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Research Paper

Bias-corrected natal dispersal estimates fill information gaps for White-headed Woodpecker conservation

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ABSTRACT. Although the White-headed Woodpecker (*Dryobates albolarvatus*) has been used as a management indicator species to guide forest management in the western U.S., basic information on the dispersal behavior of this species is currently unavailable. However, understanding dispersal can provide key information for management and conservation by revealing the mechanisms by which species colonize new areas and restored habitat. To address this information gap, we tracked the dispersal of juvenile White-headed Woodpeckers from their natal areas to their first spring home range in 2014–2018 and estimated dispersal distances using an interval-censored bias correction method with field observations and aerial telemetry surveys. We also compared habitat features between dispersal locations and spring home ranges. The median bias-corrected dispersal distance was 22.2 km in the fall (95% confidence interval [CI] = 16.4, 29.1 km), with 90% of woodpeckers dispersing >4.8 km (95% CI = 2.7, 8.3 km). The following spring, the median bias-corrected natal dispersal distance was 24.6 km (95% CI = 17.9, 32.3 km), while 10 individuals with full detection histories dispersed a median of 7.7 km to their first breeding locations (range 1.2–23.0 km). Our natal dispersal estimates for juvenile White-headed Woodpeckers were longer than those for most other woodpecker species studied to date. In addition, we found that woodpeckers settled in mid-elevation areas with greater variation in canopy cover compared to dispersal locations. There was no difference in ponderosa pine (*Pinus ponderosa*) basal area between dispersal tracks and spring home ranges. White-headed Woodpeckers are a species of conservation concern due to habitat loss in western North America, and active management in Washington state seeks to restore overstocked ponderosa pine forests to pre-settlement tree densities which could benefit this woodpecker. Our results inform conservation and forest management efforts by suggesting that dispersing juveniles have the capacity to travel long distances to colonize restored forests.

Distances de dispersion natale corrigées du biais comblant les lacunes en matière d'information pour la conservation du Pic à tête blanche

RÉSUMÉ. Bien que le Pic à tête blanche (*Dryobates albolarvatus*) ait été utilisé comme espèce indicatrice pour guider l'aménagement forestier dans l'ouest des États-Unis, des informations de base sur le comportement de dispersion de cette espèce manquent à l'heure actuelle. Toutefois, la compréhension de la dispersion peut fournir des informations clés pour l'aménagement et la conservation en révélant les mécanismes par lesquels les espèces colonisent de nouveaux endroits et milieux restaurés. Pour combler ce manque d'informations, nous avons suivi la dispersion de jeunes Pics à tête blanche depuis leur région natale jusqu'à leur premier domaine vital au printemps de 2014 à 2018 et calculé les distances de dispersion à l'aide d'une méthode de correction des biais par intervalle de relevés, ainsi que d'observations sur le terrain et de relevés télémétriques aériens. Nous avons aussi comparé les caractéristiques de l'habitat entre les lieux de dispersion et les domaines vitaux de printemps. La distance médiane de dispersion natale corrigée du biais était de 22,2 km à l'automne (intervalle de confiance à 95 % [IC] = 16,4; 29,1 km), 90 % des pics se dispersant >4,8 km (IC à 95 % = 2,7; 8,3 km). Au printemps suivant, la distance médiane de dispersion corrigée du biais était de 24,6 km (IC 95 % = 17,9; 32,3 km), tandis que 10 individus ayant un historique de détection complet se sont dispersés sur une distance médiane de 7,7 km de leur premier site de nidification (valeurs s'échelonnant de 1,2 à 23,0 km). Les distances de dispersion natale calculées pour les jeunes Pics à tête blanche étaient plus longues que celles obtenues pour la plupart des autres espèces de pics étudiées à ce jour. De plus, nous avons constaté que les pics s'installaient dans des zones de moyenne altitude dont le couvert végétal était plus varié par rapport aux lieux de dispersion. Il n'y avait pas de différence dans la surface terrière du pin ponderosa (*Pinus ponderosa*) entre les corridors de dispersion et les domaines vitaux de printemps. Le Pic à tête blanche est une espèce dont la conservation est préoccupante en raison de la perte d'habitat dans l'ouest de l'Amérique du Nord; l'aménagement actif préconisé par l'État de Washington vise à restaurer les forêts de pins ponderosa très denses, à des densités d'arbres antérieures à la colonisation pouvant être bénéfique pour ce pic. Nos résultats renseignent les efforts de conservation et d'aménagement forestier en révélant que les jeunes en dispersion ont la capacité de parcourir de longues distances pour coloniser les forêts restaurées.

Key Words: *Dryobates albolarvatus; movement; Pinus ponderosa; ponderosa pine; post-dispersal settlement; telemetry*

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INTRODUCTION

Dispersal is a key ecological process that drives gene flow and provides a mechanism for populations to colonize new or restored habitats (Nathan 2001, Ronce 2007). Dispersal also reduces competition from conspecifics and kin, thereby reducing inbreeding, and allows for species to expand their range to unoccupied or higher quality landscapes (Clobert et al. 2001, Bowler and Benton 2005). The costs of dispersal include increased energy expenditure from long-distance movements, as well as exposure to predators in novel habitats. In highly fragmented habitats, dispersing individuals may have a lower probability of successfully locating mates and suitable areas to breed because they are naïve about local conditions (Conner and Rudolph 1991, Bonte et al. 2012). Some species reduce the risks of dispersal by engaging in short-distance forays prior to dispersing, enabling them to make more informed decisions during dispersal (Williams and Rabenold 2005). Overall, effective dispersal strategies are under strong selective pressure, and the dispersal capabilities of individuals are a major factor determining the range and distributional limits of species (Clobert et al. 2001).

