

Juvenile survival of a burned forest specialist in response to variation in fire characteristics

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Abstract

1. Pyrodiversity, defined as variation in fire history and characteristics, has been shown to catalyse post-fire biodiversity in a variety of systems. However, the demographic and behavioural mechanisms driving the responses of individual species to pyrodiversity remain largely unexplored.
2. We used a model post-fire specialist, the black-backed woodpecker (*Picoides arcticus*), to examine the relationship between fire characteristics and juvenile survival while controlling for confounding factors.
3. We radio-tracked fledgling black-backed woodpeckers in burned forests of California and Washington, USA, and derived information on habitat characteristics using ground surveys and satellite data. We used hierarchical Bayesian mixed-effects models to determine the factors that influence both fledgling and annual juvenile survival, and we tested for effects of fledgling age on movement rates.
4. Burn severity strongly affected fledgling survival, with lower survival in patches created by high-severity fire compared to patches burned at medium to low severity or left unburned. Time since leaving the nest was also a strong predictor of fledgling survival, annual juvenile survival and fledgling movement rates.
5. Our results support the role of habitat complementation in generating species-specific benefits from variation in spatial fire characteristics—one axis of pyrodiversity—and highlight the importance of this variation under shifting fire regimes. High-severity fire provides foraging and nesting sites that support the needs of adult black-backed woodpeckers, but fledgling survival is greater in areas burned at lower severity. By linking breeding and foraging habitat with neighbouring areas of reduced predation risk, pyrodiversity may enhance the survival and persistence of animals that thrive in post-fire habitat.

KEYWORDS

black-backed woodpecker, fire severity, fledgling, habitat complementation, movement, *Picoides arcticus*, pyrodiversity, wildfire

1 | INTRODUCTION

A prevailing theory in ecology suggests that spatial variation in environmental features leads to greater biodiversity (Stein et al., 2014). Environmental disturbance from wildfire is a key driver of spatial variation in landscapes worldwide (Bond & Keeley, 2005), and variation in fire regime characteristics—termed pyrodiversity—can have profound impacts on the structure and function of ecological communities (He et al., 2019). Pyrodiversity can occur along multiple axes of variation including fire severity, seasonality, patch size and time since fire (Bowman et al., 2016; Martin & Sapsis, 1992), and the belief that pyrodiversity can promote biodiversity has become an influential principle guiding the management of fire-prone landscapes (Kelly & Brotons, 2017). Past studies have demonstrated strong positive relationships between pyrodiversity and biodiversity in a variety of ecosystems and taxa (Beale et al., 2018; Ponisio et al., 2016; Tingley et al., 2016), although the magnitude of these relationships depends heavily on regional context (Kelly et al., 2017; Parr & Andersen, 2006).

Pyrodiversity–biodiversity relationships are generally predicated on the idea that heterogeneity in the composition and configuration of burned habitat enhances the coexistence of multiple species, each with a specific niche in the fire regime (Beale et al., 2018; Steel et al., 2019; Tingley et al., 2016). However, the capacity for individual species to benefit from pyrodiversity and the potential mechanisms driving these benefits remain largely unexplored. One hypothesis behind the benefits of pyrodiversity for individual species is that spatial variation in post-fire characteristics may enhance a species' persistence through habitat complementation, where multiple fire characteristics are needed for

an individual to meet resource requirements (Kelly et al., 2017). Accordingly, the spatial configuration of fire characteristics may influence immediate survival through species interactions like competition and predation.

Variation in burn severity within a fire—an important component of pyrodiversity—provides an opportunity to evaluate species-specific effects of fire characteristics on animals that inhabit post-fire landscapes. The black-backed woodpecker (*Picoides arcticus*) is a post-fire specialist closely tied to coniferous forest burned by stand-replacing fire in the western U.S. (Hutto, 2008; Tremblay et al., 2016). Black-backed woodpecker populations thrive where dense stands of snags (standing dead wood) that burned at high severity provide food and nesting resources (Rota et al., 2015; Stillman, Siegel, Wilkerson, Johnson, Howell, et al., 2019). Woodboring beetles (e.g. Cerambycidae, Buprestidae) rapidly colonize burned patches to reproduce in fire-killed snags, and beetle larvae supply a key food source (Murphy & Lehnhausen, 1998). In the western U.S., local black-backed woodpecker populations follow a 'boom and decline' cycle in the first 10 years following fire (Tingley et al., 2018), likely reflecting an initial pulse of post-fire colonization followed by gradual population declines perhaps due to decreasing prey abundance (Ray et al., 2019) and decreased recruitment (Siegel et al., 2016). Although breeding black-backed woodpeckers are closely associated with high-severity burn, recent evidence has demonstrated the importance of pyrodiversity for this species (Stillman et al., 2019). In large fires of northern California, fledging black-backed woodpeckers demonstrate strong selection for areas burned at low and medium severity with higher proportions of live trees (Figure 1). The severely burned 'snag forests' frequented by adults are open, exposed environments that provide high prey densities but little protection from aerial

