships of a burned forest specialist emphasise the role of pyrodiversity in fire management

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Abstract

1. Variation in fire characteristics, termed pyrodiversity, plays an important role in structuring post-fire communities, but little is known about the importance of pyrodiversity for individual species. The availability of diverse post-fire habitats may be key for fire-associated species if they require different resources at different life-history stages.
2. We tested for age-specific habitat relationships in the black-backed woodpecker, a post-fire specialist. We used radio-telemetry to track fledgling and adult woodpeckers in burned forests and built resource selection functions to compare the effect of stand-, tree- and snag-level covariates between adults and fledglings.
3. Fledgling black-backed woodpeckers selected habitat with more live trees than adults and used more heterogeneous habitats burned at lower severity, illustrating strong age-dependent effects on habitat selection. Within selected stands, fledglings were less likely to use snags and more likely to use live trees when compared to adults, but both age classes showed strong positive selection for larger-diameter trees (live and dead). Over the 60 days after leaving their nests, fledglings showed an increasing propensity to use snags rather than live trees.
4. Our results provide evidence that the predation–starvation hypothesis, which posits a trade-off between foraging efficiency and the need to minimise predation risk, plays a role in structuring the age-dependent habitat use of a burned forest specialist. Adult black-backed woodpeckers selected resources associated with food availability, but these resources occurred in relatively open, exposed habitat. Fledglings selected habitat that provided increased cover, perhaps as a strategy to reduce predation risk.
5. *Synthesis and applications*. Globally, fires are increasing in severity and extent, leading to increased focus on fire-associated species that play keystone roles in facilitating biodiversity resilience. Our findings suggest that a diversity of patches burned at different severities may benefit post-fire specialists like the black-backed woodpecker at multiple life-history stages. The increasing prevalence of large, homogeneously high-severity ‘megafires’ may present an emerging threat

even to post-fire specialists, and we urge land managers to consider opportunities to promote pyrodiversity in the face of novel fire regimes.

KEYWORDS
black-backed woodpecker, fire severity, forest management, habitat selection, landscape heterogeneity, *Picoides arcticus*, pyrodiversity, wildfire

1 | INTRODUCTION

Wildfire is a key ecological disturbance in forests world-wide, generating successional mosaics of habitat that structure biotic communities (Kelly & Brotons, 2017). Variation in fire regime characteristics—termed pyrodiversity—creates heterogeneous post-fire habitat, which has been correlated with increased biodiversity in a variety of fire-prone systems (Beale et al., 2018; Tingley, Ruiz-Gutiérrez, Wilkerson, Howell, & Siegel, 2016). Mounting evidence in support of this 'pyrodiversity–biodiversity' hypothesis has made promoting and retaining fire heterogeneity an increasingly influential guiding principal in forest management and biodiversity conservation (Kelly, Brotons, & McCarthy, 2017). Pyrodiversity is generally believed to foster biodiversity where fire regimes yield heterogeneous patchworks of different habitats, each with its own affiliated species (Tingley, Ruiz-Gutiérrez, et al., 2016). In this view, individual species do not benefit from pyrodiversity, as species diversity is simply an emergent property of a diversity of habitats. However, the implicit view that individual species are monolithic in their habitat requirements—depending on just one component of a diverse landscape—may not be accurate (Bolnick et al., 2002; Holtmann, Santos, Lara, & Nakagawa, 2017). In particular, pyrodiversity could hold substantial benefits for populations within a single species if individuals require different habitat characteristics across their full life cycle.

Globally, the size and intensity of wildfires are on the rise (Stephens et al., 2014). In western North America, historical fire suppression and a changing climate increasingly push the region into a novel fire regime, which is characterised by exceptionally large, homogeneously high-severity fires (Miller & Safford, 2012; Stevens, Collins, Miller, North, & Stephens, 2017). These trends have led to increased focus on fire-associated species that benefit from fire and play keystone roles in facilitating biodiversity resilience. High-severity fire creates dense stands of standing dead trees (snags) that may contribute to the regional persistence of deadwood-associated species including cavity-nesting birds, saproxylic insects and cavity-using mammals (DellaSala, Bond, Hanson, Hutto, & Odion, 2014; Hutto et al., 2016). The black-backed woodpecker (*Picoides arcticus*) is a post-fire specialist that appears closely tied to areas burned at high severity across much of its range (Hutto, 2008). Black-backed woodpeckers depend on snags for nest sites and foraging (Rota, Rumble, Lehman, Kesler, & Millspaugh, 2015; Seavy, Burnett, & Taille, 2012). In the western U.S., the species primarily feeds on the larvae of wood-boring beetles (Cerambycidae and Buprestidae), which reproduce in dead and dying trees, especially after fire (Murphy & Lehnhausen, 1998). High densities of black-backed woodpeckers within recently burned areas contrast with the species' rarity in the surrounding matrix of unburned forest (Hutto, 2008). It is thus reasonable to hypothesise that the black-backed woodpecker, as a flagship for biodiversity conservation in burned forests, may benefit from trends towards increasing forest fire severity.

