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Original Article

Conditional natal dispersal provides a mechanism for populations tracking resource pulses after fire

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Animals that persist in spatially structured populations face the challenge of tracking the rise and fall of resources across space and time. To combat these challenges, theory predicts that species should use conditional dispersal strategies that allow them to emigrate from patches with declining resources and colonize new resource patches as they appear. We studied natal dispersal movements in the black-backed woodpecker (*Picoides arcticus*), a species known for its strong association with recent post-fire forests in western North America. We radio-tracked juveniles originating from seven burned areas and tested hypotheses that environmental and individual factors influence dispersal distance and emigration rates—investigating emigration while additionally accounting for imperfect detection with a novel Bayesian model. We found that juveniles were more likely to leave natal areas and disperse longer distances if they were heavier or hatched in older burned areas where resources are increasingly scarce. Juveniles were also more likely to leave their natal burn if they hatched in a nest closer to the fire perimeter. While dispersing across the landscape, black-backed woodpeckers selected for burned forest relative to unburned available habitat. Together, these results strongly support the hypothesis that black-backed woodpecker populations track resource pulses across fire-prone landscapes, with conditional natal dispersal acting as a mechanism for locating and colonizing newly burned areas. Lending empirical support to theoretical predictions, our findings suggest that changes in resource distribution may shape dispersal patterns and, consequently, the distribution and persistence of spatially structured populations.

Key words: **black-backed woodpecker, metapopulation, movement, *Picoides arcticus*, resource tracking, wildfire.**

INTRODUCTION

Dynamic landscapes are the norm in many ecosystems, producing spatial structure in plant and animal populations (Moloney and Levin 1996; Hastings 2003; Wimberly 2006). Dispersal is a key trait leading to gene flow among spatially structured populations, but the causal mechanisms driving dispersal behavior in mobile species can be difficult to test. Given the complexity of dispersal mechanisms, a variety of proximal factors are likely to act together in determining the costs and benefits of movement (Bowler and Benton 2005; Matthysen 2012). For example, resource availability changes over time in many heterogeneous landscapes due to a variety of natural and anthropogenic factors. Dispersal behavior allows mobile species to respond to resource dynamics by seeking areas with available resources and leaving areas after resources decline (Matthysen 2012). Rather than remaining stationary in habitat patches, animals in spatially structured populations are expected to exhibit life history strategies for resource tracking consistent with two hypotheses. First, populations should show patch-level population trajectories that track the rise and fall of resource availability, as mediated by changes in immigration and emigration rates (Thomas 1994; Yang et al. 2008). Second, species should exhibit conditional dispersal strategies that respond to external information, such as

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environmental quality (condition-dependence), and individual factors, such as body size (phenotype-dependence; Bowler and Benton 2005; Clobert et al. 2009). These hypotheses underscore the importance of dispersal behavior as a key parameter governing the distribution and persistence of spatially structured populations (Johst et al. 2002; Brotons et al. 2005; Reigada et al. 2015).

Patch dynamics are particularly dramatic in the instance of resource pulses—the temporary availability of drastically elevated levels of food, habitat, or other population requirements that subsequently decline over time (Holt 2008; Yang et al. 2008). Ecological disturbance is frequently overlooked as an agent of resource pulses, but many species benefit from elevated resource levels that develop during or following disturbance events. Disturbance regimes that alter landscape features may pave the way for a cascade of heightened resources in a successional context, as when immediate responses by one species produce a lagged positive response in other species through negative (e.g., predation) or positive (e.g., facilitation) interactions (He et al. 2019). Compared to conventional resource pulses, such as oak mast events—which combine low frequency, large magnitude, and short duration (Schmidt and Ostfeld 2003; Yang et al. 2008)—resource pulses following disturbance are typically longer-lasting and may extend over one or more generations of vertebrate consumers.

Disturbances from wildfire can create local conditions with elevated resource availability for many years after fire, following the gradual attrition of dead trees or the shift to early successional vegetation (Perry et al. 2011; Grayson et al. 2019). Fire often creates discrete patches of elevated resource availability—such as canopy openings for aerial foragers and herbaceous plants (Smucker et al. 2005; Perry et al. 2011)—that host unique assemblages of plants and animals, with the frequency and magnitude of these resource pulses dependent on regional fire regimes (He et al. 2019). In western North America, the pulse of dead trees immediately following stand-replacing fire attracts vast numbers of woodboring beetles which reproduce in dead and dying trees (Ray et al. 2019). Woodboring beetle larvae provide a pulsed food source for many woodpecker species, which in turn create nest cavities that are used by secondary cavity-nesting birds and mammals (Tarbill et al. 2015). Consequently, the ability of mobile species to find, colonize, and exploit post-fire resource pulses plays a key role in structuring the biotic community that arises after fire (Brotons et al. 2005; Nimmo et al. 2019).

Often called the most fire-associated vertebrate in North America, the black-backed woodpecker (*Picoides arcticus*) colonizes burned forests rapidly after fire (Hutto 2008; Tingley et al. 2018). Black-backed woodpeckers are strongly linked to post-fire areas, where they use standing dead trees (snags) for foraging on woodboring beetle larvae and excavating nest cavities (Rota et al. 2015; Stillman et al. 2019a). Previous studies have demonstrated strong effects of snag density on habitat selection, home range size, and occupancy (Tingley et al. 2014; Tingley et al. 2018; Stillman et al. 2019b). Stand-replacing fire creates a resource pulse of snags and woodboring beetle larvae, but the availability of these resources declines drastically in the decade following fire as snags decay and beetle larvae become less abundant (Grayson et al. 2019). Thus, black-backed woodpecker populations in the western United States exhibit strong spatial structure driven by the availability of burned patches and the resource levels within them (Hutto 2008).

