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Is green the new black? Black-backed Woodpecker vital rates do not differ between unburned and burned forests within a pyrodiverse landscape

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ABSTRACT

Woodpeckers often reflect rapid changes to forest health and serve as indicator species to help guide forest management decisions. The Black-backed Woodpecker (*Picoides arcticus*) is known for its strong association with recently burned forests and is a species of conservation concern due to habitat loss stemming from post-fire management of burned forest. Several studies have found the Black-backed Woodpecker occupying extensive areas of unburned (i.e., green) forests in the western part of its range during the breeding season, raising questions about whether green forests can support viable nesting populations in this region. We studied breeding Black-backed Woodpeckers in southern Oregon, USA to evaluate whether 2 vital rates critical to population recruitment—nest survival and post-fledging survival—differed between green and burned forests. During 2018, 2019, and 2021, we monitored 91 Black-backed Woodpecker nests (*n* = 34 in green forest, *n* = 57 in burned forest) and found that neither daily nest survival rate nor reproductive output (i.e., the number of fledglings per successful nest) differed between nests located in green and burned forest; however, nestling body condition was slightly enhanced in green forest. We also quantified survival of recently fledged individuals using VHF radio telemetry and found that the survival rate of birds in green forest was nearly identical to those in burned forest, with most mortalities occurring within 4 weeks of fledging. Our results indicate that Black-backed Woodpeckers in green forests were equally successful at breeding as conspecifics in recently burned forest, although densities of nesting pairs in green forest were lower than those in burned forest. Our findings indicate certain types of green forest, particularly mature lodgepole pine, can support viable populations of the Black-backed Woodpecker in the western portion of its range. This finding has conservation implications given that green forest occupies much of the forested landscape in this region and is often juxtaposed to areas subjected to high severity fire. Therefore, practices that promote pyrodiversity—landscape-level spatial and temporal variability in fire effects—as well as connectivity between green and burned forest within fire-prone landscapes are likely to provide the greatest conservation benefit for this species.

Keywords: Black-backed Woodpecker, nest survival, *Picoides arcticus*, post-fledging survival, unburned forest, wildfire

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LAY SUMMARY

- The Black-backed Woodpecker (*Picoides arcticus*) is typically found breeding within recently burned forests in the western United States.
- Two recent studies found this species in unburned, green forests during the breeding season, suggesting such forests might hold self-sustaining populations.
- Our research found that two components of breeding success—nest survival and the survival of young after fledging from the nest—did not differ between birds nesting in green forests and burned forests of southern Oregon, USA.
- Our results indicate that certain green forests, such as mature lodgepole pine, are suitable areas for Black-backed Woodpeckers to rear offspring, and they may play an important role for conservation efforts aimed at maintaining Black-backed Woodpecker populations in the western portion of its range.

¿Es verde el nuevo negro? Las tasas vitales de *Picoides arcticus* no difieren entre bosques quemados y no quemados dentro de un paisaje pirodiverso

RESUMEN

Los pájaros carpinteros a menudo reflejan cambios rápidos en la salud del bosque y sirven como especies indicadoras para ayudar a guiar las decisiones de manejo forestal. La especie *Picoides arcticus* es conocida por su fuerte asociación con los bosques recientemente quemados y es de interés para la conservación debido a la pérdida de hábitat derivada del manejo de los bosques quemados después de

los incendios. Varios estudios han encontrado que *P. arcticus* ocupa extensas áreas de bosques no quemados (i.e., verdes) en la parte occidental de su área de distribución durante la temporada reproductiva, lo que genera dudas sobre si los bosques verdes pueden albergar poblaciones de anidación viables en esta región. Estudiamos la reproducción de *P. arcticus* en el sur de Oregón, EEUU, para evaluar si dos índices vitales críticos para el reclutamiento poblacional (supervivencia del nido y supervivencia posterior al emplumamiento) diferían entre los bosques verdes y los quemados. Durante 2018, 2019 y 2021, monitoreamos 91 nidos de *P. arcticus* (*n* = 34 en bosque verde, *n* = 57 en bosque quemado) y encontramos que ni la tasa de supervivencia diaria del nido ni el rendimiento reproductivo (i.e., el número de volantones por nido exitoso) difirió entre nidos ubicados en bosque verde y quemado; sin embargo, la condición corporal de los polluelos mejoró ligeramente en el bosque verde. También cuantificamos la supervivencia de individuos recién emplumados utilizando radio-telemetría VHF y encontramos que la tasa de supervivencia de las aves en el bosque verde fue casi idéntica a la de los bosques quemados, con la mayoría de las muertes ocurriendo dentro de las cuatro semanas del emplumamiento. Nuestros resultados indican que los individuos de *P. arcticus* en bosques verdes tuvieron el mismo éxito en la reproducción que sus congéneres en bosques quemados recientemente, aunque las densidades de parejas anidando en bosques verdes fueron menores que en bosques quemados. Nuestros hallazgos indican que ciertos tipos de bosques verdes, particularmente los pinos maduros de *Pinus contorta*, pueden sustentar poblaciones viables de *P. arcticus* en la parte occidental de su área de distribución. Este hallazgo tiene implicaciones para la conservación dado que el bosque verde ocupa gran parte del paisaje boscoso en esta región y, a menudo, se yuxtapone a áreas sujetas a incendios de alta severidad. Por lo tanto, las prácticas que promueven la pirodiversidad (variabilidad espacial y temporal a nivel del paisaje en los efectos del fuego), así como la conectividad entre el bosque verde y el quemado dentro de los paisajes propensos a incendios, probablemente proporcionen el mayor beneficio de conservación para esta especie.