In birds, species-specific benefits of pyrodiversity may arise from differences in the habitat requirements of adults and fledglings, particularly where a trade-off exists between foraging efficiency and the need to minimise predation risk (Houston, McNamara, & Hutchinson, 1993). This 'predation–starvation' hypothesis may help explain foraging behaviour of birds and the ways that individuals adjust habitat selection based on perceived predation risk (Bonter, Zuckerberg, Sedgwick, & Hochachka, 2013). Past studies of habitat selection have indicated that some fledgling passerines select habitat with greater cover than adults, likely providing increased protection from predators (Jones, Brawn, & Ward, 2017; King, Degraaf, Smith, & Buonaccorsi, 2006). Habitat use in adult black-backed woodpeckers is linked to areas with high food availability (Rota et al., 2015; Tingley, Wilkerson, Bond, Howell, & Siegel, 2014), yet open, snag-dominated stands containing high food concentrations often have less cover than surrounding areas. Fledgling woodpeckers generally do not forage for themselves during the period when they are dependent on food provisioning from adults. Thus, fledgling black-backed woodpeckers may exhibit different habitat relationships than adult black-backed woodpeckers, even while using burned forests.

We studied differences between habitat selection in adult and fledgling black-backed woodpeckers in burned forests. Specifically, we addressed three predictions that stem from the predation–starvation hypothesis. First, we predicted that adult black-backed woodpeckers would select habitat that is associated with the availability of key resources for adults, including nest sites and food availability. We therefore predicted that adults would show strong relationships with snag density and areas burned at relatively high severity. Second, because young fledglings are provisioned by their parents, we predicted that fledglings would select habitat associated with higher cover than adults. In burned forests, higher cover is generally available in areas burned at relatively low severity, with abundant live trees remaining after fire. Third, we predicted that fledgling habitat use would shift to include more snags as fledglings aged and became more independent from parents. Our objective was to examine the role of pyrodiversity across life stages of a burned forest specialist in light of the predation–starvation trade-off. In addition, we sought to provide relevant information to forest managers interested in maintaining habitat for black-backed woodpeckers and other species associated with burned forests.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted our research within forests burned by six wildfires in Plumas and Lassen National Forests of northeastern California: Moonlight (burned in 2007), Wheeler/Antelope Complex (2007), Peterson Complex (2008), Sugarloaf/Hat Creek Complex (2009), Chips (2012) and Bald (2014). Study areas ranged from 2 to 10 years post-fire at the time of data collection. Four of the fires (Moonlight, Wheeler, Sugarloaf and Chips) burned predominately Sierran mixed conifer forest dominated by *Pinus ponderosa*, *P. jeffreyi*, *Abies concolor*, *A. magnifica*, *Pseudotsuga menziesii* and *Calocedrus decurrens*. The Peterson and Bald fires burned mostly eastside pine forest composed of *P. ponderosa*, *P. jeffreyi*, *C. decurrens* and *Juniperus occidentalis*.

2.2 | Woodpecker capture and tracking

We used radio-telemetry to track the movements and habitat use of adult and fledgling black-backed woodpeckers. During the breeding season between 2011 and 2016, we tagged adult woodpeckers in the Moonlight, Wheeler, Peterson and Sugarloaf fires. In 2016 and 2017, we tagged fledgling woodpeckers in the Moonlight, Chips and Bald fires. Adults were captured in mist nets or at the nest with hoop nets. To prevent nest abandonment, adults were only captured with hoop nets if nestlings were at least 5 days old. We captured nestlings 1–3 days before fledging using the hole-saw method and replaced all nestlings back into the cavity immediately after processing (Ibarzabal & Tremblay, 2006). Between 2011 and 2016, we attached a 1.6–2.0-g VHF radio transmitter (Model BD-2, Holohil Systems, Carp, Ontario, Canada) to the dorsal surface of an inner rectrix feather for each bird using two loops of monofilament and a thin layer of ethyl cyanoacrylate. In 2017, fledglings were fitted with a 1.6-g programmable connectivity tag (Model CTx Ag 392, Lotek Wireless Inc., Newmarket, Ontario, Canada) using the leg-loop harness method secured with elastic beading cord (Rappole & Tipton, 1991). All individuals were fit with a unique combination of colour bands and a numbered U.S. Fish and Wildlife Service leg band. Transmitters weighed less than 3% of average body mass for adult woodpeckers (mean mass = 67.5 g) and fledgling woodpeckers (mean mass = 61.7 g) in accordance with recommended practices to minimise transmitter impact on bird behaviour (Fair, Paul, & Jones, 2010).

We tracked adult and fledgling woodpeckers between April and August each year, attempting to locate each bird at least once every 3 to 5 days. Individuals were located using radio receivers and Model RA-7/Model RA-14K antennas (Telonics Inc., Mesa, AZ, USA). Once found, each bird was followed on foot by a team of paired observers for at least 1 hr, or until the bird landed on and ‘used’ a maximum of 20 trees. Black-backed woodpeckers were unwary of observer presence during tracking bouts and did not visibly alter their behaviour, even when observed at a distance of 3–4 m (Rota et al., 2015; Tingley et al., 2014). However, observers attempted to remain at least 10 m away from tagged birds while still maintaining a direct line of sight to record behaviour.

2.3 | Habitat use measurements

For adult woodpeckers, we defined ‘used habitat’ as each tree where the woodpecker landed, remained for at least 5 s and interacted with the tree using one of the following common behaviours: pecking, gleaning, probing, flaking or excavating. We found that adult woodpeckers exhibited these behaviours on nearly every tree on which they landed. We used a 5-s minimum threshold for ‘use’ to omit trees on which woodpeckers stopped only momentarily while travelling between habitat patches. More details on adult tracking methods can be found in Tingley et al. (2014). In contrast, fledgling black-backed woodpeckers tended to be more sedentary than adults, and they did not show the same propensity to forage on every tree on which they landed. Therefore, we modified our definition of habitat ‘use’ by fledglings to include all trees that a fledgling landed on and remained for at least 5 s. This definition of ‘use’ omits the trees that fledglings landed on only briefly while travelling between habitats, but allows for the inclusion of trees used as daytime roost sites.