As expected by the first hypothesis for spatially structured populations, black-backed woodpecker subpopulations within post-fire areas of western North America track changes in resource availability, with local occupancy peaking between 3–5 years after fire and then gradually declining over the next 5–10 years (Taillie et al. 2018; Tingley et al. 2018). Given this population trajectory, theory predicts that black-backed woodpeckers also should exhibit dispersal strategies that allow populations to track the rise and fall of fire-driven resource pulses. More specifically, dispersal behavior should respond to time since fire, with increased emigration from old post-fire sites (where snags have decayed and fallen) and selection of new breeding territories in younger burns with high densities of snags—and the beetle larvae within them—still present. Black-backed woodpecker population age structure in burned forests, with higher proportions of younger individuals in more recent burns, suggests that natal dispersal may be an important behavioral mechanism driving these population dynamics (Siegel et al. 2016). Additionally, because black-backed woodpeckers are relatively uncommon outside of burned forests in western North America (Tingley et al. 2020), burned forests are hypothesized to act as source populations, with emigrants colonizing newly burned forests or persisting at lower densities within unburned areas (Hutto 2008; Nappi and Drapeau 2009). Natal dispersal may be the key mechanism that allows this specialist to track the shifting mosaic of burned forests across the landscape and exploit post-fire resource pulses.

Here, we use dispersal data from black-backed woodpeckers to empirically test the hypothesis that species in spatially structured populations exhibit condition- and phenotype-dependent dispersal strategies to track heterogeneous resources through space and time. While past work has postulated that this hypothesis may be true for black-backed woodpeckers (Pierson et al. 2013; Rota et al. 2014; Siegel et al. 2016; Tingley et al. 2018), direct studies of dispersal behavior are lacking for this species, and some studies have argued that the species' occurrence patterns do not support the hypothesis for selection of post-fire forest during dispersal (Fogg et al. 2014). We hypothesized that black-backed woodpeckers engage in natal dispersal movements between burned areas and that dispersal behavior responds to condition- and phenotype-dependent factors. To test this, we first assessed the effects of condition-dependent environmental factors (years since fire, fire size, distance to fire boundary, distance to nearest neighboring burn, elevation) as well as phenotype-dependent individual factors (sex, body mass) on dispersal distances. Second, we developed a novel Bayesian model to evaluate how these factors influence the probability of dispersal away from the natal fire area while accounting for the imperfect detection of dispersal events and making use of incomplete dispersal data. We additionally used simulations to test the prediction that dispersing individuals are more likely to settle in burned forest relative to its availability on the landscape.

METHODS

Study area and field methods

We used radio-telemetry to track black-backed woodpecker natal dispersal in montane regions of northern California (Sierra Nevada and Southern Cascade ranges) and central Washington, USA (Cascade range). Both study regions were approximately 50,000 km^2 in area and contained a spatial network of burned areas 1–10 years post-fire. The median nearest neighbor distance between burned areas >100 ha in size was 2.2 km (interquartile range = 0.9–5.8 km) in California and 3.6 km (interquartile range = 1.6–8.7 km) in Washington. All birds in this study originated from nests within burned areas of predominantly conifer forest spanning a gradient of 1–10 years since fire. In California, we tagged birds in three areas burned by wildfires that ranged from 162.6 to 311.1 km^2 in size: the Moonlight fire (burned in 2007), Chips fire (2012), and Bald fire (2014). In Washington, we tagged birds in three prescribed fires and one wildfire: Kaboom (2009), Angel 1 (2014), Angel 2 (2016), and Meeks (2015). The Washington fires were relatively small, ranging from 4.5 to 25.1 km^2, but still included patches of stand-replacing fire > 10 ha. Post-fire logging was absent from our Washington study sites, and California study sites were predominately in unlogged areas where intact burned forest provided nesting habitat for woodpeckers.

We searched for black-backed woodpecker nests in burned forests following the methods from Stillman et al. (2019a). We captured nestlings just prior to expected fledging (mean = 1.6 days before fledging) during spring and summer 2016–2018. We used the hole-saw method to access nestlings (Ibarzabal and Tremblay 2006), conducted standard measurements on each individual, and fit birds with 1.6-g radio tags (Model CTx Ag 392, Lotek Wireless Inc. Newmarket, Ontario, Canada) with an adjustable leg-loop harness made of elastic beading cord (Rappole and Tipton 1991). CTx transmitters included a programmable on/off calendar schedule that extended battery life over a year post-deployment; we programmed each tag to transmit during three intervals: May–August, September–November, and April–June. We coated transmitters in a thin layer of epoxy as added protection against mechanical wear. Transmitters weighed less than 3% of average body mass to minimize impact on movement and survival (Fair et al. 2010). We marked nestlings with a unique combination of color bands and a numbered U.S. Geological Survey leg band before returning them to their nest cavity.

We used a combination of on-the-ground radiotracking and aerial telemetry to track natal dispersal movements. We tracked fledglings from the ground every 3–5 days until early August to record location coordinates and visually confirm survival. We found that juveniles began to disperse in August and September, so we transitioned to a more intermittent tracking schedule based on the availability of aircraft. The goal of this tracking schedule was to locate each bird three to five times between August and November using two strategies: driving road networks with vehicle-mounted antennas, and fixed-wing aerial telemetry. Aerial telemetry 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 out to >60 km from a bird's last known location. Programmable transmitters switched off during the winter to save battery life and turned back on the following spring, allowing us to use the same methods to locate birds approximately 1 year after fledging when most individuals engage in their first breeding attempt.

Over the course of this study, we conducted 15 fall aerial telemetry flights and 14 spring flights. Combined with on-the-ground search efforts, this yielded five possible re-sighting histories: 1) located in both fall and spring, 2) located in fall but missing in spring, 3) missing in fall but located in spring, 4) missing in both fall in spring, and 5) found dead during the study period. We recorded a death 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). We also recorded data from four color-banded individuals without transmitters that were opportunistically located 1 year after fledging, although these individuals were omitted from analysis where the inclusion of non-radio-tagged birds would introduce sampling bias (i.e., dispersal distributions and simulations).