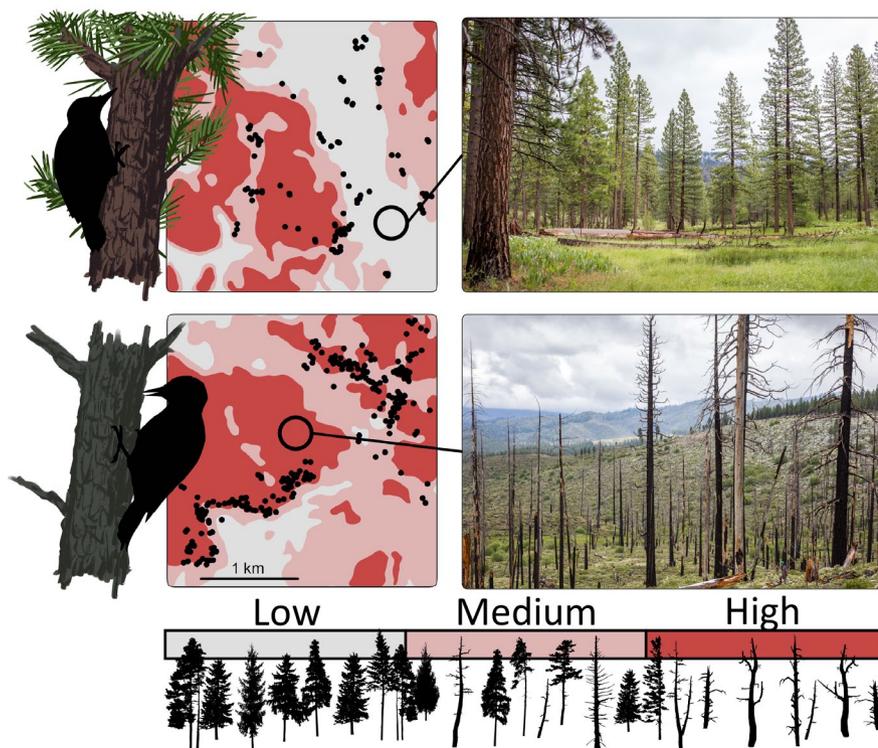


FIGURE 1 Conceptual diagram showing patterns of age-dependent habitat selection in fledgling (top) and adult (bottom) black-backed woodpeckers using burned forests. Fledglings select habitat that burned at low to medium severity, where live trees provide cover from predators, while adult woodpeckers select habitat that burned at high severity, where dead trees provide abundant prey. Data are from Stillman, Siegel, Wilkerson, Johnson, and Tingley (2019)

predators. Young fledglings may adjust to this predation–starvation trade-off by moving into areas with greater cover while they are still being provisioned by parents that largely forage in nearby areas burned at higher severity (Houston et al., 1993; Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). This behaviour suggests that fledgling survival may be lower in severely burned patches, and differences between adult and juvenile habitat may be an overlooked mechanism driving species-specific benefits of pyrodiversity.

The post-fledging period in birds is a critical life stage characterized by high juvenile mortality. Across avian taxa, outcomes of this vulnerable period impose marked effects on recruitment, population persistence and geographical distributions (Cox et al., 2014; Jenkins et al., 2016). Past studies on a variety of species have demonstrated a tendency for fledgling birds to seek areas with high cover after leaving the nest, likely as a strategy to avoid detection by predators (Gow & Wiebe, 2014; King et al., 2006). Predation is particularly high immediately after fledging, a pattern which is generally attributed to limited mobility and weak musculature (Kershner et al., 2004; Naef-Daenzer et al., 2001). In post-fire landscapes, greater variation in burn severity leads to the juxtaposition of high-cover habitats (i.e. live trees in low-severity burn) and high-severity, low-cover patches (Figure 1). For black-backed woodpeckers that use both these habitats during different life stages, determining how habitat selection decisions govern survival during the vulnerable fledgling stage is important to understanding the species' life history, ecology and conservation.

We used radio-telemetry to track the survival and movements of juvenile black-backed woodpeckers in burned forests. First, we investigated fledgling survival relationships during the period when fledglings are dependent on provisioning from parents (up to 35 days post-fledging). The contrasting habitat use patterns of adults and fledglings lends support to the hypothesis that spatial variation in burn severity benefits black-backed woodpeckers through habitat complementation, with adults and fledglings using adjacent habitats burned at different severities (Figure 1). Thus, we predicted that fledgling survival would be lower in high-severity patches but also higher in areas with greater variation in burn severity. We additionally predicted that fledgling survival would be higher in more recent burns (<5 years post-fire) due to increased food availability (Ray et al., 2019). Second, we examined the relationship between fledgling age and movement rates, both of which are predicted to decrease predation risk and increase survival probability (Kershner et al., 2004). Last, we estimated annual survival for juvenile black-backed woodpeckers and tested whether this demographic parameter is a potential mechanism behind observed population declines with time since fire (Tingley et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Study sites

We collected survival and movement data from black-backed woodpeckers in seven distinct burned areas in two U.S. states, Washington

and California (Figure 2). In northern California (Plumas, Lassen and Shasta counties), we tracked woodpeckers in the Moonlight (burned in 2007), Chips (2012) and Bald (2014) wildfires (Table 1). The Moonlight and Chips fires burned predominantly Sierran mixed conifer forest with a history of mixed-severity wildfire, and the Bald fire burned an area dominated by eastside pine forest with a historical regime of frequent, low- to mixed-severity wildfire (Agee, 1998). We also collected data from four fires in Yakima county, Washington: Kaboom (prescribed burn: 2009), Angel 1 (prescribed burn: 2014), Meeks (wildfire: 2015) and Angel 2 (prescribed burn: 2016; Table 1). These fires burned primarily Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forest types characterized by a