Understanding species' dispersal patterns and the mechanisms driving dispersal behavior can provide important conservation insights, although this information can be difficult to obtain (Nathan 2001). Given that external factors, such as resource availability and habitat configuration, can have strong effects on dispersal (Clobert et al. 2001, Bowler and Benton 2005), managers have the opportunity to identify and target key landscape parameters that influence habitat connectivity and population persistence. In some cases, information on the factors that affect dispersal movements has meant the difference between success and failure of conservation efforts. For example, models of the dispersal ecology of the endangered Red-cockaded Woodpecker (*Dryobates borealis*) have shown that habitat fragmentation leads to longer dispersal distances, a lower probability of population persistence, and ultimately a downward spiral resulting in local extirpation (Schiegg et al. 2002). An understanding of dispersal behavior is frequently a glaring information gap when determining priorities for landscape-level conservation initiatives, establishing protected area networks, or updating conservation plans for single species (Walters 2000, Nathan et al. 2008).

The White-headed Woodpecker (*Dryobates albolarvatus*) is a species of conservation concern that has been used to guide landscape-level management goals (e.g., U.S. Fish and Wildlife Service 2021) and it is a focal species for the eastern slope of the Cascade Mountains conservation strategy (Altman 2000). The White-headed Woodpecker occurs in dry, pine-dominated conifer forests of western North America (Kozma et al. 2020), where it provides cavities for secondary-cavity nesting species (Kozma 2014). In the northern part of its range, it is used as an indicator species for the restoration of ponderosa pine (*Pinus ponderosa*) forests (Gaines et al. 2007). Concerns over White-headed Woodpecker population declines due to habitat loss (e.g., fire suppression resulting in forests with high densities of small diameter trees and forest management practices that remove snags [i.e., dead trees] or large diameter trees) have prompted research on this species (Kozma et al. 2020), but information on dispersal behavior is currently limited to a few anecdotal observations (Lorenz 2016, Kozma et al. 2020). For example, a color-banded male White-headed Woodpecker was observed 35.1 km from its natal territory where it was banded the previous summer (Kozma et al. 2020). Information on dispersal movements and potential barriers to gene flow are, therefore, unavailable to guide conservation efforts for the White-headed Woodpecker, particularly in the context of forest restoration efforts and disturbance impacts. For these reasons, a better understanding of White-headed Woodpecker dispersal ecology was highlighted as a priority research need (Kozma et al. 2020).

Despite the value of understanding dispersal, it remains largely unstudied in many at-risk species due to technological limitations that hinder long-distance tracking of small animals - particularly birds (Walters 2000, Nathan et al. 2008). However, recent advancements in radio telemetry have allowed for extended battery life of lightweight transmitters suitable for tracking individual movements over the annual cycle. To aid conservation efforts for the White-headed Woodpecker, we conducted a study of natal dispersal (i.e., movement of juveniles away from the natal area) using radio-tags with an extended battery life >1 yr combined with ground and aerial telemetry. White-headed Woodpeckers are nonmigratory and breeding dispersal appears rare (Lorenz 2016, Kozma et al. 2022a), lending support to the hypothesis that effective gene flow in this species is enabled primarily by young woodpeckers dispersing in their first year of life (Kozma et al. 2020).

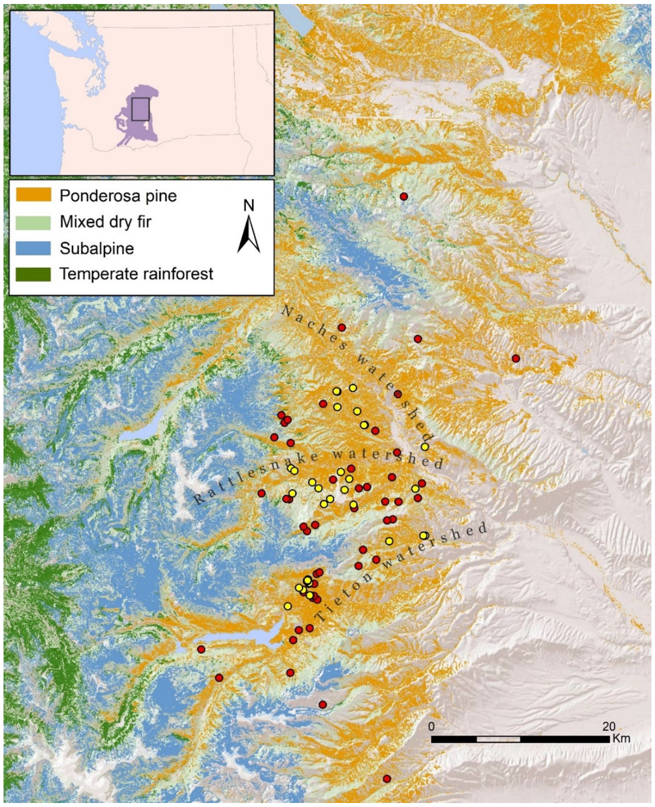
Our objectives were to quantify bias-corrected distributions of movement distances for juvenile White-headed Woodpeckers during two key periods of natal dispersal: (1) movements during the first fall after leaving natal territories, and (2) total natal dispersal between the natal nest site and the first breeding attempt the following spring. Natal dispersal has been poorly studied in North American woodpeckers, with only four species having robust dispersal distance estimates. Juvenile Red-bellied Woodpeckers (*Melanerpes carolinus*) and Acorn Woodpeckers (*M. formicivorus*) were found to disperse <10 km from their natal areas (Cox and Kesler 2012, Koenig et al. 2000), Red-cockaded Woodpecker juveniles dispersed a median distance <4 km (Kesler et al. 2010), and juvenile Black-backed Woodpeckers (*Picoides arcticus*) were found to disperse a median distance of 18 km (Stillman et al. 2022b). Based on these juvenile dispersal estimates from other woodpecker species, we predicted that juvenile White-headed Woodpeckers would disperse <10 km on average, especially if potential breeding sites are continuous on the landscape. Last, we tested for differences in forest characteristics and elevation between telemetry locations along the dispersal track and the locations of spring home ranges. Our hypothesis was that dispersing White-headed Woodpeckers cue in on habitat conditions when selecting where to settle, evidenced by differences in forest conditions between dispersal locations and spring home ranges. Given the importance of ponderosa pine for White-headed Woodpeckers in Washington (Kozma et al. 2020), we predicted that dispersing birds would settle in areas with greater ponderosa pine basal area compared to dispersal locations. Alternatively, support for the null hypothesis (i.e., no difference) would suggest that the birds either (1) show similarly strong selection for ponderosa pine habitat while dispersing across the landscape and while settling on breeding territories or (2) were selecting for a fine-scale habitat feature within ponderosa pine forest that we did not measure. We predicted that woodpeckers would settle in areas with greater variation in canopy cover, which may indicate areas with recent disturbance (e.g., timber harvest, prescribed fire, or wildfire) that have been shown to be important components of White-headed Woodpecker habitat (Lorenz et al. 2015b, Latif et al. 2015, 2020). A better understanding of White-headed Woodpecker dispersal behavior will aid forest managers in determining the ability of this species to colonize areas where dry forest restoration has occurred.