In addition to searching for dispersing birds, we conducted a series of flights to estimate the probability of transmitter detection from fixed-wing aircraft. The probability of detecting a transmitter on a single aerial survey was 0.82, and signals remained strong within 3 km of the transmitter. The probability of detection given two or three flights increased to 0.95 and 0.99, respectively. For more information on detection tests, see Supplementary Appendix S1.

Field methods were approved by the University of Connecticut Animal Care and Use Committee (Protocol A16-008), the USFS Animal Care and Use Committee (2016-007), the California Department of Fish and Wildlife (Scientific Collecting Permit #SC-8645), the Washington Department of Fish and Wildlife, and the USGS Bird Banding Laboratory (Permits 22423, 24061).

Distribution of dispersal distances

Although telemetry flights covered a vast search area, our observed dispersal distances showed a downward bias due to missing birds that likely flew beyond search boundaries. To build a distribution of dispersal distances, we applied a bias-correction method that uses interval-censored data to include information on birds with incomplete dispersal tracks (Paradis et al. 2002). This method provides added flexibility over area-ratio corrections, which require that binned dispersal distances have frequencies greater than 1 in the range of observed values (Baker et al. 1995; Cooper et al. 2008). The assumptions of area-ratio corrections may be inappropriate for studies with small sample sizes or studies where dispersers may have traveled further than the maximum observed distance, as in our case. Alternatively, interval-censored correction methods use data from individuals with known dispersal distances (uncensored data) as well as individuals with incomplete dispersal information (interval-censored data) to parameterize a bias-corrected distribution of dispersal distances. Interval-censored data comprise a minimum dispersal distance (observed or estimated) and a maximum dispersal distance, analogous to interval-censoring in survival studies (Paradis et al. 2002).

For each bird in our study with incomplete dispersal information, we estimated the minimum dispersal distance as the distance from the natal nest to the nearest area within potential habitat (i.e., >10% conifer canopy cover) that was not surveyed by aerial telemetry (Supplementary Figure S1). Although this method assumes complete detection within the search area, it provides a conservative approximation given that detection probability was high within the flight area and searches frequently extended well beyond the minimum distance (e.g., estimated distance may correspond to a gap in the flight area) (Koenig et al. 1996). We used 100 km as a feasible maximum bound of dispersal distance based on observed records and genetic evidence from this species (Yunick 1985; Pierson et al. 2013; Rota 2013), and we tested the sensitivity of our inference to this cutoff (Supplementary Table S1). We fit four potential dispersal distributions—half-Cauchy, lognormal, normal, and Weibull—to the interval-censored data using the package "fitdistrplus" in the programming language R (Delignette-Muller and Dutang 2015; R Core Team 2021). For each distribution, we estimated parameters using a maximum likelihood approach and used the distribution with the lowest Akaike's Information Criterion for inference (Burnham and Anderson 2002).

Modeling dispersal distance and dispersal probability

We tested for individual and environmental effects on three components of black-backed woodpecker dispersal behavior: 1) final dispersal distance, 2) fall dispersal status (individual either remained in the natal burn or dispersed out, see below), and 3) spring dispersal status. For birds with known post-dispersal locations (n = 19), we modeled dispersal distance as a function of covariates using a Bayesian linear regression model with a natural log-transformed response variable. Due to sample size constraints that limited power of multi-variate models, we built eight candidate models, each with a single covariate based on a priori hypotheses (Supplementary Table S2). These covariates were nestling mass, nestling sex, distance from the nest to the perimeter of the fire area, distance from the nest to the nearest neighboring burn > 100 ha in area, elevation at the nest site, years since fire, and size of the natal fire area. We also included an intercept-only model for comparison. We did not include study region (California vs. Washington) as a variable due to a strong correlation with fire size, which we considered to be a stronger hypothesis. All continuous variables were standardized by subtracting the mean and dividing by the standard deviation. Because nestlings were weighed at a range of days prior to fledging, we standardized raw mass values by subtracting the mean mass of birds tagged 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 (Stillman et al. 2021a). For all three model sets (dispersal distance, fall dispersal status, spring dispersal status), we compared models using leave-one-out cross validation (LOO) to estimate the pointwise out-of-sample prediction accuracy (Vehtari et al. 2018).

We developed a novel Bayesian model to examine the factors that influence fall and spring dispersal status while incorporating incomplete dispersal data and accounting for imperfect detection. This "false-positive event detection model" extends the occupancy modeling framework (MacKenzie et al. 2018) to cases where negative detections (0s) are known with certainty, and positive detections (1s) are either certain or uncertain. Here, the certainty of negative detections is distinct from traditional "false positive" models which typically include uncertainty in both 0s and 1s (Miller et al. 2011). We treated fall dispersal status as a binary response variable, where the observed value, y_i, for individual i is equal to 0 if a juvenile remained within the natal fire area during the fall, and $y_i = 1$ if a juvenile dispersed away from the natal fire area or if surveys failed to detect it within the fire boundary. To avoid counting potential prospecting movements, we recorded a dispersal event only if an individual remained outside the fire perimeter at the end of fall surveys. Similarly, we recorded spring dispersal status as $y_i = 0$ if a bird settled within the natal fire area the following spring, and $y_i = 1$ if a bird settled outside of the natal fire boundary or remained undetected. Observations of emigration are assumed to be imperfectly observed representations of the true dispersal status for each individual, z_i. Thus, the observed dispersal status, y_i, is modeled as:

$$y_i \sim \text{Bernoulli}(z_i + (1 - z_i) * p_i)$$

where $\mathbf{p}$ is a vector giving the measured probability of recording a false positive for each individual i. For example, an individual that remained undetected for two consecutive search flights would receive $p_i = 1 - 0.18^2 = 0.0324$, where 0.18 is the per-flight probability of inferring that the species has left the study area (i.e., not detected) when in fact it has remained in the study area and gone undetected. Likewise, an individual located with certainty outside of the natal fire area or detected within the fire boundary would receive $p_i = 0$. In this way, our model incorporates observations from individuals with incomplete dispersal data, where either fall, spring, or both fall and spring locations are missing, while incorporating the probability of detecting missing birds during aerial telemetry flights. Thus, the true dispersal status for an individual, z_i, is modeled as, $z_i \sim \text{Bernoulli}(\varepsilon_i)$, where ε_i is the probability of dispersal away from the natal fire area. We modeled the probability of dispersal separately for the spring and fall as a logit-linear function of one of the same six covariates ($\mathbf{X}$) described above, i.e. $logit(\varepsilon_i) = \beta_0 + \beta_1 X_i$.