Palabras clave: bosque no quemado, Carpintero de Espalda Negra, incendio forestal, *Picoides arcticus*, supervivencia del nido, supervivencia posterior al emplumamiento

INTRODUCTION

Species in the family Picidae—the woodpeckers—exhibit population responses to large-scale disturbances and forest management activities, making them a key group for detecting rapid changes to forest health (Drever and Martin 2010). Woodpeckers are particularly important within forest ecosystems because they can exert a disproportional influence on the ecological communities in which they occur (Virkkala 2006). Indeed, members of this group have been considered "double keystone species" in north temperate regions because they produce cavities used by other species for nesting and/or roosting, and their activities can provide access to otherwise inaccessible food resources that benefit a range of organisms (Martin and Eadie 1999, van der Hoek et al. 2017). For example, in the Pacific Northwest region of North America, 67 species of vertebrates have been documented using cavities created by woodpeckers, with 30% of these secondary cavity nesters being designated "at risk" or "potentially at risk" (Bunnell 2013). Because of their positive influence on other species, woodpeckers serve as reliable surrogates for the health of the broader ecological communities in which they are embedded (Mikusinski et al. 2001, Drever et al. 2008) and are often used as indicator species to help guide forest management decisions (Gaines et al. 2007, Tremblay et al. 2015a).

In the western United States, wildfires have increased in their extent and intensity in recent decades (Westerling et al. 2006, Dennison et al. 2014), and they are projected to increase in the future despite constraints on fuel (Flannigan et al. 2013, Abatzoglou et al. 2021). With high-severity wildfire comes the creation of ephemeral and dynamic resource pulses, such as the dead and dying trees that are used as both nesting and foraging structures by woodpeckers (Tingley et al. 2018, Ray et al. 2019). Because of their association with forest health, woodpeckers are often mentioned in the debate regarding alternative approaches for managing forests within pyrodiverse landscapes (i.e., areas that contain spatial and/or temporal variability in fire effects; Jones and Tingley 2021), including post-fire management activities such as salvage logging (Hanson and North 2008). The Black-backed Woodpecker (*Picoides arcticus*) has been featured prominently in this discussion because it has long been considered a species that requires severely burned conifer forest for population persistence (Hutto 1995, Saab et al. 2007, 2009; Hutto 2008, Tremblay et al. 2020). Research on Black-backed

Woodpeckers in recently burned forests has found that nest survival decreases with time since fire (Saab et al. 2007, Nappi and Drapeau 2009), resulting in management guidelines for this species that are aimed largely at conserving areas that have recently experienced moderate- to high-severity wildfire (Hutto 2008). Because conservation of such areas can come into conflict with post-fire forest management, this has led to concerns about the long-term viability of this species (Hanson and North 2008) that resulted in a petition for listing of the Oregon-Cascades/California population under the federal Endangered Species Act (USFWS 2017).

Despite clear evidence that Black-backed Woodpeckers use recently burned conifer forests for nesting, two recent studies have raised questions regarding the degree to which this species is restricted to breeding in burned areas in the western part of its range (Fogg et al. 2014, Verschuyl et al. 2021) and whether unburned (hereafter "green") forest can support viable breeding populations. Both Fogg et al. (2014) and Verschuyl et al. (2021) recorded Black-backed Woodpeckers using green forests extensively during the breeding season in the western United States (northern California: Fogg et al. 2014; southern Oregon: Verschuyl et al. 2021), even when burned areas were available on the broader landscape. In addition, both studies found evidence of nesting in green forest, although they reported nesting densities that were lower than what is typically found within recently burned areas (Fogg et al. 2014, Verschuyl et al. 2021). Taken together, these findings expand upon previous investigations that have found the Black-backed Woodpecker nesting in green forest in other parts of its range, including the boreal forest of eastern Canada (Tremblay et al. 2009, 2015b) and in ponderosa pine (*Pinus ponderosa*) forest of the Black Hills, South Dakota, USA, following mountain pine beetle (*Dendroctonus ponderosae*) outbreaks (Bonnot et al. 2008, Rota et al. 2014, Matseur et al. 2018). These studies further suggest that green forests may support productive nesting Black-backed Woodpecker populations in the western part of its range, which is contrary to the notion that green forests act as population sinks for this species (Hutto 1995). Whether this is the case remains unclear, as information about the productivity and habitat selection of Black-backed Woodpeckers nesting in green forests of the western United States is lacking despite the suggestion that green forests may be critical for regional population persistence in other regions (Tremblay et al. 2009,

2015b). Thus, a major research need is to assess the extent to which Black-backed Woodpecker vital rates differ between green forests and recently burned areas and determine the extent to which green forests can support successful Black-backed Woodpecker populations within dry conifer forests of the western United States (Tremblay et al. 2020). Because green forest can vary widely in its structure and composition, evaluating the extent to which different types of green forest are used by Black-backed Woodpeckers for successful nesting presents an additional knowledge gap.

In this study, our goal was to quantify Black-backed Woodpecker nest survival and post-fledging survival—two vital rates that underpin population recruitment—and evaluate the extent to which they differed between green and burned forests in fire-prone landscapes in the western portion of its range. We did this by focusing on the two forest types in which woodpeckers were regularly found nesting in our study area within the Klamath Basin of southern Oregon: unburned lodgepole pine (*Pinus contorta*) forest and conifer forests experiencing recent, high severity fire (see Results). Before experiencing more than 100 yr of fire suppression (Hagmann et al. 2019), this area was a historically pyrodiverse and frequently burned landscape, and it now experiences large, high-severity wildfires such as the 167,000-ha Bootleg Fire that burned during summer 2021. In our study, we compared measures of nest survival, reproductive output (i.e., the number of fledglings per successful nest), nestling body condition, and post-fledging survival between green and burned forest to test several hypotheses. Previous work has found that nest predators of cavity-nesting species are more abundant in closed-canopy forests (Rota et al. 2014, Squires and Reynolds 2020) and recently burned forest typically has abundant food resources (McCullough et al. 1998, Powell 2000, Saint-Germain et al. 2004, Nappi et al. 2010). Therefore, we hypothesized that Black-backed Woodpeckers nesting in green forest would have lower nest survival and decreased reproductive output than those nesting in burned forests. Because habitat quality can influence nest survival and reproductive output in woodpeckers (Wiebe 2001, Nappi and Drapeau 2009, Tremblay et al. 2014), we also hypothesized that nest-site characteristics would mediate nest survival and reproductive output in both forest types. Additionally, due to the increased food availability (Powell 2000, Ray et al. 2019) and higher offspring provisioning rates by Black-backed Woodpeckers in burned forest relative to green forest (Tremblay et al. 2016), we also hypothesized that nestlings reared in green forests would have lower body condition measures when compared to conspecifics reared in burned forests. Finally, recent work has found that fledgling Black-backed Woodpeckers were 4× more likely to survive in unburned and low- to moderate-severity burned areas when compared to areas subjected to high-severity fire, a pattern thought to be due to the greater vegetative cover in green forests (Stillman et al. 2021). Therefore, we hypothesized that juveniles reared in green forest would have greater post-fledging survival than individuals reared in burned forest.