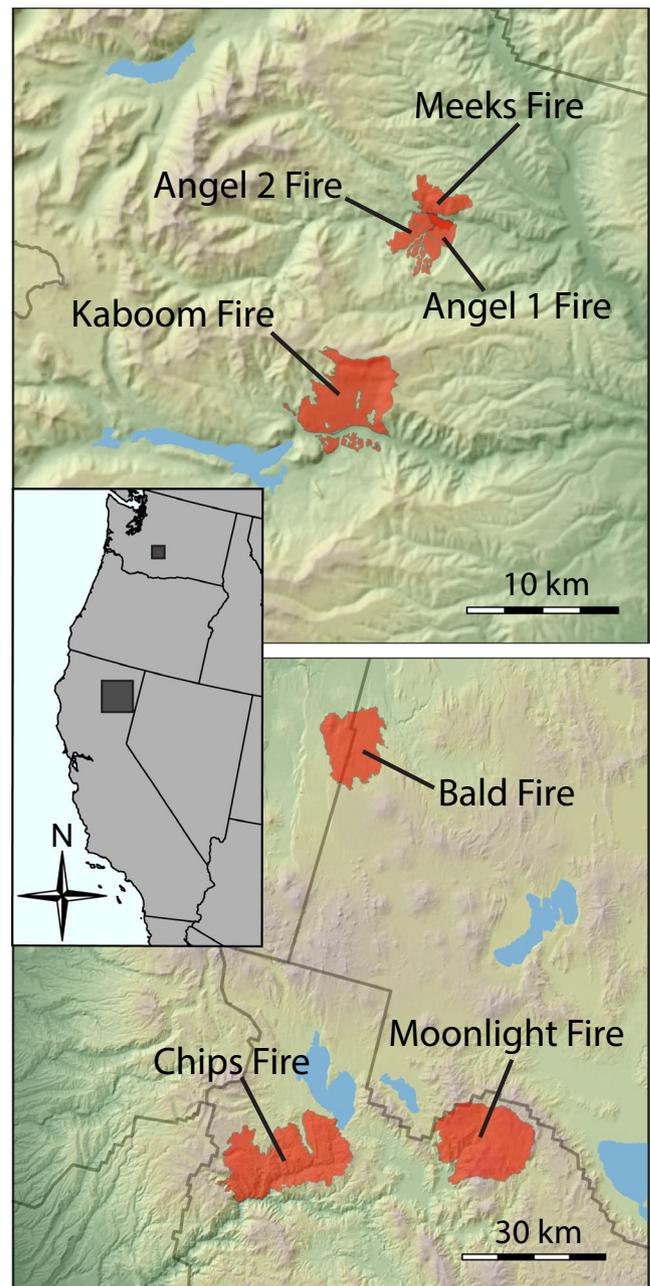


FIGURE 2 Burned areas (red polygons) where we tagged fledgling black-backed woodpeckers in Washington (top) and California (bottom). Grey lines represent county boundaries

| Region | Fire name | Size (ha) | Percent high severity ^a | Years since fire during study | Birds tagged (alive, dead) ^b |
|------------|-----------|-----------|------------------------------------|-------------------------------|---|
| Washington | Kaboom | 2,611 | 3% | 7, 8 | 14 (6, 8) |
| Washington | Angel 1 | 571 | 4% | 2 | 1 (0, 1) |
| Washington | Meeks | 552 | 6% | 2, 3 | 13 (4, 9) |
| Washington | Angel 2 | 453 | 11% | 1 | 9 (5, 4) |
| California | Moonlight | 26,509 | 44% | 9, 10 | 14 (7, 7) |
| California | Chips | 31,114 | 21% | 5, 6 | 19 (6, 13) |
| California | Bald | 16,258 | 16% | 3, 4 | 14 (9, 5) |

^aPercent of total fire area that burned at high severity (data from MTBS).

^bNumbers reflect the known fates of tagged birds during the first 35 days after fledging.

mixed-severity fire regime (Agee, 1998; Reilly et al., 2017). Although the Washington fires were considerably smaller than the California fires, they each included patches of stand-replacing fire >10 ha (Table 1), indicating approximately equal access to a diversity of post-fire habitats for individual woodpeckers. Post-fire logging occurred in some areas of the California fires, ranging from selective thinning and roadside salvage to clear-cut logging on private lands.

2.2 | Woodpecker capture and tracking

We used radio-telemetry to monitor survival and track the movements of black-backed woodpecker fledglings. During the spring and summer of 2016–2018, we captured nestlings just prior to expected fledging (mean = 1.6 days before fledging) using the hole-saw method to access nest contents (Ibarzabal & Tremblay, 2006). We conducted standard measurements on each nestling and fit birds with 1.6-g connectivity tags (Model CTx Ag 392, Lotek Wireless Inc.) using an adjustable leg-loop harness with elastic beading cord (Rappole & Tipton, 1991). A programmable on/off calendar schedule on these transmitters allowed us to extend battery life over a year post-deployment (signal transmitted May–August, September–November and April–June). In 2016, we additionally fit a subset of individuals with non-programmable 1.6-g transmitters (Model BD-2, Holohil Systems) attached to the dorsal surface of an inner rectrix feather with monofilament and a thin layer of ethyl cyanoacrylate. We marked all nestlings with a unique combination of colour bands and a numbered U.S. Fish and Wildlife Service leg band before returning them to their nest cavity. We ensured that transmitters weighed <3% of average body mass to minimize transmitter impact on behaviour and survival (Fair et al., 2010). Prior to deployment, we coated transmitters in a thin layer of quick-dry epoxy as added protection against transmitter failure during predation events.