We fit models to the data using JAGS (Plummer 2003) with the package "R2jags" in R (Su and Yajima 2021). In all cases we used vague priors: Normal(μ = 0, τ = 0.001) and Gamma(r = 0.001, λ = 0.001) for linear regression models, and Normal(μ = 0, τ = 0.2) for false-positive event detection models. We ran three chains of 15,000 iterations with a burn-in of 5000 and a thin rate of 20, yielding a final posterior sample of 1500 across all chains. We visually inspected traceplots to assess chain convergence and confirmed that the Gelman-Rubin statistic was < 1.1 for every parameter estimate (Gelman et al. 2004). We used Bayesian credible intervals on posterior samples to make inference on parameter support, with 95% credible intervals that do not cross 0 indicating "strong" support. We evaluated model fit using Bayesian P-values for test statistics summarizing the posterior predictive distribution (Conn et al. 2018; see Supplementary Appendix S2 for more information). JAGS code and input data for our models are available from the Dryad Digital Repository (Stillman et al. 2021b).

Simulation analysis

To examine whether dispersing juveniles select for burned areas, we conducted a spatially explicit simulation analysis testing our empirical results versus a null model where dispersal is random with respect to the locations of burned habitat near the nest site. For each juvenile with a known post-dispersal location, we simulated 1,000 dispersal events originating from the natal nest with distances drawn from the parameterized dispersal distribution (see methods above) and recorded the number of individuals settling in each of ten 10-km concentric distance bands centered on the natal nest. For each distance band, we then calculated the proportion of potential breeding habitat burned by wildfire or prescribed fire within the last 10 years to estimate the number of simulated birds settling in burned forest under the null model. We compared the simulated number of juveniles settling in burned forest to the observed data and calculated the probability of observing our data under the null model. For further details, see Supplementary Appendix S1.

RESULTS

Out of 81 marked nestling black-backed woodpeckers in 7 different post-fire areas, our final dataset comprised 32 radio-tagged and 4 color-banded juveniles, each with confirmed survival to at least 35 days post-fledging. We successfully relocated 23 of these 36 individuals in the fall (including 4 confirmed deaths) and 22 birds the following spring (with 3 confirmed deaths). Juvenile black-backed woodpeckers frequently moved considerable distances, and over half of radio-tagged individuals with known spring locations dispersed greater than 10 km from their natal nest. Dispersal outcomes varied among individuals, including dispersal from the natal site to a different fire (Figure 1a,d), dispersal from the natal site to unburned forest (Figure 1b,e), and dispersal from the natal territory to a different territory in the same fire area (Figure 1c,f). Dispersal events tended to occur in August and September when birds first became independent from parents.

Measured natal dispersal distances ranged from 1.6 km to 51.2 km, and the raw dispersal kernel showed high skewness and kurtosis statistics (2.4 and 10.4, respectively), indicating a fat-tailed distribution (Figure 2). The Weibull distribution provided the best fit to our interval-censored dispersal data (shape = 1.30 ± 0.24, scale = 24.30 ± 4.62; Supplementary Table S1). Bias-corrected estimates yielded a median natal dispersal distance of 18.4 km, with 75% of individuals moving at least 9 km and 5% of dispersers moving greater than 50 km from natal territories (Figure 2).

Model comparisons indicated strong support (ΔLOOIC < 2) for two variables influencing natal dispersal distance (Supplementary Table S3). First, natal dispersal distance showed a strong positive relationship with time since fire, with predicted mean dispersal distance increasing from 4 km to > 20 km as the number of years since