During each tracking bout, we marked each used tree with a numbered pin flag and recorded geographic coordinates (UTM) using a handheld GPS. We also recorded behavioural observations and the duration a woodpecker remained on each tree. After completing a tracking bout, we returned to flagged trees to record tree characteristics and measure surrounding habitat. We recorded species of each used tree, diameter at breast height (DBH) and whether the tree was alive or dead. For dead trees only, we also estimated the per cent of bark remaining (aggregated into four categories: 0–10, 11–50, 51–90, >90) and counted the number of wood-boring beetle exit holes (four categories: 0–10, 11–20, 21–50 and >51) on the trunk between 0 and 1 m above-ground as an index of past beetle activity. We measured the tree density surrounding used trees by counting the number of snags and live trees with DBH >10 cm within a 10-m radius. We assigned burn severity within a 50-m radius to one of four categories (Unburned, Low, Medium, High) based on the estimated per cent of canopy mortality (0, <25, 26–80, >80% respectively).

In addition to habitat variables collected in the field, we used data from the Rapid Assessment of Vegetation Condition after Wildfire program (https://www.fs.fed.us/postfirevegcondition/index.shtml) to extract the per cent change in canopy cover from pre-fire to immediately after fire at each use location (hereafter ‘point’). We used this measure of burn severity to create an index of pyrodiversity by calculating the standard deviation of burn severity within a 100-m radius of each point (Tingley, Ruiz-Gutiérrez, et al., 2016).

2.4 | Systematic habitat measurements

Our inference in this study centred on the relative probability of resource use for adult vs. fledgling back-backed woodpeckers. Habitat use is considered selective when certain resources are used disproportionate to their availability (Manly, McDonald, Thomas, McDonald, & Erickson, 2002), but biologically arbitrary definitions of 'available resources' can lead to bias when estimating resource selection parameters (Jones, 2001). Here, we used the Design III method, where a unique distribution of used and available habitat samples is collected for each tagged individual (Manly et al., 2002). This design was appropriate because we tracked woodpeckers across multiple fires and regions within fires, so available habitat differed between individuals.

We used a minimum convex polygon (MCP) bounding the tracking locations of each bird to define the habitat that was available for use, and we measured habitat variables at systematically spaced points on a 100-m by 100-m grid covering the MCP. We did not measure available habitat for birds with fewer than 10 tracking points. For adult woodpeckers, we collected stand-level measurements (i.e. tree density, burn severity) at alternating points in the grid, but collected tree-level measurements (i.e. size, condition, species, snag decay, beetle exit holes) at every point in the grid. To build a sample of available trees, we collected data on the snag and live tree closest to each grid point, but within 50 m. For fledgling woodpeckers with MCP >200 ha, we randomly discarded gridded survey points prior to sampling until the ratio of used points to available points was 1:3.

2.5 | Statistical analyses

Statistical inference was made in three steps. First, we tested the statistical hypothesis that patterns of habitat use are different between woodpecker age classes using *t* tests for normally distributed samples, and Mann–Whitney *U* tests or chi-squared tests for non-normal data. This preliminary analysis provided a baseline description of habitat use before accounting for availability. Second, we analysed our use-availability data using three resource selection functions, each built at a different scale of selection: stand selection, tree selection (live trees and snags) and snag selection. These models only employed data from birds where we measured available vegetation in a systematic grid. Because we were interested in characterising the habitat relationships of fledgling woodpeckers during the stage when they are dependent on parental provisioning, we included fledgling use points collected only within the first 35 days after fledging. Field observations indicated that fledglings became independent from parental provisioning after about 35 days.

We built resource selection functions in a framework that accounts for the possibility that some points in our available sample may have been used by woodpeckers outside of observation periods, a problem termed 'zero-contamination' (Lele, 2009; Lele & Keim, 2006). Models employed an unbalanced matching design, where all individuals are included within a single model for each scale of selection, but every used point is compared against the unique set of available points surveyed within the individual's MCP (Lele, Keim, & Solymos, 2017). In each of the three models, we included an interaction of age class on every covariate—the coefficient of this interaction term provides a statistical test of whether fledgling selection differs from adults for each variable.

We tested alternative link functions for each model by building exponential, logistic, probit and complementary log–log models, and selected the functional form which resulted in the lowest Akaike information criterion (AIC) (Lele & Keim, 2006). The complementary log–log resource selection probability function provided the best fit for all three models, and we used this functional form in subsequent analysis.

For our stand-level model, we included four covariates of resource use: live tree density, snag density, burn severity (in situ measurement) and σ of burn severity (a measure of pyrodiversity). As we expected the effect of incremental increases in tree density to attenuate at higher densities, we log-transformed both tree count variables.

For our tree-level model, we modelled the relative probability of use for each tree as a function of tree diameter (DBH), whether the tree was alive or dead, and tree species. We included tree species as a series of four dummy variables based on the following groupings: *Pinus* (pines), *Abies*/*Pseudotsuga* (white fir, red fir and Douglas-fir), *Calocedrus* (incense cedar) and all other non-dominant species.

For our snag-level model, we modelled the relative probability that a woodpecker would use a snag as a function of DBH, the amount of bark remaining (which we considered an index of snag decay) and the number of wood-boring beetle exit holes on the lowest metre of trunk. We included the categorical estimate of per cent bark remaining as a continuous variable with values 1–4. For the number of beetle exit holes, we assigned each category (0–10, 11–20, 21–50 and >51) integers between 1 and 4; including these data as a continuous variable reflected our observation that the underlying relationship between beetle holes and woodpecker use was loglinear (Supporting Information Figure S1). In all three models, we centred and standardised continuous covariates to aid comparisons between coefficient estimates.