After a nest successfully fledged (mean fledge date = June 16th), we tracked tagged fledglings on foot approximately every 3–5 days until early August. Once located, observers recorded whether the bird was alive or dead and attempted to follow individuals for 30–60 min. We recorded location coordinates at each tree that a fledgling used during a tracking bout and assigned the burn severity within 50 m to one of four potential burn severity categories based

TABLE 1 Fire characteristics and sample size for study sites where we tracked fledgling black-backed woodpeckers

on tree canopy mortality (unburned: 0%, low: >25%, medium: 26%–80%, high: >80%). Although we only tagged birds from nests within fire boundaries, fledglings moved freely across burn perimeters and sometimes used the surrounding unburned forest. We considered each tracking bout as a single survival observation (alive or dead) and used repeated locations within a bout to assess habitat use.

We recorded an individual as dead if remains were found with a transmitter or if the transmitter was found with evidence of predation (e.g. blood on harness, beak indentations on coating), and we completed necropsies on two birds found with full-body remains (Washington Animal Disease Diagnostic Laboratory, College of Veterinary Medicine, Washington State University). Seven individuals went missing within 6 days of fledging, and we were unable to locate these birds despite tracking their siblings, searching over an extensive area and observing their parents as they provisioned young. We assumed that these seven individuals died and their transmitters were either destroyed or carried outside of the study area, and we included these assumed mortality events in subsequent analyses.

After August 1st each year, we transitioned to a more intermittent tracking schedule with the goal of locating each bird at least 3–5 times between August and November. We found that many birds dispersed from natal breeding grounds during this time period, and we employed two strategies to locate dispersing individuals. First, we drove road networks near natal territories with handheld and vehicle-mounted antennas. Second, we conducted aerial telemetry flights with fixed-wing aircraft. These flights included a series of concentric circles around previous locations and systematic search transects with 5-km spacing. We concentrated flight effort within 35 km of natal sites, but specific searches sometimes extended >60 km away from a bird's last-known location. If a transmitter signal was located from the air, we recorded location coordinates and visited the area on foot to determine if the bird was alive or dead. Programmable transmitters switched off during the winter and turned back on the following spring, allowing the use of on-the-ground surveys and aerial telemetry for tagged birds over 1 year after fledging. Of 34 birds that survived to August 1st, we located 21 in the fall and 14 the following spring. Birds that were lost >6 days after fledging were censored after their last location, and not assumed deceased (see modelling details, below).

2.3 | Survival covariates

We assessed spatial fire characteristics using 30×30 m rasters of categorical burn severity from Monitoring Trends in Burn Severity (MTBS; <https://www.mtbs.gov/>). Burn severity was defined using the relativized difference in normalized burn ratio (RdNBR; Miller & Thode, 2007), a standard measure of fire effects on vegetation, and classified as unburned, low, medium or high burn severity. The three prescribed fires in our study area (Kaboom, Angel 1 and Angel 2) did not meet thresholds for inclusion in the MTBS dataset, so we calculated RdNBR using regional composites of the normalized burn ratio for the year before and after each fire (Miller & Thode, 2007; Reilly et al., 2017). Within prescribed fires, we validated RdNBR thresholds for burn severity classes by calculating RdNBR values for the nearby Meeks wildfire, applying the classification thresholds, and comparing these to the Meeks MTBS data using a spatial sample of 1,000 random points. This confirmed that our RdNBR and classified burn severity layers produced results that were correctly scaled and tightly correlated with MTBS (Pearson's correlation: RdNBR $r = 0.83$, classified $r = 0.76$).

We calculated an index of fine-scale variation in burn severity—a component of pyrodiversity—for each tracking bout using the inverse Simpsons index of diversity ($1/D$) for all classified burn severity pixels within a 100-m buffer of tracking points (Ponisio et al., 2016). In this case, the inverse Simpsons index ranges from 1 (all pixels equal) to 4 (pixels equally distributed between four different severity classes). This metric conveys information about the representation and evenness of severity classes, providing a single metric of variation that may be useful to land managers. In addition, we used field-collected data to assign a binary variable to each tracking bout indicating whether or not a fledgling spent >50% of observation time in high severity burn. For points where field-based burn severity was lacking ($n = 152$ of 2,735), we extracted the value from the classified burn severity raster. While 50% of observation time in high-severity burn represents an arbitrarily conservative threshold, we explored model sensitivity to this cut-off and found that results did not qualitatively change based on threshold levels, even with thresholds as low as 25% (Table S1).

Because nestlings were weighed at a range of days prior to fledging, we standardized raw mass values by subtracting the mean mass of birds banded 0–2 days before fledging and 3+ days before fledging separately. Mass of nestlings at capture was variable, with a slight increase in average mass 2 days before fledging (Figure S1).

2.4 | Survival analysis

We examined fledging survival relationships using logistic exposure models fit within a Bayesian framework (Schmidt et al., 2010). We developed two separate models based on our quantities of interest: (a) the probability of surviving to 'independence', which

occurs approximately 35 days after fledging (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019) and (b) the probability of surviving approximately 9 months, to the beginning of the next breeding season. We assumed that the survival of individual i over interval j followed a Bernoulli distribution $y_{i,j} = \text{Bernoulli}(\theta_{i,j})$ where $y_{i,j} = 1$ if individual i survived interval j , $y_{i,j} = 0$ if the individual died, and $\theta_{i,j}$ is the probability of individual i surviving interval j . Here, θ represents the daily survival probability, s , raised to the length of the risk exposure period such that $\theta_{i,j} = s^{t_{i,j}}$, where $t_{i,j}$ is the length of interval j for individual i . We modelled $s_{i,j}$ using a logit-link function $\text{logit}(s_{i,j}) = \beta X$, where β represents a vector of intercept and slope coefficients and X represents a matrix of covariates. In this way, the model allows for uneven sampling intervals and the inclusion of interval-specific covariates such as habitat use. We included a nest-level identifier as a random intercept in each model to account for repeated observations of individuals from the same nest, which generally shared similar covariate values (e.g., same fledging date for siblings). All survival models used a $\text{Normal}(\mu = 4.00, \tau = 0.25)$ prior distribution on the overall intercept coefficient, which centres the prior on a reasonable value for daily survival rate. We used agnostic priors with slight regularization, $\text{Normal}(\mu = 0, \tau = 0.25)$, on all fixed effects and a uniform prior (0.1, 3) on the random effect standard deviation.