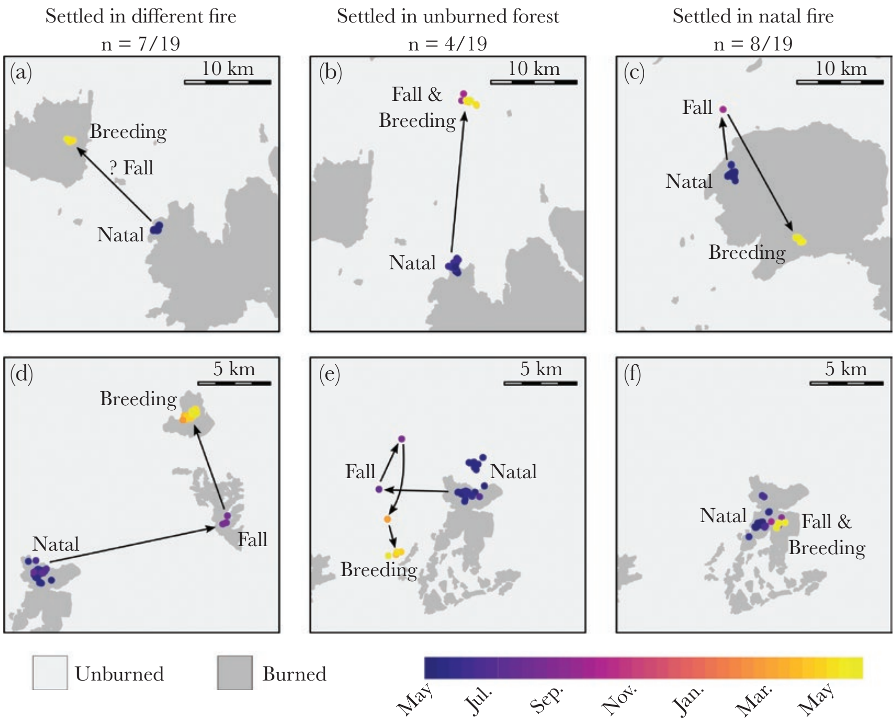

Figure 1

Example natal dispersal tracks for six black-backed woodpeckers in California (top row) and Washington, USA (bottom row). All juveniles originated from natal territories in burned forest, but dispersal strategies showed wide variation: (a, d) juvenile disperses from natal fire area to a different burned forest, (b, e) juvenile disperses from natal fire area and settles in unburned forest, and (c, f) juvenile disperses to a breeding territory within its natal fire area.

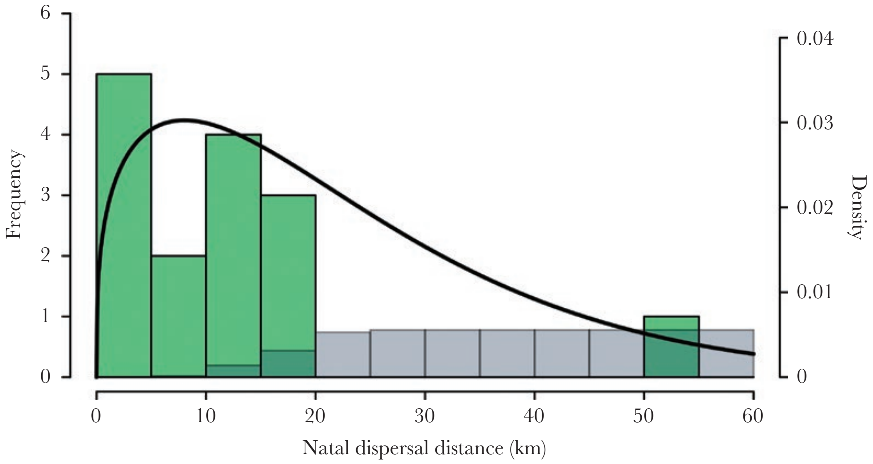

Figure 2

Distribution of black-backed woodpecker natal dispersal distances. Green bars show raw data (left axis) from 15 individuals with known dispersal distances, while overlaid gray bars indicate the aggregate probability density for 13 interval-censored individuals (right axis). The line shows the best-fit Weibull distribution corrected for sampling bias using both observed dispersal distances and interval-censored data from missing birds.

the natal fire burned increased from 1 to 10 years. Second, natal dispersal distance increased as nestling mass increased (Figure 3).

The number of years since a fire burned also had a strong, positive effect on the probability that a juvenile left the natal fire area in the fall (Figure 4a), and this was the only fall dispersal model with ΔLOOIC < 2 (Supplementary Table S4). A one-year increase in time since fire doubled the odds of leaving the natal fire area (odds ratio = 2.14; 95% CrI = 1.21, 4.68).

Two candidate models of spring dispersal status had strong support: standardized nestling mass and distance to fire perimeter (Figure 4, Supplementary Table S5). Juveniles with higher mass prior to fledging were more likely to settle outside of natal fire boundaries, and each 1-g increase in mass increased the odds of settling outside the natal fire area by a factor of 1.27 (95% Crl = 1.04, 1.66). Juveniles from nests close to the fire perimeter were more likely to settle outside the natal fire area (odds ratio = 0.93, 95% CrI = 0.84, 0.99). Posterior predictive checks demonstrated that models generally provided good fit to the data (Supplementary Figures S1 and S2).

We found strong evidence that juvenile black-backed woodpeckers select for burned forests relative to available breeding habitat when dispersing across the landscape. Under the null model assumption that dispersal is random with respect to fire locations, our simulations predicted that a median of 11% of individuals (2 of 18) would settle within burned forest (range 0–50%, Figure 5a), either within the natal fire area or in a different burned forest. By comparison, 78% of observed individuals (14 of 18) in our dataset settled in burned forest. There was no overlap between our null model simulations and our observed data, indicating that juvenile black-backed woodpeckers are much more likely to settle in burned forest relative to availability ($P < 0.001$). Among birds that left their natal fire area and settled in an area burned by a different fire ($n = 7$), our observations indicate a tendency to settle in fires that burned more recently than their natal fire (Figure 5b). Selected burns were a median of 5 years younger than natal burns, although limited sample sizes prevent robust estimates (one-sided sign test, $P = 0.11$).

DISCUSSION

Species that persist in spatially structured populations face the challenge of locating and colonizing discrete habitat patches (Thomas 1994; Hanski 1999). For species that track post-fire resources, like the black-backed woodpecker, the temporary nature of patches may catalyze high dispersal propensity and condition-dependent drivers of dispersal (Clobert et al 2009; Matthysen 2012). Our results provide empirical support for the hypothesis that conditional dispersal enables resource specialists to track heterogeneous resources through space and time at the population level. While past field and experimental work has tested this hypothesis using a variety of invertebrate taxa (Hanski 1999; Yang 2006), our study presents novel evidence from a vertebrate associated with post-fire resource pulses and sheds light on the multiple drivers of dispersal in spatially structured populations. Natal dispersal distances in black-backed woodpeckers were longer for heavier individuals and for individuals from older post-fire areas. Relatedly, juveniles were more likely to leave their natal fire area if the fire was older, their body mass was greater, or they came from a nest closer to the fire perimeter. Our finding that dispersing juveniles selectively immigrate into burned forests over all other types of available habitat lends further support to the hypothesis that natal dispersal strategies in black-backed woodpeckers have evolved in response to the shifting mosaic of resource patches in fire-prone landscapes.