METHODS

Study Area

We studied Black-backed Woodpeckers during the 2018, 2019, and 2021 breeding seasons (May–August) within a ~165,000-ha study area in the Klamath Basin of southern Oregon covering public lands that included the Klamath, Coquille, and Chemult Ranger Districts of the Fremont-Winema National Forest, the Diamond Lake Ranger District on the Umpqua National Forest, and the Sun Pass State Forest (Figure 1). Our study sites ranged from 1,280 to 1,950 meters above sea level (m.a.s.l.) in forests comprised of stands characterized by lodgepole pine, ponderosa pine, mixed conifer, and mixed pine. We defined mixed conifer stands as those containing white fir (*Abies concolor*), red fir (*Abies magnifica*), grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and/or mountain hemlock (*Tsuga mertensiana*), and mixed pine stands as those containing lodgepole pine, ponderosa pine, western white pine (*Pinus monticola*), and/or sugar pine (*Pinus lambertiana*). Lower elevation sites were typically drier and characterized by increased abundance of lodgepole pine on coarse pumice soils, whereas higher elevations had more moisture and harbored more ponderosa pine, mixed pine, and mixed conifer (Hagmann et al. 2019). Historically, this region experienced frequent, widespread wildfire accompanied by low mortality rates of trees, with fire return intervals averaging 13 yr (range: 7–25 yr) until fire exclusion began in approximately 1918 (Hagmann et al. 2019). Average temperatures during the Black-backed Woodpecker breeding season in our study area averaged 10–12°C with a range of –6°C (2018) to 34°C (2021), with precipitation ranging from 30 mm (2021) to 224 mm (2019) (SNOTEL weather station, Sun Pass, Oregon, 1,646 m.a.s.l.). Contemporary forest management in our study area is conducted in collaboration with the Klamath Tribes with the goals of reducing hazardous fuel loads, improving habitat quality for species of conservation interest, and undertaking sustainable timber production that enhances older age classes of ponderosa pine (Charnley et al. 2017). Nearly all harvesting operations on the Fremont–Winema National Forest portion of our study area take place via thinning of trees between 18 and 76 cm diameter at breast height (DBH) depending on the species and averaging ~4,200 ha treated annually (Charnley et al. 2017). On the Sun Pass State Forest, group selection harvests of 0.2–2 ha are implemented with a target of 14,000–28,000 m^3 yr^{-1} and lodgepole pine is clearcut in 8.1–20.2 ha sized blocks on 80-yr rotations (Charnley et al. 2017).

Nest Searching and Monitoring

During each year of the study, we searched for Black-backed Woodpecker nests starting the first week of May and continuing until mid-July. To cover the range of green forest used by Black-backed Woodpeckers in the broader landscape, we targeted our searches to green forest that was classified as 1 of the 4 composition types described above (i.e., lodgepole pine, ponderosa pine, mixed conifer, and mixed pine) and contained potential nest trees of a minimum of 15-cm DBH (Verschuyl et al. 2021). The green forest areas we nest-searched were generally absent of major disturbance, differentiating our study from prior research in green forest dominated by beetle-killed trees (Bonnot et al. 2008, Rota et al. 2014, Matseur et al. 2018, Tingley et al. 2020). We also searched for nests in recently burned conifer forest in areas that were interspersed with green forest throughout our focal landscape (Figure 1), including the 2017 North Pelican Fire (1,452 ha), the 2017 Blanket Creek Fire (13,484 ha), the
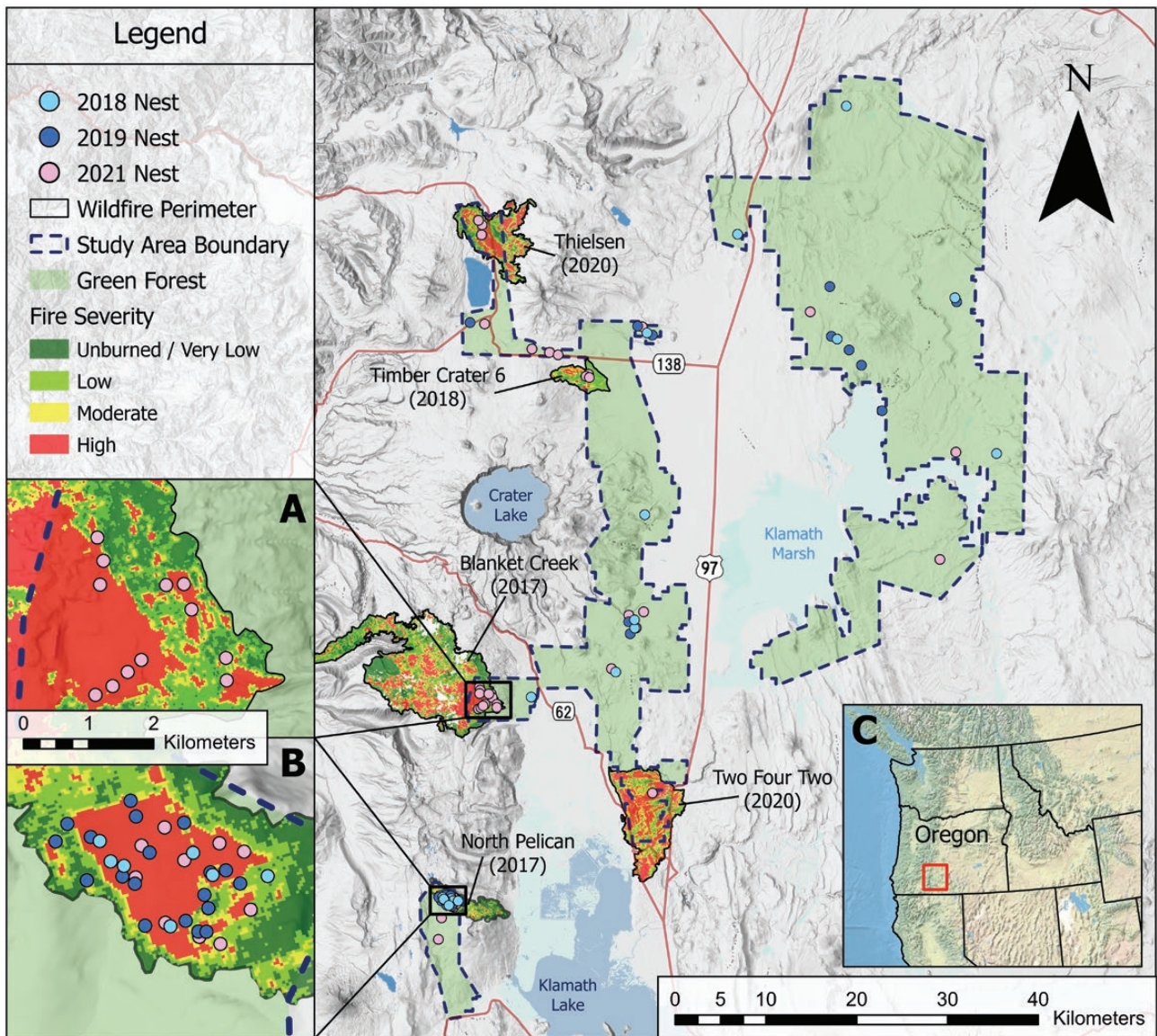
FIGURE 1. The ~165,000-ha study area in which Black-backed Woodpecker vital rates were assessed during the course of this study. Green (unburned) conifer forest where nest-searching occurred is shown in light green; burned conifer forest where nest-searching took place is outlined by solid black lines and illustrated by fire severity categories based on the 4-class Composite Burn Index (Key and Benson 2006, USFS 2022). Nest sites are shown as cyan (2018), dark blue (2019), or pink filled circles (2021). Insets show nest distributions in the (**A**) Blanket Creek Fire and the (**B**) North Pelican Fire, as well as (**C**) the location of the study area relative to Oregon and the Northwestern U.S.