METHODS

Data collection

We studied White-headed Woodpecker juvenile dispersal in the Yakima River watershed of the Cascade Range, central Washington, USA (46.816° and -121.054°; Fig. 1). The study area is bounded on the west by the Cascade Crest and on the east by the non-forested shrub steppe zone of the Columbia Basin. Forest composition varied based on aspect, slope, elevation, and longitudinal distance from the Cascade Crest. In the eastern half of our study area, ponderosa pine was dominant or codominant in forests between 600 and 1500 meters above sea level (m a.s.l.). The western half of our study area was wetter and higher in elevation, with increasing amounts of Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*) in the dry mixed-fir zone, and followed by high-elevation subalpine forest containing lodgepole pine (*Pinus contorta*), subalpine fir (*A. lasiocarpa*), and mountain hemlock (*Tsuga mertensiana*) toward the Cascade Crest (Fig. 1). Small portions of temperate rainforest containing western hemlock (*T. heterophylla*), silver fir (*A. alba*), and Douglas-fir occurred mostly on the west side of the Cascade Crest. Most of the study area is public land managed for multiple uses, such as timber production, grazing, and recreation. We estimated that with the exception of designated wilderness areas, the entire area was harvested for timber at least once after 1950, based on U.S. Forest Service timber harvest activity reports and Washington State Department of Natural Resources forest practice applications. Most harvests were described as either complete or partial removal of the entire mature overstory. We estimated that 10% of our study area had been burned with mixed-severity prescribed fire or wildfire within 10–15 yr of the start of this study, and portions were actively grazed by domestic sheep and cattle in summer and fall.

Fig. 1. Study area in the Washington Cascade Range, showing locations of natal sites for all juvenile White-headed Woodpeckers (*Dryobates albolarvatus*; yellow dots) and their last fall locations (red dots), for both interval censored and uncensored individuals, central Washington, 2014–2018. Unshaded areas on the eastern portion of this map are non-habitat. Inset map shows location of this study area in central Washington (black box) and purple shading is the area we searched for woodpeckers from the air.



We used radio telemetry to monitor juvenile White-headed Woodpecker dispersal from 2014 to 2018. We searched for active nests using playbacks of calls and drumming to locate adult birds and then followed adults until we located their nest cavities. We considered nests occupied if we heard or saw nestlings or if adult behavior, such as adults remaining in the cavity for extended periods or returning to the cavity with food, indicated that incubation or nestling feeding was underway. We tagged nestling woodpeckers 1–2 days before the estimated fledging date in late June or early July. We used the hole saw method (Ibarzabal and Tremblay 2006) to open cavities and randomly chose 1–4 nestlings (i.e., the typical brood size; Kozma and Kroll 2012) from each brood to affix with a programmable 1.0 to 2.0 g VHF transmitter (Model A1005, Advanced Telemetry Systems [ATS], Islanti, Minnesota, USA and Model CTx Ag 392, Lotek Wireless, Newmarket, Ontario, Canada). The number of nestlings that received a transmitter from each brood depended on the number of available transmitters. We used an elastic leg-loop harness (Rappole and Tipton 1991) that stretched to accommodate different sizes of nestlings. All transmitters used in this study weighed <3% of average body mass (61.1 g; Kozma et al. 2020, Fair et al. 2010). The ATS and Lotek transmitters resulted in different amounts of data collected each year. In 2014, we used refurbished ATS transmitters in which the batteries died that October or November. In 2015, we used newly purchased Lotek transmitters with a programmable on/off calendar schedule that transmitted from May to November and then again from April to June. In 2016 and 2017, we deployed Lotek transmitters that we recovered, refurbished with new batteries, and these transmitters operated continuously for up to 13 months. We coated transmitters in a thin layer of quick-dry epoxy as added protection against mechanical wear and damage. We noted the sex of each juvenile, determined by the extent of red feathering on the head, before returning them to their nests and there were no mortalities or injuries from our trapping or tagging. All juveniles retained their transmitter until fledging. This research was conducted in compliance with the Guidelines to the Use of

Wild Birds in Research and birds were handled under Federal Bird Banding permit #24061. This project was approved under the U.S. Forest Service, Institutional Animal Care and Use Committee permit #2016-007.

We began radio tracking juveniles within 1–2 days of fledging and tracked them every 1–3 days until they became independent of parents. We defined the date of “independence” from parents as three days after the final observation of juveniles begging for food from a parent, where the added three days accounted for potential missed observations of begging. We obtained point locations by homing to individuals until we observed the bird and then tracked each individual as continuously as possible for 20–60 minutes to gather multiple locations per bird. We alternated the order in which birds were tracked each day to reduce temporal bias.