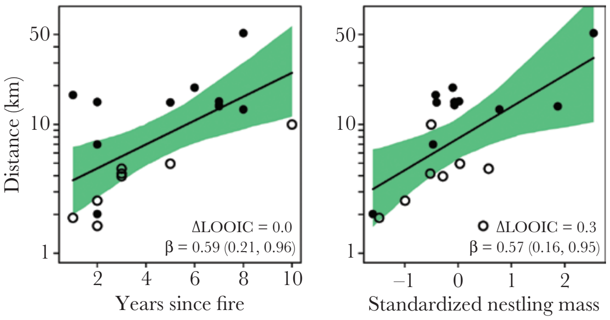

Figure 3

Model selection results indicated strong support for two variables influencing natal dispersal distance: the number of years since the natal fire burned, and the standardized mass of the dispersing individual. Filled dots show birds that settled outside of the natal fire area, and open dots are birds that settled within the natal fire area. ΔLOOIC values give the difference between each model and the model with the lowest LOOIC. Slope estimates are shown with 95% credible intervals. Note that the y-axis (dispersal distance) is on the log scale.

The challenge of imperfect detection in studying dispersal

Despite the demonstrated importance of dispersal to gene flow, metapopulation dynamics, and species distributions (Johst et al. 2002; Bowler and Benton 2005), the drivers of dispersal behavior remain enigmatic in many species. This is partially because quantities like dispersal rates and dispersal distances are exceedingly difficult to measure accurately in the field, particularly for lightweight and highly mobile species like birds (Koenig et al. 1996). Incomplete datasets and partial dispersal tracks are the norm, and there has been considerable effort to develop analytical approaches to glean biological information from imperfectly detected datasets. Bias-correction methods can be applied to scale observed dispersal distances according to some probability of detection (Baker et al. 1995; Cooper et al. 2008), although these methods fail to make use of the partial information researchers might have on certain individuals (e.g., last recorded location). Interval-censored data can be used to fit distributions to datasets with partial dispersal tracks (Paradis et al. 2002), but researchers are often precluded from using these incomplete datasets when assessing the factors that may drive condition- or phenotype-dependent dispersal and emigration rates. Integrating data on observed emigration rates with estimated probabilities of detection presents a novel opportunity to analyze the proximate factors governing dispersal probabilities.

In this study, we developed a false-positive event detection model to evaluate the conditions that influence emigration rates while accounting for imperfect detection during aerial surveys. Even with fixed-wing aerial telemetry over large study areas, detection probability may still downwardly bias dispersal observations, and we encourage future studies to incorporate tests to estimate detection probability into their study designs. The false-positive event detection model employed here could be easily extended to other datasets involving imperfectly detected animal emigration events, such as the movement behavior of birds at migration stopover locations. While the miniaturization of robust global positioning system loggers and transmitters may eventually solve the quandary of lost long-distance dispersers, for many species—including the vast majority of birds—our ability to track where individuals

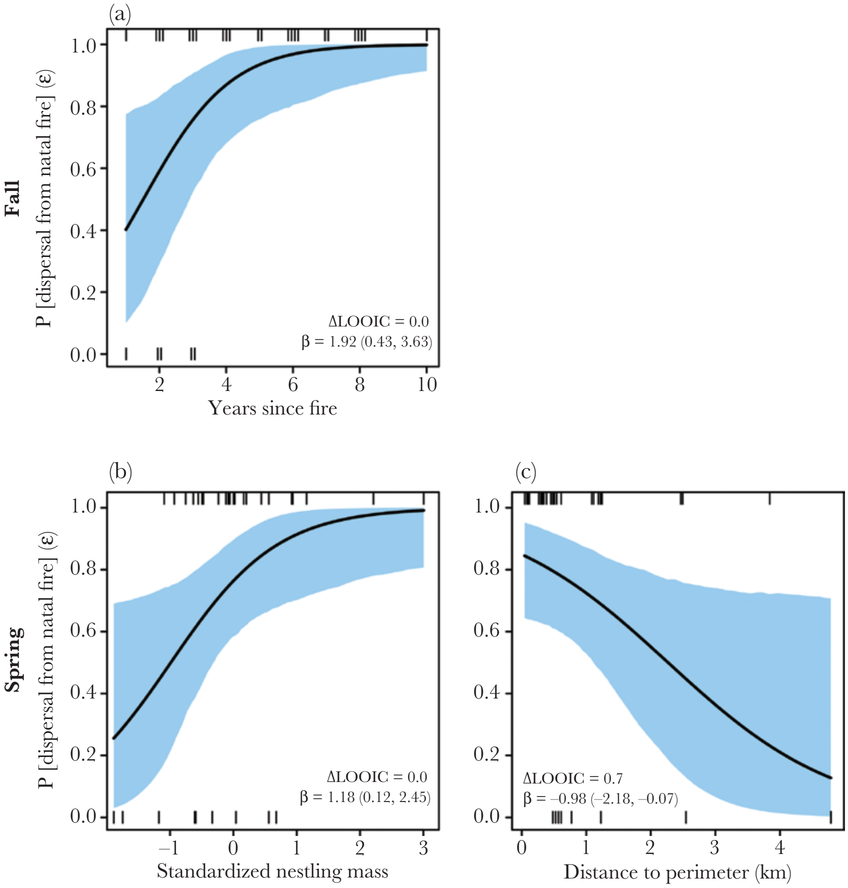

Figure 4

Modeled relationships showing the results of strongly supported model(s) for (a) the probability of a juvenile black-backed woodpecker dispersing away from its natal fire area in the fall, and (b, c) the probability of settling outside the natal fire area in the spring, accounting for false positives. Data rugs show naïve occurrence, where 0 = within natal fire, and 1 = outside of natal fire (jittered to enhance visibility). ΔLOOIC values give the difference between each model and the model with the lowest LOOIC, and slope estimates are shown with 95% credible intervals.

have dispersed remains limited by where we can physically search for signals.