2018 Timber Crater 6 Fire (1,265 ha), the 2020 Thielsen Fire (4,037 ha), and the 2020 Two Four Two Fire (5,857 ha). Our initial nest-searching efforts revealed that (1) Black-backed Woodpecker nests in green forests were most likely to occur in lodgepole pine stands, (2) Black-backed Woodpeckers were most likely to be found nesting in recently burned areas that experienced moderate- to high-severity fire, and (3) Black-backed Woodpecker nesting densities were greater in recently burned forest relative to green forest. To maximize our sample sizes, we therefore undertook greater cumulative search effort in lodgepole pine relative to other green forest types, greater cumulative search effort in moderate- to high-severity burned areas relative to low-severity burned areas, and greater cumulative search effort in green forest relative to burned forest. Importantly, our primary goal was to obtain a representative sample of nests in both green and burned forests, and we have no reason to believe this nest-searching

approach would have resulted in any biases when estimating vital rates. Additionally, we note that although we refer to unburned lodgepole pine forest as "green" forest and forest recently disturbed by high-severity fire as "burned" forest, we recognize these coarse descriptions may not be suitable for characterizing the full spectrum of forest types that the Black-backed Woodpecker may use in other parts of its range (Tremblay et al. 2020).

To locate nests, we used a combination of systematically targeted and opportunistic ground-based surveys dispersed across our study area (Figure 1). Our surveys included passive searches in potential nesting habitat for Black-backed Woodpecker activity, as well as active surveys where we used a game caller (FOXPRO NX4, FOXPRO Inc., Lewistown, PA, USA) to locate territorial individuals by broadcasting vocalizations and drumming sounds recorded in the Pacific Northwest (Macaulay Library of Natural Sounds, Cornell

Laboratory of Ornithology, Ithaca, NY, USA). Our broadcasted recordings were audible to a human observer 500 m distant within open forest (authors, personal observation), so we assumed that woodpeckers could detect recorded vocalizations at least 500 m distant from our broadcasting locations. Once a Black-backed Woodpecker was detected, we followed it for up to 2 hr to determine whether it was paired and showed signs of nesting behavior or appeared to be unpaired and was not nesting. We located nests by following adults to their nest sites, observing adult activity at the nest tree (e.g., excavating, nestling provisioning), or by detecting nesting begging calls emanating from nest trees. After we located nests, we re-visited them approximately every 4 days (range: 1–8 days) to monitor their status and determine their fate. During our visits we visually checked nests using a wireless cavity inspection camera (www.ibwo.org; Little Rock, AR) that was mounted on a telescoping pole and allowed us to view the contents of nest cavities as small as 3.8 cm in diameter and up to 14 m in height; this allowed us to obtain a visual record of the nest contents during the majority of our nest checks (i.e., 84% of n = 728 cumulative visits).

We assigned the nest initiation date to each nest as the day the first egg was laid, either through direct observation or by back-dating using photos of nestlings taken by our inspection camera in known-age nests from our study area. For back-dated nests, we estimated nest initiation date based on the observed number of unique offspring (i.e., eggs or nestlings) observed in the nest together, and we assumed an incubation period of 13 days (Stillman et al. 2019a) that commenced on the day the penultimate egg in the clutch was laid. When clutch sizes were unknown, we assumed a clutch size of 4 eggs, the average clutch size across the Black-backed Woodpecker's geographic range (Tremblay et al. 2020) which was the typical clutch size in our study in nests for which we had complete laying data (authors personal observation). We considered a nest to be successful if it fledged at least one nestling, which was based on observations of tagged fledglings outside of the nest cavity, or nests that were no longer active on the expected fledge date with no signs of predation. We considered unsuccessful nests as those found empty prior to the expected fledge date, had clear evidence of predation (e.g., eggshell fragments), or contained a brood in which all nestlings had died. We calculated reproductive output as the number of young considered to have fledged from each nest based on its individual history.