To document natal dispersal behavior, we tracked juveniles every 3–7 days after independence until snowfall prevented us from tracking (i.e., early November). In 2015–2018, we resumed tracking in March or April to record spring movements when snowmelt permitted access to field sites. We searched for tagged juveniles by driving forest roads with vehicle-mounted antennas and via fixed-wing aircraft with wing-mounted antennas. We searched for juveniles using aircraft, that we were unable to locate while driving, starting at the location each individual was last detected and moving outward from that location in concentric circles or belt transects. For juveniles that remained missing after one or two searches, we continued to monitor their signals daily from the ground with scanner receivers or from aircraft. We conducted 25 fall flights and 10 spring flights; most of which lasted 3–6 h and covered ~2500 km². Aerial tracking was necessary to locate most dispersing woodpeckers and most dispersal movements were detected with airplanes (estimated at >90%).

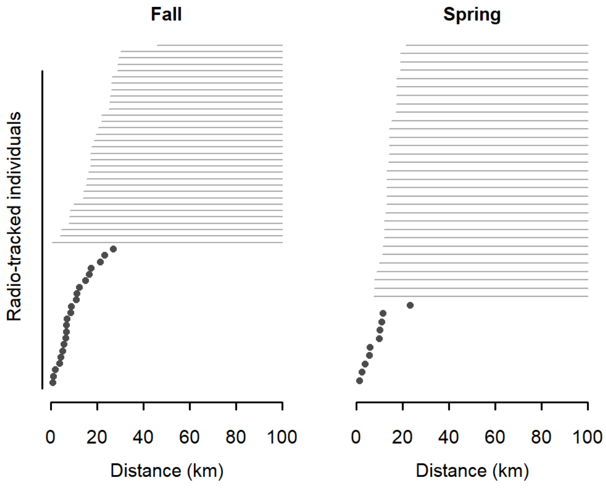
We conducted two test flights to estimate the probability of detecting woodpeckers from the air. We placed five to six radio transmitters at random locations in our search area and then provided 10 possible frequencies (the average number of birds we tracked per flight) for an experienced pilot/tracker team to scan for from the air. The team then flew a survey route without knowing the number or locations of deployed transmitters. After completing the test flights, we estimated a detection probability of 0.82 after one flight and 0.95 after two flights.

Statistical analysis

Estimating dispersal distances

We estimated the fall distance from natal site as the straight-line distance between the natal site and the last known location in fall. We estimated the spring distance from natal site as the straight-line distance between the natal site and the first recorded nesting tree. Thus, this value represents a total estimate of natal dispersal in the first year of life. If no spring nesting site was found, we used the centroid of the spring tracking locations. Despite our large search area, the distribution of fully observed dispersal tracks is likely subject to downward bias, a common issue when some dispersers go undetected due to long-distance movements outside the study area (Koenig et al. 2000). To counter some of this bias, we applied a bias-correct method that incorporated information from individuals with incomplete detection histories using interval-censored data (Paradis et al. 2002, Stillman et al. 2022b). Rather than omitting individuals with partial information, this approach allows these individuals to inform the dispersal kernel by calculating a probable distance interval for each bird (Fig. 2). This method provides benefits over conventional area-ratio corrections, which require that binned dispersal distances have frequencies greater than one in the range of observed values (Baker et al. 1995, Cooper et al. 2008). Thus, the assumptions of area-ratio corrections may be inappropriate for telemetry studies with relatively small sample sizes where, as in our study, dispersers likely traveled farther than the maximum observed distance. While a downward bias in dispersal distances is typical for naïve estimates from telemetry studies, we also note that undetected transmitter failure could potentially introduce an upward bias when using interval censored methods. We found that reinforcing transmitters with an epoxy coat greatly improved transmitter recovery from predated birds, even when transmitters were stowed in tree cavities or buried underground. We assume that transmitter battery failure was low because transmitters continued to function well beyond the data collection period for each bird.

Fig. 2. Cumulative distributions of distances from natal sites for individual juvenile White-headed Woodpeckers (*Dryobates albolarvatus*) in fall (left) and spring (right), central Washington, 2014–2018. Points indicate woodpeckers with known final dispersal locations. Horizontal lines show the distance band within which censored (i.e., missing final location) birds most likely settled.



In order to estimate a dispersal interval for birds with missing observations, we first estimated an individual-level minimum dispersal distance using the approach of Stillman et al. (2022b). For each bird that disappeared from the study area, we calculated the distance between the natal site and the nearest pixel within a reasonable elevation band that was not surveyed by aerial telemetry (Stillman et al. 2022b). We used an inclusive elevation band of 600-1800 m a.s.l., bounded on the lower end by the distribution of forested habitat and on the higher end by the highest ridge within the search area. For individuals with some dispersal locations, but who were eventually lost during dispersal, we computed the distance from the natal site to the farthest point tracked. Next, we used the higher of these two values as the minimum dispersal distance in our interval-censored dataset. Similar to Stillman et al. (2022b), we used 100 km as the maximum bound of dispersal distances to capture the vast majority of dispersal movements while also allowing for outlier cases based on reports of rare movements >100 km in related species (e.g., Yunick 1985, Rusk et al. 2013).

We were not able to track juveniles continuously from the time they left their natal territories in the fall until they settled in an area the following spring. Thus, we considered fall and spring distances from the natal site separately in our analysis. We fit four distributions to our interval censored dispersal data using the *fitdistrplus* package (Delignette-Muller and Dutang 2015) in R version 4.3.1 (R Core Team 2023): Weibull, lognormal, Half-Cauchy, and normal distributions. We compared support for these distributions using Akaike's Information Criterion and estimated parameters using maximum likelihood approaches.