For our model of 35-day fledgling survival ($n = 439$ visit intervals), we developed a set of candidate models based on a priori hypotheses about survival relationships (Table 2). We started with a single model that included only the covariates for which

TABLE 2 Model selection results for six a priori candidate models of 35-day fledgling survival for black-backed woodpeckers in burned forests of Washington and California, USA. We employed leave-one-out cross-validation to compare Bayesian models using the information criterion LOOIC, presented here on the deviance scale. Models are shown in order of increasing LOOIC (lower value = better relative fit)

| Model | LOOIC | Δ LOOIC |
|---|-------|----------------|
| High severity + Diversity in burn severity + Years since fire + Days since fledging + Ordinal fledging date | 307.2 | 0 |
| High severity + Diversity in burn severity + Years since fire + Days since fledging | 308.4 | 1.2 |
| High severity + Diversity in burn severity + Years since fire + Days since fledging + Region | 309.4 | 2.2 |
| High severity + Diversity in burn severity + Years since fire + Days since fledging + Sex | 311.4 | 4.2 |
| High severity + Diversity in burn severity + Years since fire + Days since fledging + Mass | 311.5 | 4.3 |
| High severity + Diversity in burn severity + Years since fire + Days since fledging + Ordinal fledging date + Region + Sex + Mass | 315.4 | 8.2 |

we had strong, directional predictions for their effects on survival: high severity burn, diversity in burn severity classes, years since fire and days since fledging. Next, we iteratively tested this model with the addition of one of the following covariates: ordinal fledging date, study region (California or Washington), sex and mass. These four variables all have associations with survival supported in the literature (Cox et al., 2014; Kilgo & Vukovich, 2012; Naef-Daenzer et al., 2001), but were not the main focus of our study and therefore we considered them as potential nuisance variables. Model comparisons also included a full model with all eight predictors. We compared models using leave-one-out cross validation (LOO) to estimate the pointwise out-of-sample prediction accuracy (Vehtari et al., 2018). We also performed model comparisons using the widely applicable information criterion (WAIC; Watanabe, 2010) and confirmed that results were similar (Table S2). We made inference using the best supported model based on ΔLOOIC (Arnold, 2010).

We used covariates from the top 35-day survival model to parameterize a model of annual juvenile survival that included all tracking bouts from the first year after birds were tagged ($n = 638$ visit intervals). This model did not include habitat characteristics as predictors because birds often moved extensively during the long intervals between consecutive visits. Although some birds likely dispersed beyond the boundaries of our aerial telemetry searches, our censorship criteria meant that daily survival estimates were only informed by detected transmitters and that mortality was not confounded by emigration. We calculated annual juvenile survival by summarizing the posterior distribution of cumulative survival probability for the first 350 days after fledging, which represents the time period between the average ordinal nest fledging date (June 16th) and June 1st of the following year, when most pairs have initiated nesting.

2.5 | Analysis of movement rates

We calculated a metric of fledgling mobility, km moved per hr, for all tracking bouts that lasted longer than 25 min during the first 35 days post-fledging. Using the R package `ADEHABITATLT` (Calenge, 2006), we summed the straight-line distances between all consecutive trees where we observed an individual during a tracking bout, divided this distance by the total minutes of observation time and multiplied by 60 to obtain the distance travelled per hour of observation. We modelled movement rate as a function of days since fledging using a Bayesian lognormal regression. We used vague prior distributions, $N(\mu = 0, \tau = 0.01)$, on fixed effects, and we included a nest-level random effect with a vague prior distributed as $\Gamma(r = 0.001, \lambda = 0.001)$.

2.6 | Bayesian inference

We fit all models in R version 3.6.3 using JAGS and the package `R2JAGS` (R Core Team, 2020; Su & Yajima, 2015). Each model ran 3

chains of 20,000 iterations with a burn-in of 5,000 and a thin rate of 10, giving a final posterior sample of 4,500. We confirmed that the Gelman–Rubin statistic was <1.1 for every estimate and visually inspected traceplots to assess convergence (Youngflesh, 2018). All continuous variables were centred and standardized prior to modelling, and we made inference using 95% Bayesian credible intervals. To evaluate model fit, we conducted posterior predictive checks with Bayesian p values (Gelman et al., 1996) for test statistics representing apparent survival rates and the mean and standard deviation of log-transformed movement rates.