After nests fledged, we quantified vegetation around nest sites to determine whether nest-site conditions influenced nest survival. We measured nest vegetation in 10-m radius plots centered on each nest tree, and within each plot we counted the number of small (10–30 cm DBH), medium (30–60 cm DBH), and large (>60 cm) live trees and standing dead trees (i.e., snags). We also quantified basal area of all trees and snags using variable-radius plots centered on the nest tree. We quantified additional characteristics of nest trees that included species, DBH, tree height, cavity height (measured from cavity center), cavity orientation, tree decay class (1 = live; 2 = live but declining; 3 = recently dead; 4 = snag with loose bark; 5 = snag with no bark; 6 = broken snag with no bark, top, or branches; or 7 = decomposing snag; Maser et al. 1979), and the average canopy cover taken over the 4 cardinal directions from the base of the nest tree.

Measuring and Tagging Nestlings

When nestlings were ~20 days old (±2 days), we returned to nests to band them, measure their body condition, and, to a subset of the brood, attach a VHF radio telemetry tag to assess post-fledging survival. For nest trees, we deemed safe for climbing, we accessed nest cavities using aluminum sectional ladders that were secured directly to the bole, allowing us to access nest cavities up to 19 m high. For nests that were unsafe for direct climbing, we erected a free-standing 12 m extension ladder that was secured with 4 opposingly anchored static climbing ropes that allowed access to nest cavities (Rohwer 1988). Once at the nest cavity, we used a hole saw to remove a wooden plug from the outside wall of the tree below the cavity entrance to create an access hole that allowed for safe extraction of nestlings (Ibarzabal and Tremblay 2006). Of note, we did not penetrate the inner wall of the cavity with the hole saw; instead, we used a chisel to manually remove the wooden plug that was created by the hole saw to access the nest. Once nestlings were extracted (n = 133), we banded them with an aluminum U.S. Geological Survey leg band and 1–3 colored plastic leg bands (Avinet Research Supplies, Portland, ME, USA) to allow for individual identification after release, and then measured body mass and right tarsus length to calculate an index of size-corrected body condition. Finally, we attached a VHF telemetry tag to a subset of nestlings (n = 69), randomly selecting at least one nestling per brood for tagging that was of sufficient size based on research permit guidelines. To attach tags, we used the leg-loop method of Rappole and Tipton (1991) with beaded elastic cord to allow for flexion, and each individual received either a standard beeper tag (model Ag393, Lotek Wireless, Newmarket, ON) or a similarly constructed tag whose activity periods could be programmed prior to attachment (model CTx Ag393, Lotek Wireless, Newmarket, ON). All tags weighed 2.8%–4.0% of each individual's body mass and were within permit guidelines. After tagging, we immediately returned nestlings to their nest, wrapped the outside edge of the wooden plug with duct tape to account for kerf caused by removal, placed it back into the hole from which it was removed, and then secured it in place with two wood screws. Our nestling removal approach provided a safe and efficient method for removing nestlings from the nest, with no instances of subsequent nest abandonment in our study. Indeed, we documented several instances of nests from which we removed nestlings being used by secondary cavity nesting species in subsequent years, indicating that the cavities retained their integrity and remained suitable for nesting and roosting after being modified (Ibarzabal and Tremblay 2006).

Post-fledging Survival

After we returned nestlings to their nest cavity, we continued to monitor nests until they fledged after which we attempted to relocate radio-tagged individuals using the homing method every 3–5 days until approximately the first week of September. Individuals that survived until the end of our tracking period were 41–84 days old, which extended beyond the period when fledgling Black-backed Woodpeckers become independent from their parents (~35 days; Stillman et al. 2019b). During each relocation, we recorded an individual's status (i.e., alive/dead) and their location using a handheld GPS unit. When individuals were not relocated during a scheduled search, we attempted at least 3 additional relocations in the

vicinity of their last known location, after which we periodically checked for telemetry signals of missing birds throughout the rest of the season. Additionally, we attempted to relocate all missing individuals during mid-August of each year by conducting aerial telemetry flights over the study area using fixed-wing aircraft. If an individual was not detected after ≥3 regular consecutive searches nor during our aerial telemetry searches, we assumed it dispersed from the study area and was therefore right-censored in our analysis, along with individuals known to be alive during their last encounters. We considered a tagged bird to have undergone mortality when we recovered a tag that was severely damaged without a carcass, was tracked to raptor nest or roost site, or was found with considerable quantities of feathers near the tag.

Statistical Analyses

We performed all analyses using the R statistical environment (R Core Team, 2021; v4.1.2). Given our objectives, we constructed 2 separate types of models: (1) design-based models that we initially used to quantify how the 4 primary responses variables we measured (i.e., daily nest survival, reproductive output, body condition, and post-fledging survival) differed between green and burned forests and (2) covariate-based models that we assessed within a model selection framework (Burnham and Anderson 2002) to explore which covariate(s) had the strongest effect on the primary response variables (Rivers et al. 2019). All design-based models were constructed similarly in that they included 1 of the 4 primary response variables with forest type (2 levels: green forest, burned forest) as a fixed effect. For covariate-based models, we tested a priori hypotheses that were based on biological processes (as outlined in Supplementary Material Tables 1–5), and we used the *AICcmodavg* package (Mazerolle 2020) to calculate Akaike's Information Criterion corrected for small sample size (AIC_c) to determine the top model in each candidate set (Burnham and Anderson 2002).