Habitat use during dispersal

We tested the hypothesis that dispersing White-headed Woodpeckers cue in on habitat conditions when selecting where to settle, evidenced by differences in forest conditions between dispersal locations and spring home ranges. For 10 individuals with complete dispersal tracks, we considered tracking points to represent actively dispersing birds when three conditions were satisfied. First, the point must occur outside of the natal home range, which we approximated using a circular 176 ha buffer around natal nest locations. This buffer represents the mean 95% kernel density home range for 23 tagged juveniles in this study with at least 20 tracking points prior to independence (mean home range = 176.3 ha). Area observation curves indicated that home range size reached an asymptote after 20 locations. Second, the point must occur before May 1, which is the approximate time of year that many woodpeckers in our study settled onto breeding territories. Third, for each individual we excluded all tracking points that fell within a 500 m buffer around the 95% kernel density estimate of tracking points after May 1. This approach omitted tracking points on or near home ranges when assigning dispersal status.

We extracted four forest measurements from dispersal locations at the coordinates of observed birds: basal area of ponderosa pine, conifer quadratic mean diameter, conifer canopy cover, and the standard deviation of canopy cover within a 100-m buffer of tracking locations (30-m resolution; Landscape Ecology Modeling, Mapping, and Analysis Team 2020). These variables represented our *a priori* hypotheses about the factors affecting post-dispersal settlement based on published studies of White-headed Woodpecker habitat selection (Hollenbeck et al. 2011, Latif et al. 2015, 2020). We used variation in canopy cover as a proxy for recent fire or other disturbances (and therefore snag availability) because seamless spatial data on disturbance history and snag availability were not available for this area.

We extracted the same four forest measurements from the spring home range area by randomly sampling 50 points from a 125 ha buffer around the "final" spring location. Here, the buffer represented the average spring home range from a previous study of 35 radio-tracked individuals (Lorenz et al. 2015b), and the final spring location represented either the nest site (for breeders) or the centroid of spring locations (for nonbreeders confirmed alive). We compared dispersal and spring home range (i.e., post-dispersal) points using a generalized linear mixed effects model to estimate the parameters of the exponential resource selection function. We modeled the probability of a given point coming from the dispersal track ($y = 0$; $n = 212$) versus the spring home range ($y = 1$; $n = 500$) as a function of ponderosa pine basal area, conifer quadratic mean diameter, conifer canopy cover, variation in canopy cover, and a quadratic effect of elevation. The model only used data for 10 birds with complete dispersal tracks, and we included a random intercept for each individual. We fit the model in a Bayesian framework using STAN (Carpenter et al. 2017) called via the *rstanarm* R package (Goodrich et al. 2020). The model used slightly regularized, vague prior distributions on all parameters following default recommendations. We ran three chains for 2000 iterations with a warmup of 1000, and we assessed model convergence using the potential scale reduction factor (Rhat) and the number of effective samples. Parameters estimated from frequentist models are presented ± their 95% confidence intervals (CI), and empirical Bayesian parameter estimates are presented ± their 95% Bayesian credible intervals (BCI).

RESULTS

We tagged 83 juvenile woodpeckers from 2014 to 2017 and we included data from 54 of them that survived to independence to calculate dispersal estimates (Table 1; Fig. 2). We excluded all 13 birds from the 2014 cohort from estimates of spring distance from natal site because their transmitter batteries died during the fall. The average age at independence was 31.4 days (range 16-45 days) and the average date of independence from parents was July 31 ± 8.5 days (mean ± SD). The earliest date of independence was July 9, with all juveniles independent by August 15.

Table 1. Parameter estimates, Akaike's Information Criterion (AIC), and the difference in AIC (compared to the top-ranked model) for four distributions fit to data on White-headed Woodpecker (*Dryobates albolarvatus*) natal dispersal (km) in fall and spring in central Washington, 2014–2018. Dispersal distributions were fit to a combination of fully observed and interval-censored dispersal measurements.

Distribution	Parameter estimate (± SE)	AIC	ΔAIC
Fall distances from natal sites (n = 54)			
Weibull	Shape: 1.23 ± 0.15 Scale: 29.94 ± 4.25	210.3	0
Lognormal	Meanlog: 2.91 ± 0.16 SDlog: 1.11 ± 0.11	221.6	11.3
Normal	Mean: 24.40 ± 2.97 SD: 15.79 ± 2.60	223.8	13.5
Half-Cauchy	Sigma: 21.05 ± 4.02	224.7	14.4
Spring distances from natal sites (n = 41)			
Weibull	Shape: 1.49 ± 0.24 Scale: 31.41 ± 5.76	102.8	0
Lognormal	Meanlog: 22.26 ± 3.51 SD: 11.28 ± 2.84	105.9	3.1
Normal	Mean: 3.03 ± 0.17 SDlog: 0.92 ± 0.11	111.3	8.5
Half-Cauchy	Sigma: 24.08 ± 5.25	118.1	15.3

For 43 juveniles with tracking locations, median distance between natal site and known dispersal location in their first July was 3.0 km (range 1.1–8.9 km, $n_{\text{observed}} = 14$). Dispersal distances increased through the fall, with a median of 5.1 km (range 1.1–23.2 km, $n_{\text{observed}} = 43$) at the end of August, 8.1 km (range 1.3–47.1 km, $n_{\text{observed}} = 35$) at the end of September, and 11.0 km (range 2.0–26.7 km, $n_{\text{observed}} = 20$) at the end of October. The sample size of dispersing woodpeckers increased between July and August as more individuals became independent and began dispersing. The number of missing birds more than doubled from August (n = 11) to October (n = 26).