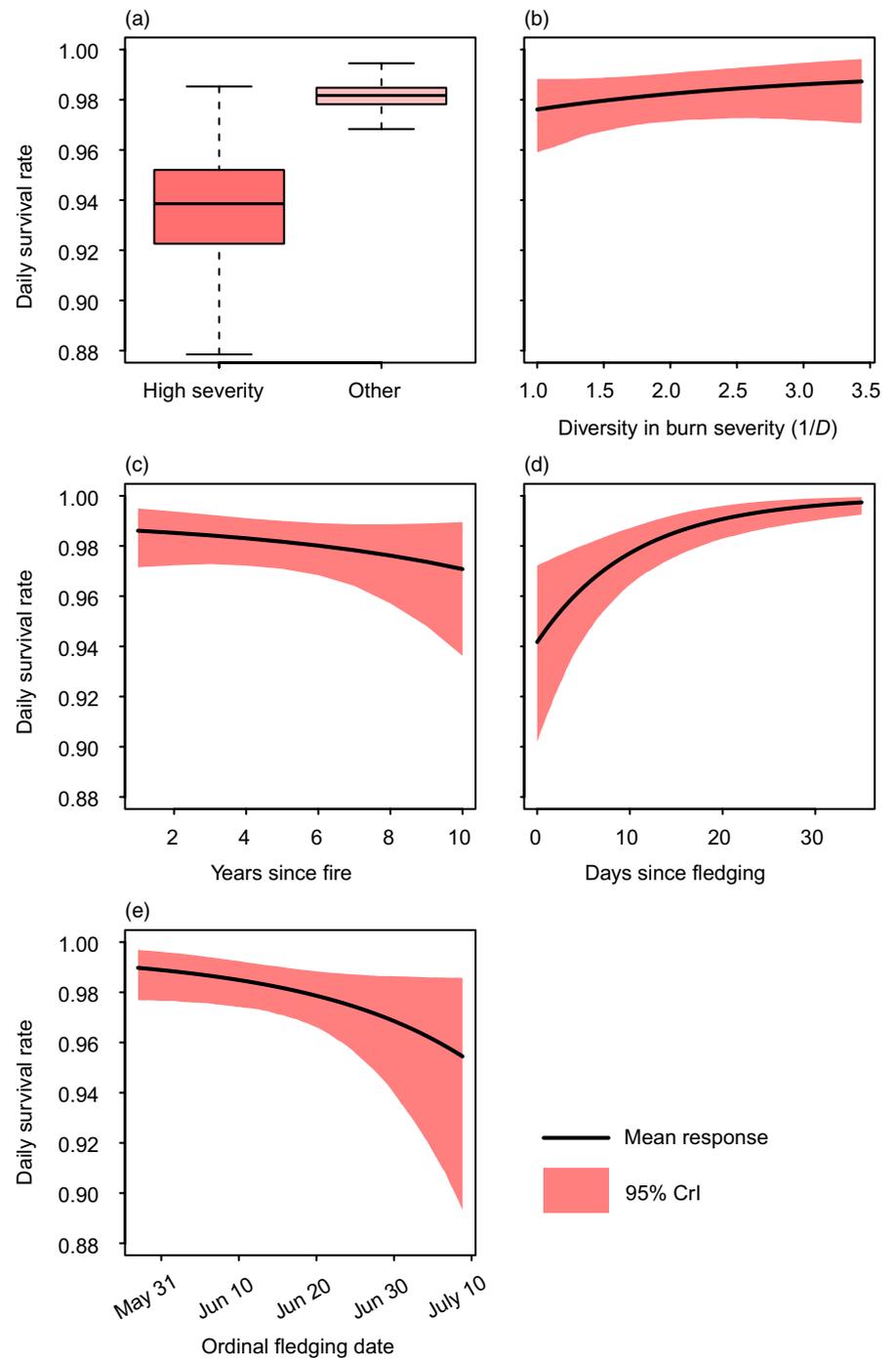
3 | RESULTS

We tracked the survival of 84 fledgling blacked-backed woodpeckers from 39 nests in seven different post-fire areas. Nests generally contained 2–3 young (mean = 2.5), and parents tended to split the brood after nests fledged, with each parent separately provisioning 1–2 offspring. In total, we collected tracking data at 2,735 points during 722 tracking bouts, with an average of 8.6 bouts per bird. Of 439 tracking bouts on dependent fledglings, 53 of 220 were assigned to high-severity burn ($>50\%$ of observation time in high severity) in California, and 35 of 219 were assigned to high-severity burn in Washington. Apparent survival to independence 35 days after fledging was 44% (47 deaths; Table 1) with seven additional deaths recorded 35–350 days post-fledging.

Most deaths could be attributed to predation by hawks or owls, and we frequently found transmitters surrounded by body remains or plucked feathers. Two transmitters were recovered below northern goshawk (*Accipiter gentilis*) nests and one transmitter each was located in—or next to—the nests of a red-tailed hawk (*Buteo jamaicensis*), western screech owl (*Megascops kennicottii*) and Cooper's hawk (*Accipiter cooperii*). Of five deaths with full body remains, three were found in exposed habitat within high-severity burns directly after unusually severe weather (e.g. early summer thunderstorms). A necropsy on another fledgling revealed the presence of tapeworms, and a necropsy on a final bird detected the presence of pneumonia, although bodily damage suggested that predation may have been the proximate cause of death.

We made inference using the best supported model for fledgling survival to independence, which included fixed effects of burn severity, diversity in burn severity, years since fire, days since fledging and ordinal fledging date (Table 2). Daily fledgling survival probability showed a strong relationship to burn severity, with lower survival in areas with high burn severity compared to unburned, low- and medium-severity burn (Figure 3a; Table 3). The cumulative probability of a fledgling surviving 35 days in unburned to medium-severity burned forest was 0.53 (95% CrI = 0.37–0.70), but survival decreased to 0.13 (95% CrI = 0.02–0.33) for birds using only high-severity patches. Controlling for burn severity, years since fire and diversity in burn severity did not show strong relationships, but predicted values showed a slight increase in survival with increasing diversity in burn severity and a weak decrease in survival in older fires.