To model daily nest survival, we used the *RMark* (Laake 2013) package to construct logistic exposure models that incorporate exposure time and can account for nests that were discovered at different ages after initiation (Shaffer 2004). For the design-based model for daily nest survival, we constructed a logistic exposure model with forest type as a fixed effect. For the covariate-based models of daily nest survival, we assembled a set of 14 candidate models that included forest type, as well as temporal, nest-tree, and nest-site habitat variables (Supplementary Material Table 1). We did not include nest age in daily nest survival models because predation events were uncommon and occurred throughout both incubation and nestling stages (Supplementary Material Figure 1). To calculate the probability of nest success, we raised the estimated daily survival rate to the 40th power because the Black-backed Woodpecker nestling period is ~40 days (Tremblay et al. 2020).

To model reproductive output, we constructed a general linear model that assumed a Poisson distribution and had forest type (2 levels) as a fixed effect for the design-based model. For the covariate models, we assessed 9 additional models that included forest type and a suite of nest-site and temporal covariates (Supplementary Material Table 2). Because clutch size, egg hatchability (i.e., the proportion of eggs in a clutch that hatched), and nestling survival (i.e., proportion of nestlings that fledged relative to those that hatch) each has the potential to drive differences in nest survival and reproductive

output, we also tested whether these secondary response variables varied between forest type. To do this, we constructed separate general linear models for each response variable with forest type as a fixed effect.

To evaluate nestling body condition, we constructed 2 separate general linear models—one for each sex because of size-based sexual dimorphism (Tremblay et al. 2020)—whereby we log-transformed body mass and regressed it on log-transformed right tarsus length (Labarbera 1989, Jakob et al. 1996, Schrader et al. 2003), with nest identity as a random effect to account for non-independence of nestlings reared in the same nest. We then took the residuals from this regression as size-corrected, unitless measures of body condition that allowed us to compare relative size of individuals against the population mean. As described above, we constructed a general linear model for our design-based model with forest type as a fixed effect. For covariate models, we developed a set of 13 models based on 5 potential covariates (Supplementary Material Table 3) that related to a priori hypotheses, including forest type.

Finally, to assess post-fledging survival we constructed Cox Proportional Hazard (CPH) models (Sara et al. 2012, Fox and Weisberg 2018) using the *survminer* (Kassambara et al. 2021) and *survival* packages (Therneau 2021). For our design-based model, we modeled the number of days of exposure with forest type as a fixed effect; for our covariate models we developed a set of 12 candidate models covering six potential covariates, including forest type (Supplementary Material Table 4). For all CPH models, we included nest identity as a random effect in all models to account for non-independence between tagged fledglings originating from the same nest. Assumptions were upheld for all statistical models.

RESULTS

Across 3 breeding seasons (2018, 2019, and 2021) we spent a total of 995 and 184 person-hours nest searching in green and burned forests, respectively; we located 10–13 nests per year in green forest (n = 34 total) and 8–28 nests per year in burned forest (n = 57 total). In green forests, 97% of the nests we found (33 of 34) were located within lodgepole pine stands, with 94% (32 of 34) of those nests located in mature lodgepole pine trees, despite searching in the 4 types of green forest that occur in our study area. In addition, 76% of green forest nests (26 of 34) were in live trees. The majority of nests in burned forest (77%) were found in high-severity fire patches, with only n = 8 and n = 5 nests occurring in low- and moderate-severity fire patches, respectively. Across years, peak nest initiation dates of nests in burned forest was centered on May 11 and occurred ~8 days earlier than the peak of nest initiation in green forest (Wilcoxon one-sided rank sum test, P = 0.04; Figure 2A). For successful nests in burned forest (n = 48), median fledging date was June 21 with 75% of nests fledging between June 14 and July 15. For successful nests in green forest (n = 29), median fledging date was June 28, with 75% of nests fledging between June 22 and July 6. Of the 9 nests that failed in burned forest, 3 were depredated during the incubation stage with the remaining nests failing when nestlings were 5–18 days old (Supplementary Material Figure 1). Of the 5 nests that failed in green forest, 3 were depredated during the incubation stage, and one when nestlings were 6 days old. An additional nest in green forest was abandoned for unknown reasons when nestlings were 8 days old.
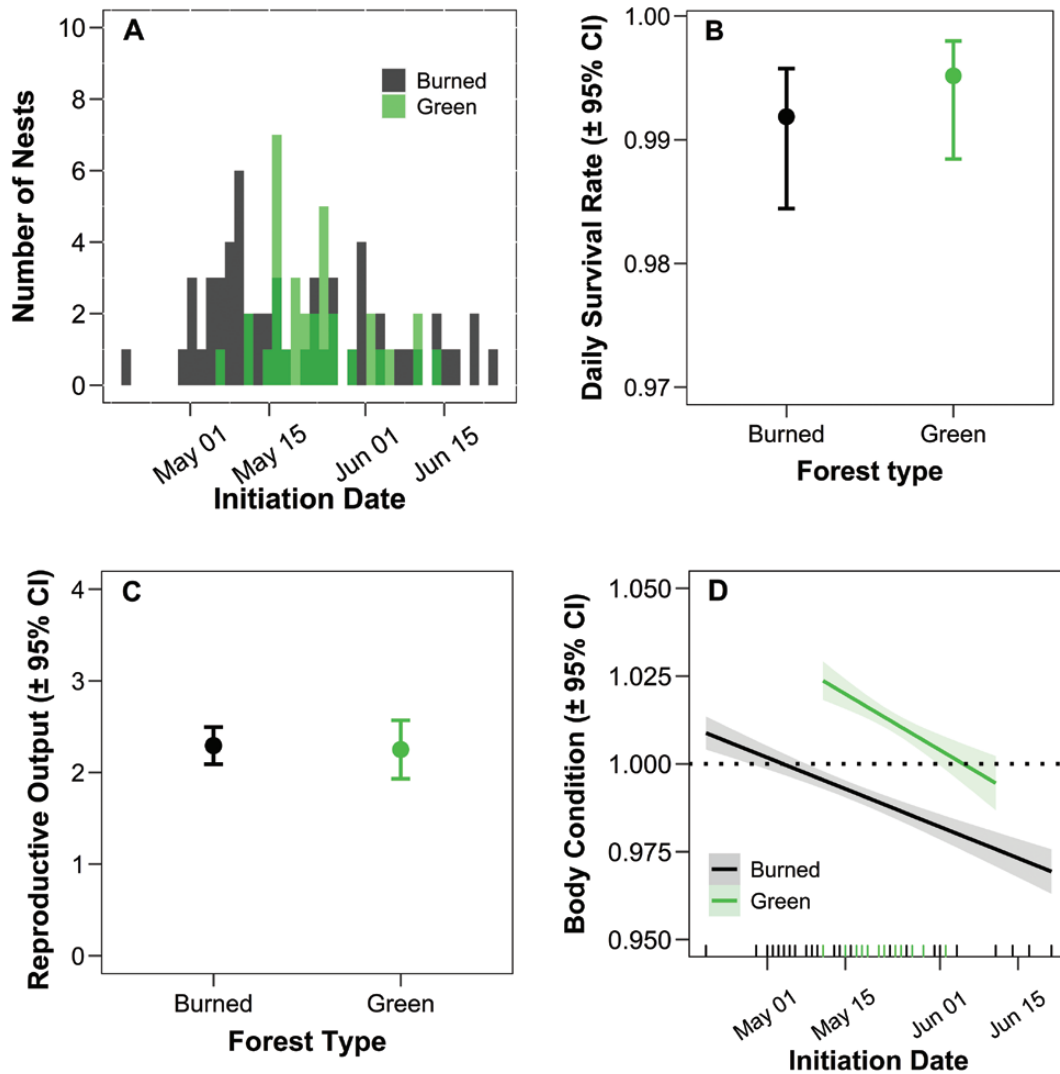
FIGURE 2. Black-backed Woodpecker (**A**) nest initiation date peaked 8 days earlier in burned forest than green forest; in contrast, no differences were detected between burned and green forests for (**B**) daily nest survival rate or (**C**) reproductive output (i.e., number of young fledged per successful nest). (**D**) Body condition of Black-backed Woodpecker nestlings was slightly improved in green forest relative to burned forest and declined with nest initiation date in both forest types. In (**D**), the dotted line represents the average expected body condition of a nestling given its size-corrected body mass; nestlings in better body condition have values >1, whereas nestlings in worse body condition have values <1. In all panels, green forest is denoted by green circles and lines whereas burned forest is denoted by black circles and lines. Mean point estimates are shown with 95% confidence intervals.