Dispersal distances

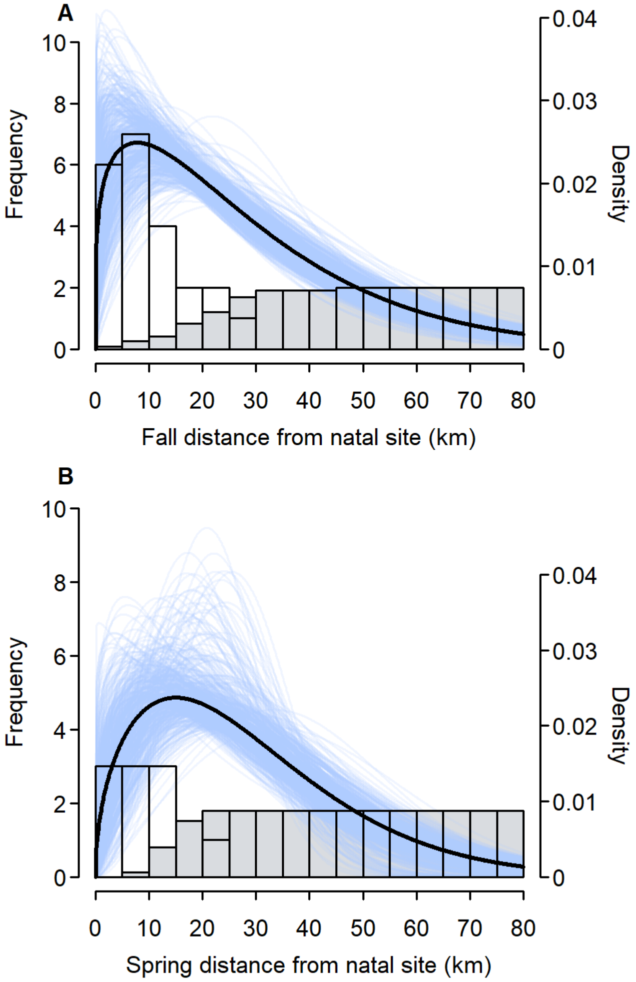
Among the 20 woodpeckers we tracked to their final fall location, the median distance between their natal nest and their final fall location in October was 11.0 km, but this estimate omits birds with partial dispersal tracks, some of which dispersed farther before evading detection or leaving the search area (e.g., one male dispersed 47.2 km by October 3). The Weibull distribution received the highest support for fall distance from natal site using interval-censored data from all 54 woodpeckers (Table 1; Fig. 3). Using this distribution, we predicted that in the fall, 50% of woodpeckers dispersed at least 22.2 km (95% CI = 16.4, 29.1 km) from their natal site (Table 2). The bias-corrected Weibull distribution predicted that 90% of woodpeckers dispersed at least 4.8 km (95% CI = 2.7, 8.3 km) and 5% dispersed at least 72.9 km (95% CI = 55.7, 86.2 km).

In spring, we tracked 10 woodpeckers to a nest site or spring home range, and the median observed dispersal distance from natal areas was 7.7 km (range 1.2–23.0 km). When incorporating additional data from 19 woodpeckers with interval-censored data, the Weibull distribution showed the strongest support (Table 1; Fig. 3). Based on the Weibull distribution, we estimated that 50% of woodpeckers dispersed at least 24.6 km (95% CI = 17.9, 32.3 km) from their natal site by spring of their first breeding season (Table 2) and 90% of woodpeckers dispersed at least 7.0 km (95% CI = 3.9, 12.7 km). The long tail of this distribution indicated that, under the assumption of a Weibull dispersal kernel, up to 5% of birds may disperse distances over 65.5 km from the nest.

Relationship between dispersal and forest type

We found evidence that White-headed Woodpeckers select forest types during natal dispersal, which are similar to their breeding habitats, but they also cue in on nuanced heterogeneity in forest cover when selecting where to first breed. The standard deviation of canopy cover was higher within spring home ranges compared to tracking locations along the dispersal path. However, the other forest characteristics that we measured (i.e., ponderosa pine basal area, conifer quadratic mean diameter, and canopy cover) did not show differences between dispersal and spring home range locations (Table 3, Fig. 4). We also found a strong quadratic effect of elevation, suggesting that dispersing woodpeckers use areas at higher and lower elevations compared to the mid-elevation territories where they eventually settle (Table 3, Fig. 4). The model R^2 was 0.11 (95% BCI = 0.06, 0.16).

Fig. 3. Distributions for (A) distance from the natal site in fall (n = 54) and (B) natal dispersal distance, measured as the distance between the natal site and the first breeding attempt in spring (n = 41), for juvenile White-headed Woodpeckers (*Dryobates albolarvatus*), central Washington, 2014–2018. The frequencies of known dispersal distances are shown with white bars, and the frequencies of interval censored dispersal distances are shown with gray bars. The solid bold line shows probability density for the best-supported Weibull distribution, and thin blue lines show potential variability of Weibull parameter estimates based on 500 bootstrapped simulations.



DISCUSSION

A basic understanding of dispersal distances can fill important information gaps for conservation efforts, yet many challenges remain when measuring dispersal behavior (Koenig et al. 2000). In this study, we radio-tracked dispersing juvenile White-headed Woodpeckers and estimated the bias-corrected distribution of natal dispersal distances in the fall and spring following fledging and independence from adults. Estimated dispersal distances were much greater than we predicted based on past studies of North

Table 2. Estimates of the minimum distance (with 95% confidence interval) juvenile White-headed Woodpeckers (*Dryobates albolarvatus*) dispersed in central Washington by their first fall and spring, 2014–2018. Quantiles are based on a Weibull distribution fit to the combination of fully-observed and interval-censored dispersal data. Estimates for the first spring represent total natal dispersal from fledging to first breeding attempt.