FIGURE 3 Modelled relationships for daily survival rate of fledgling black-backed woodpeckers during the first 35 days after fledging, when young typically depend on their parents for provisioning. The strongest predictors of survival were burn severity (a) and days since fledging (d). Diversity in burn severity (b), years since fire (c), and ordinal fledging date (e) showed weak effects



Fledgling survival was strongly related to the number of days since fledging, with lower survival in younger individuals. The ordinal date that a nest fledged showed a weak, negative relationship, indicating a tendency for earlier nests to produce fledglings with higher survival (Figure 3; Table 3).

We found a strong positive relationship between fledgling movement rate and the number of days since fledging ($\beta = 0.82$, 95% CrI = 0.57–1.07; Figure 4). Immediately after leaving the nest, many fledglings travelled to forest patches with live trees where they moved infrequently and received provisioning from adults. As fledglings grew older, activity increased and fledglings moved between trees more often. As they neared independence, we observed

fledglings accompanying foraging adults and attempting to forage independently in low- and high-severity burn patches.

Survival rates generally remained high once fledglings reached independence. In all habitats combined, a juvenile woodpecker had a cumulative survival probability of 0.23 (0.05, 0.45) from fledging to the first breeding attempt the following spring. The number of days since a juvenile left the nest was the strongest predictor of survival probability, with mean daily survival rates rising from an average of 0.972 (0.954, 0.985) during the dependent fledgling period to 0.998 (0.996, 0.9997) after independence (Table 4). Once surviving to independence, the cumulative probability of additionally surviving to June 1st the following spring was 0.60 (0.25, 0.92).

TABLE 3 Posterior means and 95% credible intervals for estimated parameters from two models of fledgling black-backed woodpecker survival during the first 35 days after leaving the nest. Inference was made using the top model with the lowest LOOIC; the full model including all parameters is shown for reference. Items in bold indicate 95% credible intervals that do not overlap zero

| Covariate | Top model | Full model (Δ LOOIC = 8.2) |
|----------------------------|-----------------------------|---------------------------------------|
| Intercept | 3.99 (3.48, 4.57) | 3.18 (1.22, 5.35) |
| High severity | -1.26 (-2.02, -0.54) | -1.27 (-2.04, -0.52) |
| Diversity in burn severity | 0.20 (-0.13, 0.56) | 0.21 (-0.15, 0.57) |
| Years since fire | -0.23 (-0.67, 0.19) | -0.35 (-0.89, 0.17) |
| Days since fledging | 0.97 (0.50, 1.49) | 0.97 (0.50, 1.49) |
| Ordinal fledging date | -0.38 (-0.84, 0.04) | -0.33 (-0.82, 0.13) |
| Region (California) | — | 0.26 (-0.75, 1.26) |
| Sex (female) | — | 0.30 (-0.50, 1.07) |
| Mass | — | 0.19 (-0.35, 0.75) |

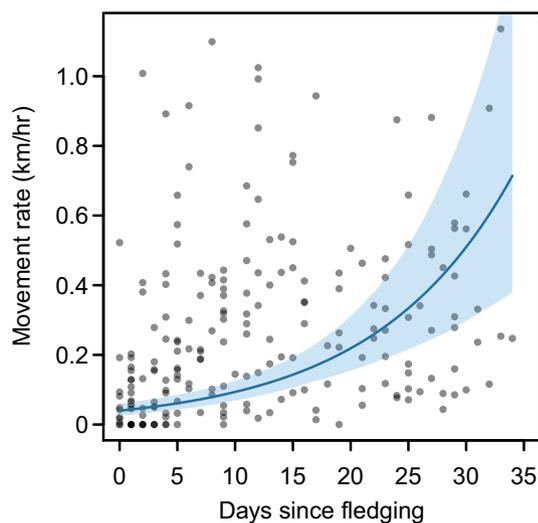


FIGURE 4 The relationship between the number of days since a fledgling black-backed woodpecker left the nest and movement rate recorded during radio-telemetry tracking bouts. Mean prediction and 95% CrI are shown in blue, and dots represent raw data with transparency added to visualize overlapping points

TABLE 4 Posterior means and 95% credible intervals from the model of juvenile black-backed woodpecker annual survival in burned forests of Washington and California, USA

| Covariate | Estimate (95% CrI) |
|-----------------------|---------------------|
| Intercept | 3.48 (2.92, 4.08) |
| Years since fire | -0.18 (-0.79, 0.35) |
| Days since fledging | 0.35 (0.17, 0.72) |
| Ordinal fledging date | -0.37 (-1.00, 0.19) |

3.1 | Model evaluation

Both the 35-day and annual survival models closely approximated the apparent interval survival rate for fledgling black-backed woodpeckers and showed no evidence for lack of model fit (35-day survival $p_b = 0.21$, annual survival $p_b = 0.38$). Posterior predictive tests also indicated no significant lack of fit for our model of fledgling movement rates based on the mean and standard deviation of observed data (p_b for the mean = 0.49, p_b for standard deviation = 0.48).

4 | DISCUSSION

Spatial variation in fire characteristics can structure not only the biotic community arising after fire but also the populations of individual species using burned areas (He et al., 2019; Kelly & Brotons, 2017). Here, we demonstrate that spatial fire characteristics interact with fledgling survival rates in a post-fire specialist. Despite the importance of high-severity patches for black-backed woodpecker foraging and reproduction in our study region (Hutto, 2008), survival to independence was four times higher for fledglings that avoided high-severity patches compared to fledglings that primarily used high-severity, even when controlling for effects of fledgling age, mass, sex, fledging date and years since fire. This result supports the hypothesis that fledgling habitat selection confers fitness benefits consistent with the predation-starvation hypothesis: while fledglings are provisioned by adults, they can avoid exposed areas with increased predation risk (Houston et al., 1993; Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019).