Nest Survival and Reproductive Output

Against our initial predictions, we did not detect an effect of forest type on daily nest survival ($z = 0.8$, $P = 0.44$). Estimated daily survival rates for green forest nests was 0.995 (95% CI: 0.988, 0.998) and in burned forest was 0.992 (95% CI: 0.984, 0.996; Figure 2B). Estimated probability of nest success was 0.83 (95% CI: 0.63, 0.92) in green forest and 0.72 (95% CI: 0.53, 0.84) in burned forest. When assessing the covariate-based models for daily nest survival ($\Delta AIC_c < 2$) we found that nest initiation date was the only measured variable with a consistent influence (Table 1; top model: $\beta = -0.042$ [95% CI: -0.085, 0.001], $z = -1.9$, $P = 0.06$). For every additional day a nest was initiated later during the breeding season, daily nest survival rate was reduced by 4.1% (95% CI: 0.2%, 8.4%). The probability of nest success for nests in burned forest dropped below 70% for nests initiated after May 26; in green forest the probability of nest success dropped below 70% for nests initiated after June 6.

Similar to our estimates of daily nest survival, we did not detect differences in the number of young fledged per successful nest between the forest types ($t = -0.2$, $P = 0.82$; Figure 2C). Successful nests in burned forests ($n = 48$) were estimated to fledge an average of 2.3 young (95% CI: 2.1, 2.5), which was the same estimate for the number of young fledged in successful green forest nests (2.3 young [95% CI: 1.9, 2.7], $n = 29$). In our covariate-based models, we did not detect a measurable effect from any of the covariates we examined as the top model included only the intercept (Table 2). We also did not detect any differences between the forest types in either clutch size, egg hatchability, or nestling survival (see Supplementary Material Figure 2).

Nestling Body Condition

Across the 3 years of the study, we obtained body condition measurements on $n = 133$ nestlings from 60 nests (i.e., 52 nestlings from 24 green forest nests, 81 nestlings in 36

TABLE 1. A comparison of candidate models used to evaluate factors influencing Black-backed Woodpecker daily nest survival. Nest initiation date was the top variable among models, with daily nest survival decreasing as nests initiation date increased. See Supplemental Table 1 for an explanation of the biological significance of covariates include in candidate models.

Model	K^a	ΔAIC_c	W_i^b	ER^c
Initiation date [d]	2	0	0.37	–
Initiation date + forest type	3	1.52	0.17	2.13
Intercept only	1	1.64	0.16	2.27
Forest type	2	3.03	0.08	4.56
Tree DBH + forest type	3	4.79	0.03	10.95
Canopy cover + forest type	3	4.91	0.03	11.66
Snag count + forest type	3	4.93	0.03	11.78
Cavity height + forest type	3	4.99	0.03	12.13
Tree count + forest type	3	5.04	0.03	12.40
Tree count + snag count + initiation date + forest type	5	5.42	0.02	15.06
Canopy cover + cavity orientation + forest type	4	5.44	0.02	15.21
Cavity height + tree DBH + cavity orientation + canopy cover + initiation date + forest type	7	7.24	0.01	37.33
Cavity height + tree DBH + cavity orientation + canopy cover + forest type	6	8.55	0.01	71.88
Decay class + forest type	7	9.31	0.00	104.96

[a]Denotes number of parameters in model.
[b]Relative likelihood of model (*i*) based on AIC_c value.
[c]Evidence ratio.
[d]AIC_c value for the top model = 115.03.