We evaluated our resource selection models using a fivefold cross validation technique designed for presence/available data (Boyce, Vernier, Nielsen, & Schmiegelow, 2002). To create training/test data, we iteratively withheld 20% of the used and available points for each bird, without replacement. We assessed model performance by examining Spearman rank correlations between predicted values, divided into 10 equally sized bins, and area-adjusted frequencies. Strong positive correlations and low *p*-values ($p < 0.05$) indicate good predictive performance of a model (Boyce et al., 2002).

Finally, we examined the effect of fledgling age on the probability of snag use to test the prediction that fledgling woodpeckers gradually shift resource use as they become independent from adult provisioning. We built a binomial mixed-effects model to examine the effect of fledgling age, measured as days since fledging, on the logit-transformed probability of snag use. We included a random slope for each individual to account for repeated

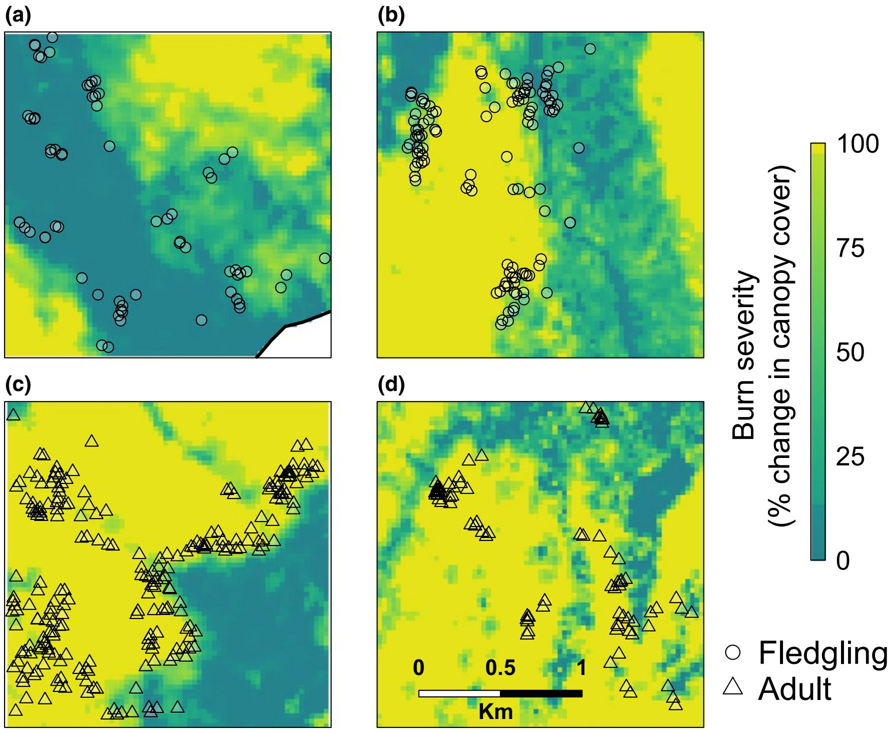

FIGURE 1 Example observed locations of black-backed woodpeckers in post-fire forests for fledglings in (a) the Moonlight and (b) Bald fires, and for adults in (c) the Wheeler and (d) Sugarloaf fires, demonstrating apparent juvenile preference for areas of lower burn severity (blue–green) and adult preference for areas of greater burn severity (green–yellow)

observations of fledglings. All analyses were performed in R version 3.5.1 using the packages lme4 (Bates, Mächler, Bolker, & Walker, 2014) and ResourceSelection (Lele, 2009; Lele et al., 2017; R Core Team, 2018).

3 | RESULTS

We recorded habitat use data for 49 adult and 22 fledgling black-backed woodpeckers between 2011 and 2017, and we sampled available habitat for 41 adults and 15 fledglings. Overall, we characterised used habitat at 5,352 adult points and 915 fledgling points, and we measured 4,242 and 1,896 available points for adults and fledglings respectively.

3.1 | Habitat use

Patterns of habitat use differed between adult and fledgling black-backed woodpeckers. Adults tended to use areas burned at medium or high severity, but fledglings showed proportionally greater use of habitat burned at medium and low severity (Figures 1 and 2). Even within large patches of forest burned at relatively high severity, fledglings tended to associate with small 'island' patches of lower burn severity or boundaries between high and low-severity burn stands (Figure 1). Fledglings used areas with significantly greater variation in burn severity within a 100-m radius than adults ($t = -2.03$, $df = 1{,}119.3$, $p < 0.01$; Figure 2). The per cent change in canopy cover pre-fire to post-fire was significantly lower for fledgling (38.33 ± 1.30%) than adult woodpeckers (adult mean = 64.05 ± 0.53%; $U = 1{,}411{,}000$, $p < 0.001$). This pattern was strongest during the first 10 days after fledglings left the nest. Woodpeckers tended to nest in high-severity stands, but newly fledged young generally left the nest stand and associated with surrounding areas of low and medium burn severity, where they sought daytime roost sites in or near live trees and received provisioning from adults. During 84 hr of fledgling behavioural observations, individuals between 0 and 10 days post-fledge spent 26.6% of their time in habitat classified as low severity from field-based assessment, compared to 15.1% for fledglings over 20 days post-fledge, and 7.1% for adults (based on 213 observation hours).