Predicted fledgling survival to independence was notably low for fledglings that primarily used high-severity burned patches (mean = 13% survival), but we caution that the majority of fledglings used a mix of burn severities during their first 35 days after leaving the nest. Still, 16 birds in our sample used >50% high-severity habitat during every tracking bout, and of these, 15 of 16 (94%) did not survive to independence. In addition, subtle differences in forest type, management history and fire size between Washington and California could represent sources of variation in our dataset. However, the survival model that included an effect of region (i.e. U.S. state) received little support, indicating that underlying survival relationships were similar across sampling sites.

Of the non-habitat covariates that we examined, the number of days since fledging had the strongest effect on fledgling survival. We also found that movement rates increased substantially as fledglings grew older, likely reflecting post-fledging muscle development and the gradual shift towards independent foraging during the first 35 days out of the nest. New fledglings experience high predation rates in many bird species, especially when fledglings are weak fliers or engage in vocal begging behaviours (Fisher & Davis, 2011; Kershner et al., 2004). In our study, 53% of deaths occurred within the first 3 days after fledging. We hypothesize that the strong positive relationship between fledgling age and survival in our study corresponds to an increase in mobility and predator evasion as

fledglings grow older. In the field, we observed gradual decreases in fledgling 'begging' behaviours and increases in independent foraging during the first 35 days after fledging.

The day of year that a nest fledged had a weak, negative effect on fledgling survival, with slightly higher survival in early-season fledglings. This relationship may stem from seasonal effects, such as changes in predation and food availability, or the quality of breeding adults (Naef-Daenzer et al., 2001; Perrins, 1970). Previous work on black-backed woodpeckers has shown a strong negative day-of-year effect on nest survival (Stillman, Siegel, Wilkerson, Johnson, Howell, et al., 2019), which suggests that a similar mechanism may affect both vital rates with carry-over effects from one life stage to another. Within the burned forests that we studied, it is possible that more experienced breeders nest earlier in the breeding season and have higher offspring survival compared to less-experienced conspecifics (Perrins, 1970).

We did not find evidence for a strong relationship between juvenile survival and years since fire, although parameter estimates of this effect were negative for both 35-day and annual survival models. These results suggest that juvenile survival is not the principal demographic mechanism driving the observed decline of local populations within burned areas during the first decade following fire (Rota et al., 2014; Tingley et al., 2018). Juvenile recruitment may influence local population size through variation in the probability of long-dispersal dispersal rather than survival (Siegel et al., 2016), although this hypothesis has not been empirically tested. In addition to influencing black-backed woodpecker population density, the number of years since fire also has a marked effect on the structure of forests burned at high severity. Snags fall over time (Grayson et al., 2019), food resources may decline (Ray et al., 2019) and high-severity patches become even more open and exposed to aerial predators with increasing years since fire. These successional changes may incrementally increase predation risk for fledglings in high-severity patches over time, although our data do not support this as a strong effect.

More broadly, our results provide evidence to support the role of habitat complementation in generating species-specific benefits of pyrodiversity over the full life cycle of animals (Kelly et al., 2017). Variation in burn severity within post-fire habitat yields high-severity areas that are close to forest patches with live trees (low-severity burn or unburned), which may provide needed habitat structure for multiple life stages in close proximity. This is evidenced in adult black-backed woodpeckers, which select foraging and nesting sites near ecotones between high- and low-severity burn (Stillman, Siegel, Wilkerson, Johnson, Howell, et al., 2019; Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). As the proximate cause of mortality, fledgling predation may exert selective pressure for adults to nest near low-severity or unburned forest, where fledglings with limited flying ability may seek cover rapidly after leaving the nest. Taken together, these habitat selection and survival patterns support the idea that the distribution of species on the burned landscape is driven not only by habitat quality but also by the presence of higher trophic levels and spatial patterns of predation risk (Creel et al., 2005; Kelly et al., 2017). By linking resource-rich foraging and breeding habitat

with areas of reduced predation risk, variation in burn severity—as well as other aspects of pyrodiversity—may enhance the survival and persistence of animals that specialize on post-fire habitat. Although our study only focused on a single fire-associated species, the expected mechanisms underlying this phenomenon may apply broadly to other animals, particularly prey species, in fire-prone landscapes of western North America.

We note that our study occurred in a region historically dominated by a mixed-severity fire regime, where previous research has shown positive relationships between pyrodiversity and biodiversity (Ponisio et al., 2016; Steel et al., 2019; Tingley et al., 2016). Although other species likely benefit from variation in spatial fire characteristics, we caution that the role of pyrodiversity in animal conservation must be considered at a regional level, where the effects of pyrodiversity are evaluated in the context of a historical fire regime (Kelly & Brotons, 2017; Parr & Andersen, 2006). Fire regimes in the western U.S. show a pattern of increasing fire intensity and larger high-severity patches in recent decades (Steel et al., 2018; Stevens et al., 2017). These changes may lead to overall decreases in pyrodiversity, including important ecotones between low- and high-severity patches (Stevens et al., 2017). In addition to potential community-level effects of increased habitat homogeneity after fire, our research suggests that declining pyrodiversity may also influence individual species through stage-dependent effects of post-fire habitat structure on demographic rates.

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AUTHORS' CONTRIBUTIONS

A.N.S., T.J.L., R.B.S., R.L.W. and M.W.T. conceived the ideas and designed the methodology; A.N.S., T.J.L. and P.C.F. collected the data with substantial help from all co-authors; A.N.S. and M.W.T. analysed the data and led manuscript preparation. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Input data and model code in JAGS language are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.0rxwdbzrt> (Stillman et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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