Our study used lightweight VHF transmitters to track woodpecker movements, but the high amount of search effort required per tagged bird resulted in sample sizes that limited our analysis to univariate models. This precluded our ability to test for potential interactions between variables. In addition, we were unable to test for potential social influences on dispersal such as population density or intruder pressure, which likely play a role in the emigration and patch colonization process (Clobert et al. 2009; Kesler et al. 2010). The complex process of dispersal in this system likely responds to multiple drivers, and additional study—perhaps facilitated by future advances in tracking technology—is warranted to decompose the complex interactions between dispersal and resource availability, population density, and fire regimes.

Long-distance movement and environmental effects on dispersal

Black-backed woodpecker dispersal distances measured in this study (median = 18.4 km) exceed typical distances reported from other North American woodpecker species and showed evidence for a "fat-tailed" dispersal kernel after correcting for detection bias. In comparison, a long-term study of red-cockaded woodpeckers (*Leuconotopicus borealis*) — cooperatively breeding fire-associated species—documented median natal dispersal distances from 2.9 to 3.3 km (Kesler et al. 2010). Natal dispersal distances for pair-breeding resident red-bellied woodpeckers (*Melanerpes carolinus*) ranged from 1.1 to 5.0 km (*n* = 18) in central Missouri, USA (Cox and Kesler 2012a). Although not directly tied to natal movements, some seed-eating birds in boreal North America are known to respond to spatiotemporal fluctuations in annual food availability across larger scales (e.g., 100s of km) via facultative migration (Koenig and Knops 2001; Newton 2012). While our study focused on natal dispersal movements in response to localized resource pulses, black-backed woodpeckers—particularly in eastern North America—may also engage in long-distance irruptive movements beyond normal range limits (Yunick 1985; Rota et al. 2015).

Theoretical work has demonstrated that dispersal can increase metapopulation persistence through increased couplings between disparate patches (Johst et al. 2002), suggesting that inter-patch distances between burned forests may be a selective force driving the evolution of high dispersal capacity in black-backed woodpeckers, and potentially other spatially structured populations. In addition, landscape permeability between patches can have strong effects on dispersal distance (Ricketts 2001). Forested regions of the western United States have recently exhibited increased tree mortality due to drought and bark beetle outbreaks (Preisler et al. 2017), which may increase the permeability of unburned forests for dispersing

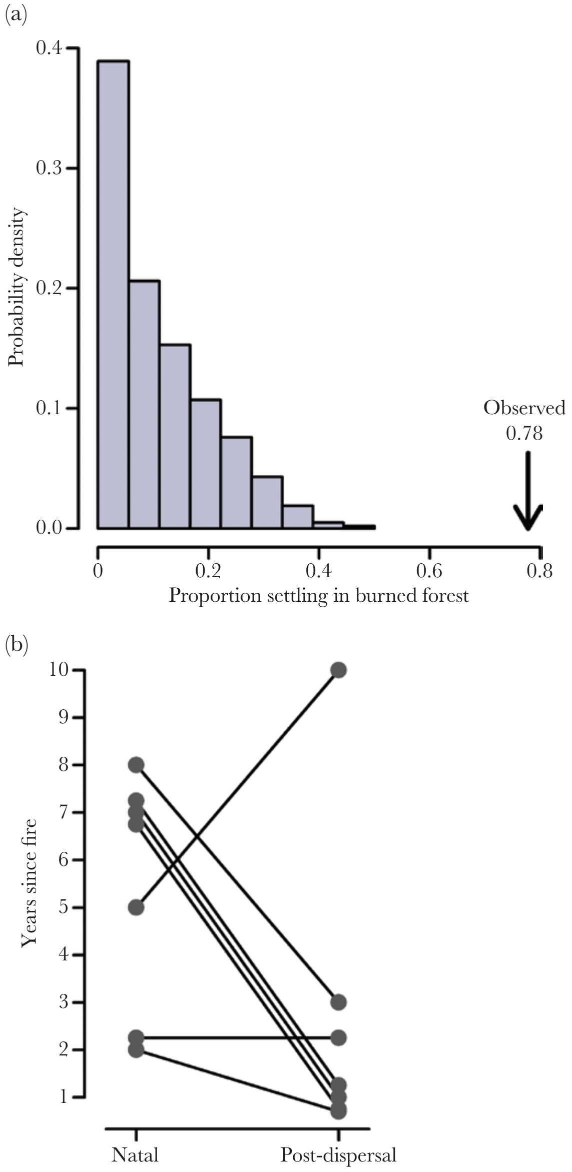

Figure 5
Simulated and observed data showing black-backed woodpecker selection for newly burned forests during natal dispersal. The histogram in (a) shows the number of expected individuals settling in burned forest from a simulation analysis under a null model assumption with no directional selection for burned forest. These values are compared to the observed data, where 14 of 18 birds settled in burned forest. Panel (b) compares years since fire between natal and post-dispersal habitat for birds that dispersed out of the natal fire area and settled in a different burned area (n = 7). Years since fire values are jittered on the y-axis to enhance visibility.

black-backed woodpeckers. Although patches of beetle-killed forest can host breeding pairs (Fogg et al. 2014; Tingley et al. 2020), our results indicate that burn-to-burn dispersal is a frequent occurrence when burned patches are available. An important caveat, however, is that the relative rarity of nests in unburned forests in our study region prevented us from studying dispersal behavior of juveniles in unburned areas, and the dispersal patterns for these individuals are currently unknown. The potential role of disturbance dynamics on dispersal behavior also highlights the importance of forest management actions that modify burned and unburned forests, as these actions could have potential effects on metapopulation dynamics, the cost of interpatch movements, and the spatial genetic structure of species tracking post-fire resources (Pierson et al. 2013).