Vegetation measurements at used points showed further differences in habitat use between adults and newly fledged birds. On average, fledglings used areas with lower snag density ($t = 14.92$, $df = 1{,}324.3$, $p < 0.001$) and higher live tree density ($t = -11.42$, $df = 1{,}144.6$, $p < 0.001$) than adults (Figure 2). Both adults and fledglings used snags more frequently than live trees, but fledglings used a greater proportion of live trees than adults ($\chi^2 = 358.87$, $df = 1$, $p < 0.001$; Figure 2). The mean DBH of trees used by fledgling woodpeckers was 44.4 cm, compared to a mean DBH of 39.2 cm for adults ($t = -6.35$, $df = 1{,}097.5$, $p < 0.001$). Both adult and fledgling woodpeckers primarily used fir and pine trees, which in our study areas included white fir, red fir, Douglas-fir, ponderosa pine and Jeffrey pine.

Fledglings showed changing habitat preferences with time since fledging. The probability of a fledgling using a snag increased with the number of days since the fledgling left the nest (odds ratio: 1.03, 95% CI: (1.01, 1.06), $p = 0.014$, Supporting Information Figure S2). Thus, the odds of a 3-week-old fledgling using a snag were two times greater than a 1-day-old fledgling.

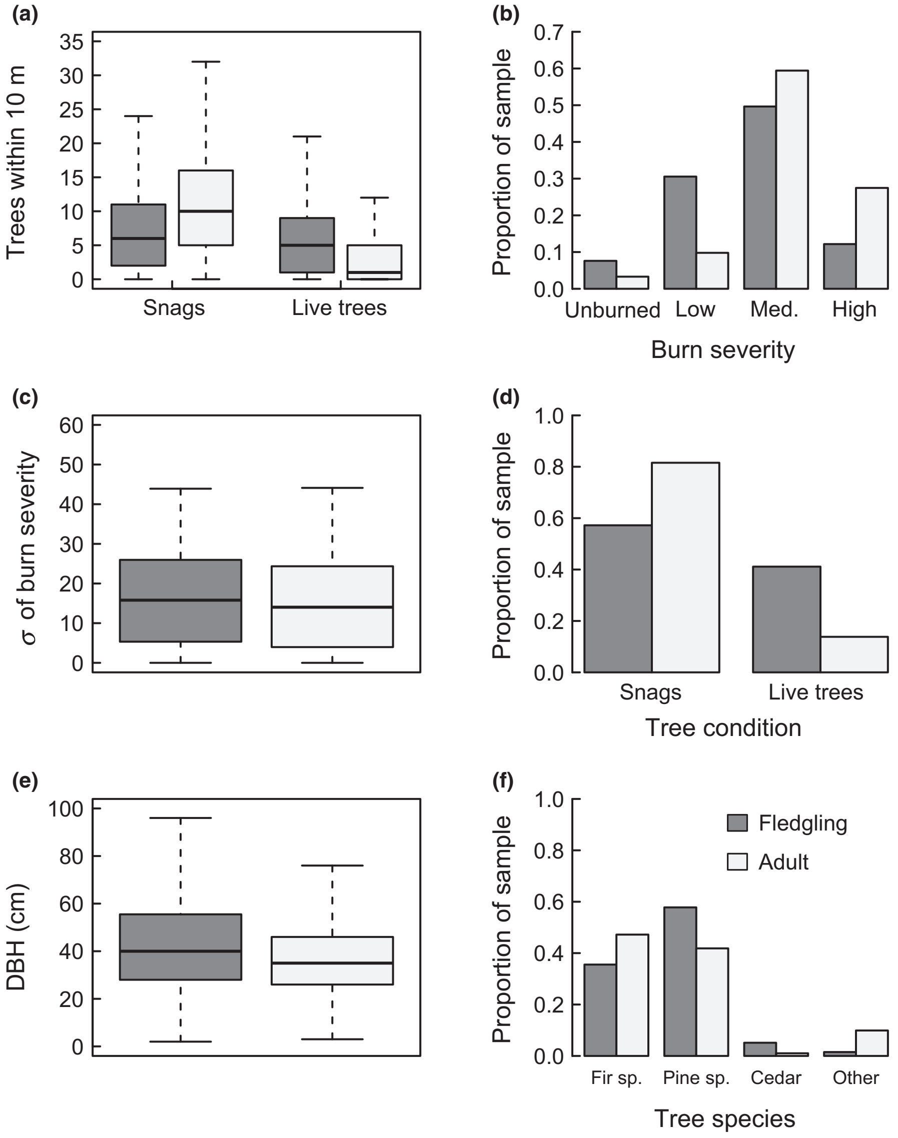

FIGURE 2 Summary of habitat used by adult and fledgling black-backed woodpeckers in post-fire forests, pooled across all individuals per age group. Plots show (a–c) stand-level measurements and (d–f) tree-level measurements. All comparisons showed significant differences between fledgling and adult habitat use ($p < 0.01$)

3.2 | Resource selection

We used resource selection functions to estimate the effect of stand-, tree- and snag-level characteristics on the relative probability of woodpecker resource use while accounting for availability. The sample size of used/available points was 6,132/3,969, 5,818/6,416 and 4,733/5,724 for the stand-, tree- and snag-level models respectively.