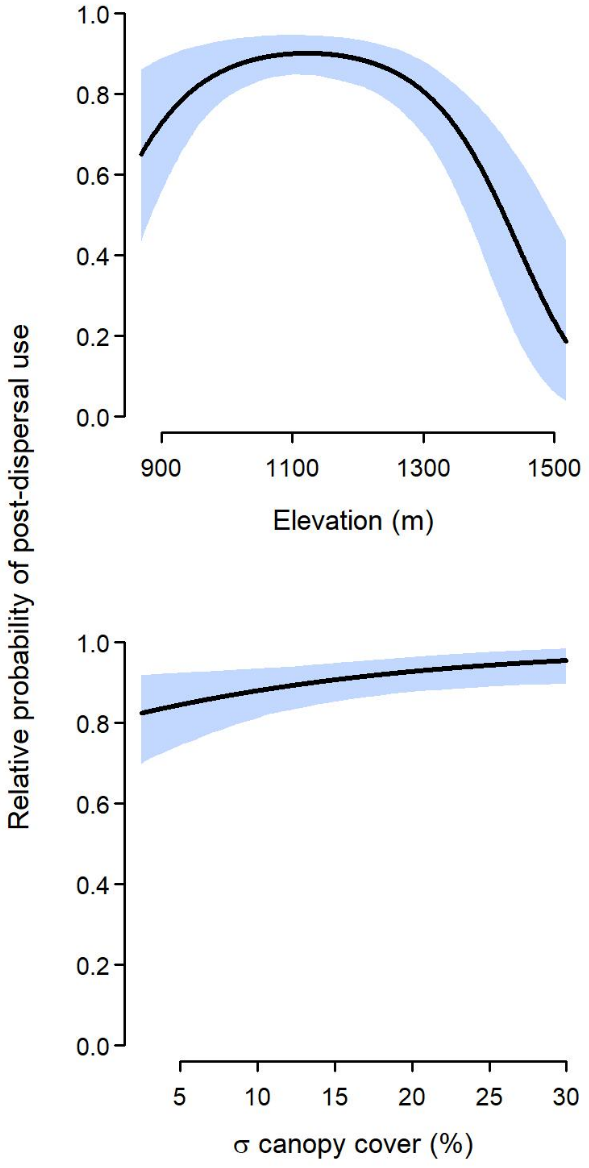
Minimum percentage of dispersed woodpeckers	Distance (in km) in the first fall (95% CI)	Distance (in km) in the first spring (95% CI)
5%	72.9 (55.7, 86.2)	65.5 (40.0, 76.0)
10%	58.9 (45.7, 69.3)	54.9 (35.4, 64.2)
50%	22.2 (16.4, 29.1)	24.6 (17.9, 32.3)
75%	10.9 (7.1, 16.2)	13.6 (8.9, 20.3)
90%	4.8 (2.7, 8.3)	7.0 (3.9, 12.7)

Table 3. Parameter estimates from a model comparing habitat use between dispersal locations and post-dispersal home range locations for juvenile White-headed Woodpeckers (*Dryobates albolarvatus*) in central Washington (n = 621 locations). For linear predictors, positive estimates indicate that a habitat characteristic is more likely to occur within the spring home range versus during dispersal. Covariate effects with 95% Bayesian credible intervals (BCI) that do not cross zero are highlighted in bold.

Covariate	Estimate (95% BCI)
Intercept	2.22 (1.67, 2.82)
Elevation	-0.21 (-0.65, 0.13)
Elevation^2	**-0.58 (-0.83, -0.34)**
Basal area of ponderosa pine	0.04 (-0.19, 0.28)
Conifer canopy cover	-0.15 (-0.38, 0.09)
σ canopy cover	**0.28 (0.04, 0.52)**
Conifer quadratic mean diameter	-0.11 (-0.19, 0.28)

American woodpecker species, which generally disperse <10 km from natal sites. We estimated that 50% of the juvenile woodpeckers we tracked dispersed at least 24.6 km from their natal territory to their first breeding site the following spring. In comparison, studies of Red-cockaded and Red-bellied woodpeckers show that a portion of juveniles do not leave the natal territory or opt for an adjacent territory (Daniels and Walters 2000, Cox and Kesler 2012), which contrasts sharply with White-headed Woodpeckers where all juveniles left the natal territory and dispersed at least 2 km. Median natal dispersal distances were less than 5 km in the cooperatively-breeding Red-cockaded Woodpecker, although dispersal behaviors in this species are strongly affected by social breeding structure and the availability of cavity trees (Walters et al. 1988, Kesler et al. 2010). Similar to White-headed Woodpeckers, Northern Flickers (*Colaptes auratus*) in British Columbia exhibited relatively low local recruitment rates (<4%) with anecdotal evidence for long dispersal distances over 100 km (Wiebe 2020).

Fig. 4. Compared to locations along the natal dispersal path, White-headed Woodpeckers (*Dryobates albolarvatus*) tended to settle at medium elevations and in areas with greater heterogeneity in canopy cover. Bold solid lines and shaded areas show the mean and 95% Bayesian credible interval describing the relationship between each variable and the probability of using a habitat type after settling versus during dispersal (n = 621 locations).



Contrary to our predictions, we did not find evidence that larger trees, higher canopy cover, or higher ponderosa pine basal area increased the probability of settling. Rather, our results suggest that birds exhibit similar selection for forest type while dispersing compared to breeding, but they tend to establish breeding territories in mid-elevation areas with higher variation in canopy cover. White-headed Woodpeckers in our study area may avoid breeding in the lowest and highest elevation areas due to lower availability of ponderosa pine, which becomes sporadic at low elevations and at higher elevations is replaced by other conifer species. In addition, birds may be responding to different prescribed fire and disturbance regimes at different elevations. In support of this, woodpeckers selected areas with higher variation in canopy cover, which may reflect increased heterogeneity in forest structure from disturbances, such as mixed-severity fire, variable density thinning, or tree mortality from insects and disease. These areas are often characterized by patches of higher snag abundance, which provide nest sites, adjacent to live forest used for foraging (Stillman et al. 2022a). Similar habitat mosaics have been shown to be important for nesting by White-headed Woodpeckers in Washington, Oregon, and Idaho (Latif et al. 2015, Lorenz et al. 2015b, Miller-ter Kuile et al. 2023).