Our results show evidence for condition-dependent dispersal strategies in response to temporal changes in habitat quality as post-fire resources decline in the years following fire. Increasing emigration rates in older post-fire forests likely reflect the process of resource pulse attenuation as snags decay and food availability declines (Grayson et al. 2019; Ray et al. 2019). Although greater years since fire increased the probability of juveniles emigrating in the fall, it did not have a strong effect on whether a juvenile settled within the natal fire area in the following spring. This counterintuitive result may stem from the availability of recently burned forests on the landscape—if juveniles do not find suitable breeding areas during fall dispersal, they may return to their natal fire area. We observed this particular behavior several times in our dataset, including one individual that dispersed from a 10-year-old fire area into an unburned matrix with low availability of new fires, only to return to its natal fire area by the following spring (Figure 1c).

In addition to individuals seeking out non-natal burned forest, juveniles that dispersed from one post-fire patch to another predominantly selected areas that had burned more recently than their natal patch (Figure 5b). This apparent selection for "greener pastures"—which deserves to be secondarily validated with larger sample sizes—raises questions about how individuals may integrate information about habitat quality while moving across the landscape. If black-backed woodpeckers selectively search for higher-quality burned patches as they disperse, then an even greater mystery is how they might find such patches. Given that natal dispersal generally occurs during the active fire season in our study regions (Tingley et al. 2018), it is possible that juveniles could use olfactory cues—in addition to other non-exclusive mechanisms such as conspecific attraction or natal imprinting—to find very recently burned forests or even forest fires in progress. Indeed, anecdotal observations in the course of this study suggest that juveniles may actively orient toward new fires—we observed two tagged individuals that emigrated from an old fire area to a new prescribed fire 10 km away, arriving within 3 weeks of the burn.

Relationship between body mass and dispersal

Body mass is sometimes expected to have a negative relationship with dispersal in resource-limited systems because smaller, competitively inferior individuals are excluded from high-quality habitats close to the natal site (Bowler and Benton 2005; but see Delgado et al. 2010; Waters et al. 2013,). For example, in more social species, delaying dispersal or settling in more familiar habitat may confer long-term fitness benefits (Stacey and Ligon 1991). We found the opposite pattern in the pair-breeding black-backed woodpecker, where individuals with higher nestling body mass dispersed farther and were more likely to settle outside of the natal fire area. The reversal of this common pattern may be due to the location of "high-quality" habitat relative to natal territories. The fitness benefits of seeking a new resource patch may outweigh the benefits of remaining in a familiar patch with waning resources, particularly for juveniles in older fires. If, in a constantly attenuating, resource-pulse situation, the "high-quality" habitat frequently exists outside the natal patch, then the phenomenon observed here could arise. Larger individuals, which have more reserves for energetically costly dispersal, may gain a fitness advantage if they are capable of immigrating into a more recent burn (Bonte et al. 2012).

Moreover, the potential interaction between time, habitat quality, and parental experience yields an intriguing hypothesis. In contrast to movement-prone juveniles, adult black-backed woodpeckers are generally site-faithful (Rota 2013), and older post-fire forests tend to have older adults, which can live up to at least 8 years (Siegel et al. 2016). Given that adult breeding experience generally correlates with growth and survival of young (Perrins 1970), we predict that nestlings in older fires may have higher body mass than nestlings from young parents in newer fires, despite the general decline in available high-quality habitat within these older fires. If true, this causal chain suggests that older fires may produce larger juveniles that are physiologically predisposed to disperse from the natal patch in response to other proximate factors like territory competition or resource availability. Indeed, we found a weak, positive correlation ($r = 0.30$, $P = 0.07$) between time since fire and nestling mass in our dataset, lending preliminary evidence to support this hypothesis. A similar hypothesis is that young black-backed woodpeckers from older fires may be predisposed to disperse via maternal effects. This phenomenon has been documented in the dispersal polymorphism of western bluebirds (*Sialia mexicana*), where breeding females adjust egg-laying order in a way that leads to dispersal-prone, aggressive male offspring when resources are scarce (Duckworth 2009). While this hypothesis warrants further investigation, we note that our study did not detect any relationships between juvenile sex and dispersal behavior.

Population dynamics and resource pulses

Local population trajectories in black-backed woodpeckers track the pulse and decline of post-fire resources, but the mechanisms underlying these dynamics have remained elusive (Tingley et al. 2018). Previous research has shown limited effects of years since fire on nest survival, juvenile survival, adult survival, and adult breeding dispersal (Rota 2013; Rota et al. 2015; Stillman et al. 2019a; Stillman et al. 2021a). Our results suggest that natal dispersal may be the primary mechanism driving the local population dynamics of this resource pulse specialist. Adult breeding dispersal, in contrast, may remain relatively rare due to the high costs of dispersal or the fitness benefit of breeding in familiar habitat (Bonte et al. 2012; Cox and Kesler 2012b; Rota 2013). We hypothesize that rapid post-fire colonization can be largely attributed to relatively long-distance, directed movements by juveniles dispersing from older burns nearby, although some colonizers may also originate from nearby unburned forest. Initial increases in woodpecker density in early post-fire years may stem from juvenile recruitment and continued colonization, while decreases in density > 5 years post-fire may reflect increased juvenile emigration rates as resources wane and competition for resources increases. Similar dynamics are likely at play in other resource pulse specialists, where natal dispersal behavior may allow specialists to locate and colonize new resource pulses while also tracking local declines in resources through conditional emigration (Holt 2008; Yang et al. 2008). Consistent with predictions from theory (Johst et al. 2002; Reigada et al. 2015), our empirical results suggest that changes in the spatial distribution of resources can shape dispersal patterns, which in turn may help explain the long-term persistence of spatially structured populations in ephemeral habitat mosaics.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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