Among stand-level characteristics, snag density had an important effect on the relative probability of use for both fledglings and adults (Table 1). For example, a point with 10 snags within a 10-m radius was five times more likely to be used by adults than a point with one snag (Figure 3). Live tree density also had a positive effect on both adult and fledgling stand use, but this effect was significantly stronger in fledglings (Table 1). Plots of fitted probabilities showed that fledglings had the highest relative probability of use in stands burned at medium severity and lowest relative probability of use in stands burned at high severity (Figure 3), although after accounting for tree density, the fledgling relationship to high severity did not differ from adults (Table 1). By comparison, adults showed high relative probability of use in stands burned at both medium and high severity (Figure 3) but selected low and medium severity significantly less than fledglings (Table 1). In addition, both age classes demonstrated a significant positive relationship with burn severity heterogeneity; this relationship was stronger in fledglings (Table 1).

The resource selection model of tree covariates demonstrated further differences between adults and fledglings. Adult black-backed woodpeckers showed significantly stronger selection for snags than fledglings, and both selected trees with greater DBH. Across age classes, relative probability of use was substantially greater for fir and pine trees compared to incense cedar and non-dominant species, although fledglings showed significantly greater selection of incense cedar than adults (Table 1; Figure 4).

Fledglings and adults also showed differential selection in the types of snags used (Table 1). Both age classes selected snags with larger DBH, but this relationship was significantly stronger in adults. Relative probability of use also decreased with increased snag decay.

TABLE 1 Coefficient estimates, 95% confidence intervals and *p*-values for factors affecting resource selection in fledgling and adult black-backed woodpeckers. Results are shown for three models representing different types of resource use: stand use, tree use and snag use. Main effects provide the relative selection strength for adults and interaction effects show fledgling effect relative to adults

	Main effects (adults)		Interaction effects (fledgling effect)	
Covariate	**Estimate**	***p*-value**	**Estimate**	***p*-value**
Stand model: characteristics of habitat surrounding used and available trees				
Intercept	−2.23 (±0.35)	<0.001	−1.54 (±1.92)	0.422
Live tree density	0.19 (±0.02)	<0.001	0.51 (±0.02)	<0.001
Snag density	1.26 (±0.04)	<0.001	0.06 (±0.04)	0.434
Burn severity				
High	−0.58 (±0.22)	0.008	0.34 (±0.41)	0.406
Medium	−0.20 (±0.22)	0.375	1.26 (±0.40)	0.002
Low	−0.04 (±0.23)	0.874	1.36 (±0.44)	0.002
Unburned	0.30 (±0.26)	0.256	0.21 (±0.51)	0.678
σ of burn severity	0.16 (±0.02)	<0.001	0.25 (±0.05)	<0.001
Tree model: characteristics of used and available trees (live and dead)				
Intercept	−5.05 (±0.19)	<0.001	2.54 (±0.62)	<0.001
DBH	1.32 (±0.06)	<0.001	−0.12 (±0.21)	0.555
Snag (vs. live tree)	2.78 (±0.09)	<0.001	−2.09 (±0.19)	<0.001
Fir sp.	2.42 (±0.19)	<0.001	−0.45 (±0.57)	0.430
Pine sp.	2.10 (±0.18)	<0.001	−0.23 (±0.56)	0.688
Incense cedar	−0.40 (±0.23)	0.075	1.26 (±0.59)	0.032
Snag-only model: characteristics of used and available snags				
Intercept	0.50 (±0.12)	<0.001	−1.53 (±0.33)	<0.001
DBH	2.57 (±0.13)	<0.001	−1.81 (±0.36)	<0.001
Bark decay	−0.17 (±0.04)	<0.001	−0.06 (±0.10)	0.536
Beetles	0.25 (±0.05)	<0.001	−0.34 (±0.11)	0.002