The juvenile dispersal distances we observed are similar to those documented by Stillman et al. (2022b) for juvenile Black-backed Woodpeckers in fire-prone forests of California. Stillman et al. (2022b) found that juvenile Black-backed Woodpeckers dispersed a median of 18 km and exhibited conditional dispersal strategies, where juveniles search widely for burned forest and leave natal burns when resources become scarce. However, Black-backed Woodpeckers are closely associated with recently burned forests (Hutto 2008, Stillman et al. 2019a, Tingley et al. 2020), whereas White-headed Woodpeckers more readily occupy unburned forest (Kozma et al. 2020). The long natal dispersal distances we observed may initially seem puzzling because our study area contained extensive tracts of ponderosa pine forest, which contrasts with the disjunct, rare availability of recently burned forests for Black-backed Woodpeckers. However, our results suggest that White-headed Woodpecker habitat quality is not defined simply by the presence of ponderosa pine, or by the availability of large trees. Rather, this species appears to select ponderosa pine forests with greater canopy cover heterogeneity (e.g., containing canopy gaps or openings created by disturbance) near to closed-canopy forests that provide foraging habitat (Latif et al. 2015, Lorenz et al. 2015b, Latif et al. 2020). These habitat associations draw parallels to Black-backed Woodpeckers, which select heterogeneous (i.e., "pyrodiverse") forest stands after fire with adjacent patches of live and dead trees (Stillman et al. 2019b, Stillman et al. 2023). Similar to Black-backed Woodpeckers, the limited availability of high-quality breeding habitats for White-headed Woodpeckers may be associated with long natal dispersal distances to seek breeding territories. In addition, social factors may also lead to long natal dispersal when high-quality habitats are rare. For example, White-headed Woodpeckers in our study may have dispersed over potential breeding habitat because these areas were already occupied by territorial individuals.

Recent studies have concluded that dispersal is a multistage process influenced by multiple internal and external factors, such as social status, sex, body condition, age, genetic predisposition, food availability, landscape configuration, population density, and predation pressure (Bowler and Benton 2005, Nathan et al. 2008, Robles et al. 2022). A multistage dispersal process could explain the dispersal movements we observed in both fall and spring. For example, movements throughout fall may have occurred if woodpeckers initially settled in areas with abundant food but little or no access to roosting cavities (Kozma et al. 2020). Additional movements in the spring could be explained by some birds moving from their fall territories in search of higher snag densities for nesting. In order to excavate a nest cavity, woodpeckers require snags that have the proper decay characteristics (Schepps et al. 1999, Kozma et al. 2022b). Because few snags in our study area are properly decayed for cavity excavation at any given time (Lorenz et al. 2015a), White-headed Woodpeckers may select areas to settle in that have a higher abundance of snags. In support of this, Lorenz et al. (2015b) found White-headed Woodpecker breeding territories in this area occurred disproportionately in areas with small burned forest patches that contain high snag densities adjacent to larger areas of intact forest. If some or all of these habitat components were patchily distributed on the landscape, this could account for the long dispersal distances we observed.

Study limitations

Because we employed a conservative procedure when interval-censoring partially observed dispersal tracks, the bias-corrected distances reported in this study may have a downward bias (e.g., median distance could be biased low). We used the best technology available at the time of this study, but future advances in tracking technology hold promise for more certain dispersal estimates in the future, particularly for birds that move long distances. Furthermore, we acquired the best dispersal information for juveniles in the center of our study area, near their natal areas, and in areas we visited on a daily basis. We focused search effort within 10 km of natal areas, but aerial telemetry flights covered an area of ~ 2500 km². Based on our findings, we recommend that future studies should design their methods to maximize aerial search effort as much as possible, coupled with improved tracking technology (Koenig et al. 2000, Cooper et al. 2008).

Management implications

We found evidence for relatively long-distance natal dispersal in juvenile White-headed Woodpeckers, indicating that juvenile White-headed Woodpeckers are capable of moving extensive distances to find areas in which to settle. While it is encouraging that this species is mobile enough to navigate a large landscape (e.g., Trakhtenbrot et al. 2005), the long dispersal distances we observed suggest that high-quality and unoccupied habitat for White-headed Woodpeckers may be patchily distributed in our study area. Our results also show that White-headed Woodpeckers settle in areas with high variation in canopy cover, suggesting that disturbances and forest gaps are important for the species, not just ponderosa pine basal area per se. Ponderosa pine plantations, which have high basal area but low heterogeneity, may support dispersing individuals but may not be high-quality areas to settle. At the regional scale, homogeneous stands of ponderosa pine could still assist with landscape connectivity between suitable patches even though they are not selected for nesting. Future restoration projects to improve habitat for White-headed Woodpeckers should focus on creating areas with abundant snags, promoting heterogeneity in canopy cover, and avoiding large, homogenous, even-spaced stands. Land managers should be encouraged by our results because dispersing juvenile White-headed Woodpeckers have the capacity to travel long distances to colonize restored ponderosa pine forests while maintaining genetic connectivity across a larger, spatially structured population. New data and novel approaches to understand the dispersal strategies of at-risk species, including the ability for these species to colonize restored habitats, will prove a fruitful avenue for future research.

Author Contributions:

T.J.L. and P.C.F. conceived the idea, design, and experiment; T.J. L. and P.C.F collected data and conducted the research; T.J.L., J. M.K, and A.N.S. wrote the paper; and A.N.S. and T.J.L. developed the methods and analyzed the data.

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