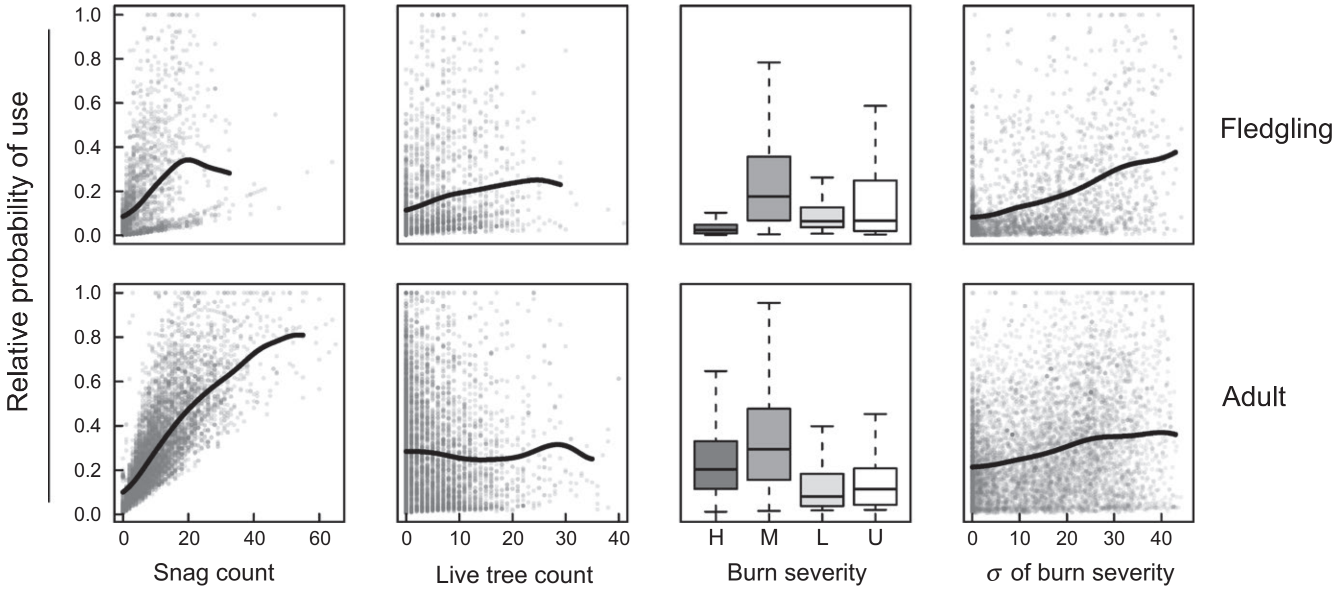

FIGURE 3 Fitted values from the stand-level resource selection function, ordered across the range of a single covariate of interest. Scatterplot dots show the relative probability of use for each point in the dataset, standardised between 0 and 1 by dividing by the maximum fitted value for each individual. Black lines show a nonparametric regression function through the mean. Note that this plot does not depict the coefficient relationship while holding all other variables constant. Rather, it plots the same set of fitted values based on the covariates of the model and orders them according to the change in a single covariate (Avgar, Lele, Keim, & Boyce, 2017)

Adult woodpeckers alone, however, showed a significant, positive relationship between snag use and the number of wood-boring beetle exit holes present (Table 1).

3.3 | Model evaluation

Using fivefold cross validation, area-adjusted frequencies were positively correlated with resource selection function predictions for all three models. Spearman rank correlations between area-adjusted frequency and binned model predictions ranged from 0.952 to nearly 1, providing no evidence for lack of model fit or poor model performance (mean $r_s = 0.980$, $p < 0.001$).

4 | DISCUSSION

Information on wildlife-habitat relationships in burned forests is key to understanding the potential effects of changing fire regimes on wildlife in fire-prone systems and the implications of post-fire forest management practices. We tested three predictions regarding (a) habitat selection in adult black-backed woodpeckers, (b) habitat selection in fledglings and (c) change in habitat use as fledglings grew older. Our results demonstrated clear differences between adult and fledgling habitat and highlight the role of pyrodiversity in fire management. Adult black-backed woodpeckers selected stands burned at high or medium severity and with high snag density, and they preferentially used snags relative to live trees. In contrast, fledgling black-backed woodpeckers selected stands burned at medium to low severity and did not show strong selection for snags over live trees. We also found that the probability of fledglings using snags increased as fledglings grew older.

Fledgling black-backed woodpeckers positioned their natal home ranges in areas that, in general, incorporated more live trees when compared to adults (Supporting Information Figure S3). This trend meant that the baseline distribution of available habitat differed between adults and fledglings due to selection at the home range scale (second-order selection; Johnson, 1980). To show evidence of selection in our analysis, a woodpecker additionally needed to display disproportionate use of a habitat relative to its availability to that individual. Thus, we assessed selection of resources from within the home range and not selection of the home range itself, leading to conservative estimates of the differences between adults and fledglings. It is important to note that even within home ranges dominated by low burn severity, we still found that fledglings selected areas associated with tree cover and avoided high burn severity patches.

Black-backed woodpeckers are known for their strong association with high and medium severity burned forests in western North America (Hutto, 2008), but our results indicate that landscape-level pyrodiversity plays a key role in meeting the habitat requirements of black-backed woodpeckers across life-history stages. Maps of woodpecker space use revealed a tendency for woodpeckers to use edge areas between high and low-severity patches of burned forest (Figure 1), and both age classes demonstrated a positive relationship between habitat use and burn severity variation. This pattern may arise from the need for fledglings and adults to maintain proximity to each other (e.g. for provisioning) while still selecting for different habitat characteristics.

Resource selection functions for snag use indicated that adult black-backed woodpeckers selected snags that were larger in diameter, exhibited relatively less bark decay and showed greater sign of past beetle activity. These results are consistent with findings based on adult black-backed woodpeckers in eastern Canada, which showed preference for larger, less deteriorated snags (Nappi,

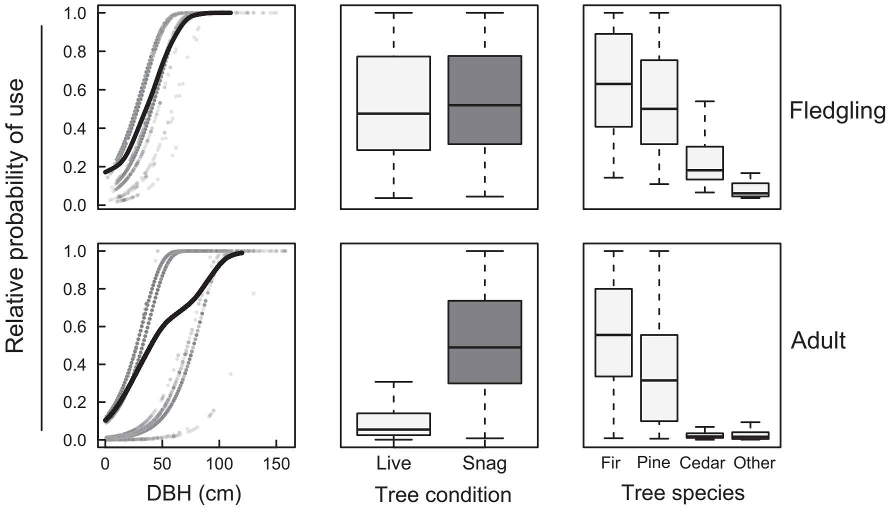

FIGURE 4 Fitted values from the tree-level resource selection function, ordered across the range of a single covariate of interest. Scatterplot dots show the relative probability of use for each point in the dataset, standardised between 0 and 1 by dividing by the maximum fitted value for each individual. Black lines show a nonparametric regression function through the mean. Note that this plot does not depict the coefficient relationship while holding all other variables constant. Rather, it plots the same set of fitted values based on the covariates of the model and orders them according to the change in a single covariate (Avgar et al., 2017)

Drapeau, Giroux, & Savard, 2003). In our study, fledgling woodpeckers also showed positive relationships with snags that were larger and less deteriorated, but evidence of past beetle emergence did not have a significant influence on snag selection. The ratio of snag use to live tree use gradually increased in older fledglings, even while they were still dependent on parental provisioning. Our field observations indicated that this might be due to fledglings spending an increasing amount of time accompanying parents on foraging trips as they grew older.

The predation–starvation hypothesis provides theoretical support for the importance of pyrodiversity in meeting habitat needs across life stages of black-backed woodpeckers in burned forests. Foraging woodpeckers encounter the highest densities of wood-boring beetle larvae, their primary food source, in areas characterised by high snag density resulting from high-severity fire. However, these 'snag forests' are open, exposed habitats (DellaSala et al., 2014); woodpeckers using these areas may incur higher risks of predation from aerial predators such as hawks. Young fledgling woodpeckers, which are provisioned by parents, may adjust to this trade-off by selecting habitat with a greater live tree component to provide cover from overhead predators. In addition, live trees may provide thermal cover in an otherwise hot, exposed environment. Our anecdotal observations indicated that much of the time, young fledglings adopted daytime roost sites in dense stands of live trees, which served as 'nurseries' for the birds while provisioning parents conducted trips back and forth between the fledgling and high-severity foraging stands. The importance of fledgling access to high-cover vegetation has been demonstrated in many passerine bird species (Jones et al., 2017; King et al., 2006); in addition, these high-cover hideouts have been implicated in higher fledgling survival rates relative to low-cover areas (Anders, Dearborn, Faaborg, & Thompson, 1997; King et al., 2006). We suggest that additional research focus on the fitness consequences of these habitat use patterns, including the relationship between selection for cover and fledgling survival.

4.1 | Implications for management under novel fire regimes

Recently, the western U.S. has experienced unprecedented increases in the size and severity of forest fires (Miller & Safford, 2012; Stevens et al., 2017). Transitioning fire regimes are yielding increases in the frequency and extent of 'megafires', that is, large, severe wildfires >10,000 ha in extent (Stephens et al., 2014). These trends have generated concern over the conservation of forest species (Ganey, Wan, Cushman, & Vojta, 2017; Jones et al., 2016), but the effect of more severe, more homogeneous fires on fire-associated species also needs to be considered. Past studies have provided evidence that some severe forest fire has neutral or beneficial effects on wildlife (Hutto et al., 2016), and black-backed woodpeckers are frequently considered a specialist on severe fires. Despite this, our results indicate that black-backed woodpecker habitat preferences vary by life stage. Consequently, heterogeneity in post-fire systems may be critical to meet habitat requirements across the full life history of this post-fire specialist. As megafires burn more homogeneously, providing less access to low and moderate severity areas juxtaposed with high-severity areas (Stephens et al., 2014), our results suggest that shifting fire regimes may pose an emerging threat to certain post-fire specialists that thrive on pyrodiverse landscapes.

More information on the effects of megafires on wildlife populations is urgently needed, particularly regarding the potential effects of high-severity fire when it occurs homogeneously over large, continuous areas. While the largest wildfire we studied comprised 30,897 ha, much of our sampling occurred in areas characterised by moderate to high variation in burn severity instead of homogeneous high-severity landscapes. We also caution that our study does not test for differential fitness among habitats (Jones, 2001), particularly whether fitness is lower in areas with more homogeneous burn severity. We recommend that future research focus on measuring the effects of pyrodiversity on fire-associated species, including links between habitat use patterns and individual fitness.

Forest fires, and the post-fire habitats that they create, can be managed in ways that promote biodiversity. Effective management strategies rely on knowledge of the characteristics of fire that enhance species' use of post-fire landscapes and the ways that variation across a fire regime can affect population dynamics (Kelly & Brotons, 2017; Tingley et al., 2018). Our results point to the crucial need for information on the resources that structure wildlife-habitat relationships beyond breeding-season adults—sound management strategies will incorporate information from full life histories. We provide novel evidence suggesting that black-backed woodpeckers may depend on mixed-severity fires to meet the needs of fledglings. Indeed, woodpecker densities within recent homogeneous megafires, such as the 102,925-ha Rim fire, fall well below predicted values based on current habitat suitability models (Tingley, Wilkerson, Howell, & Siegel, 2016). Our results suggest that these low densities may stem from low habitat heterogeneity in these fires, possibly denying adequate cover for predator avoidance by fledgling woodpeckers. The proximity of habitat burned at different severities may benefit wildlife that need heterogeneous habitat to meet different resource requirements, and we recommend that managers interested in promoting post-fire biodiversity consider the proximity of high-severity stands to unburned areas and stands burned at low to medium severity.

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AUTHORS' CONTRIBUTIONS

R.B.S., R.L.W., M.W.T., and A.N.S. conceived the ideas and designed methodology; R.L.W., R.B.S., and A.N.S. oversaw data collection with support from M.J.; A.N.S. and M.W.T. analysed the data and A.N.S. led writing the first draft of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.h5h7v20 (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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