TABLE 2. A comparison of candidate models used to evaluate factors influencing Black-backed Woodpecker reproductive output (i.e., number of offspring fledged). The top model included the intercept only model when comparing among candidate models. Although the size of nest trees (tree DBH) was a competitive model we considered it to be an uninformative parameter (Arnold 2010). See Supplementary Material Table 2 for an explanation of the biological significance of covariates include in candidate models.

Model	K^a	ΔAIC_c	W_i^b	ER^c
Intercept only [d]	1	0	0.33	–
Tree DBH	3	0.18	0.3	1.09
Forest type	2	2.11	0.12	2.87
Cavity height + tree DBH	4	2.14	0.11	2.92
Initiation date	3	3.56	0.06	5.93
Cavity height	3	4.29	0.04	8.52
Cavity orientation	3	4.29	0.04	8.56
Decay class	7	11.89	0.00	382.44
Decay class + cavity orientation + tree DBH + cavity height + forest type	10	15.82	0.00	2,731.10

[a]Denotes number of parameters in model.
[b]Relative likelihood of model (*i*) based on AIC_c value.
[c]Evidence ratio.
[d]AIC_c value for the top model = 205.38.

burned forest nests). Models with the greatest weight indicated that nestling body condition was reduced as nest initiation date increased for individuals in both forest types (top model β: –0.0004 [95% CI: –0.0009, 0.0000], *t* = –1.9, *P* = 0.07). Nestlings from burned forest were estimated to have a 4% decrease in body condition across the core of the breeding season (May 8 through June 18; Figure 2D); likewise, nestlings from green forest experienced an estimated 3% reduction across that same period. Forest type was included in several of our top models and the model with forest type alone performed better than the intercept only model (Table 3). Nestling body condition was slightly enhanced in green forest when compared to nestlings from burned forest (*t* = 2.0, *P* = 0.05); our top model estimated that body condition of nestlings in green forest (1.012 [95% CI: 1.015, 1.009])

was improved by ~2% over their burned forest counterparts of the same size (body condition = 0.993 [95% CI: 0.989, 0.996]), when averaged across the nesting period (Figure 2D).

Post-fledging Survival

We radio tagged *n* = 35 nestlings from 21 green nests and *n* = 34 nestlings from 28 burned nests (2018: *n* = 10 nestlings tagged, 2019: *n* = 23, 2021: *n* = 36 in 2021). Of the 19 mortalities that we documented, 84% occurred prior to 35 days post-fledging, the age at which Black-backed Woodpeckers are expected to be independent of parental care. We found that most mortalities appeared to be due to predation by raptors with 8 and 5 instances of apparent raptor predation documented in green and burned forest, respectively, as evidenced by tags being tracked to raptor nests and/or roost sites

TABLE 3. A comparison of candidate models used to evaluate factors influencing Black-backed Woodpecker nestling body condition. The top model included forest type, nest initiation date, and age at banding when comparing among candidate models. See Supplementary Material Table 3 for an explanation of the biological significance of covariates include in candidate models.

Model	K^a	ΔAIC_c	W_i^b	ER^c
Forest type + initiation date + banding age [d]	5	0	0.18	–
Forest type	3	0.38	0.15	1.21
Intercept only	2	0.5	0.14	1.28
Forest type + initiation date	4	0.61	0.14	1.36
Banding age	3	1.33	0.09	1.94
Forest type + year + banding age + clutch size	6	1.77	0.08	2.42
Initiation date	3	1.83	0.07	2.50
Clutch size	3	2.1	0.06	2.85
Year	4	3.14	0.04	4.80
Forest type + year	5	3.24	0.04	5.05
Number fledged	3	15.18	0.00	1,973.99
Number fledged + year	5	18.71	0.00	11,577.90
Number fledged + year + forest type	6	18.81	0.00	12,175.86

[a]Denotes number of parameters in model.
[b]Relative likelihood of model (*i*) based on AIC_c value.
[c]Evidence ratio.
[d]AIC_c value for the top model = −510.43.
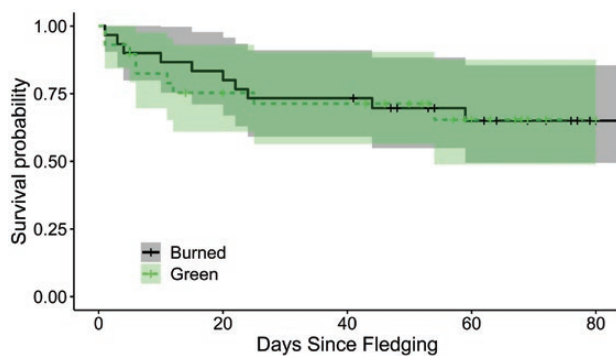
FIGURE 3. No differences in post-fledgling survival probability were detected between individual Black-backed Woodpeckers reared in green (dashed green line) and burned (sold black line) forest. Vertical dashed lines indicate instances when individuals were censored, and shading indicates 95% confidence intervals.

(Supplementary Material Figure 3). Other suspected mortality agents included snakes and/or small mammals when tags were relocated inside or adjacent to burrows, as well several mortalities in both forest types that were due to unknown causes (Supplementary Material Figure 3).

We did not detect an effect of forest type on post-fledging survival (β = 0.04 [95% CI: −90.12, 90.20], hazard ratio = 1.04 [95% CI: 0.45, 2.41], χ^2 = 0.51, *P* = 0.47; Figure 3), as overall survival during the post-fledging period was almost identical between the two forest types (green forest: 0.654 [95% CI: 0.489, 0.875], burned forest: 0.650 [95% CI: 0.494, 0.855]). Survival to independence (35 days) for juveniles from green forest was 0.708 (95% CI: 0.556, 0.902) and in burned forest was 0.733 (95% CI: 0.591, 0.810). Although radio-tagged Black-backed Woodpeckers in green forests experienced a steeper decline in survival probability immediately after fledging, this difference was not maintained once tagged individuals had been out of the nest for ~20 days, and juveniles from both forest types had similar chances of surviving

to the end of the relocation period (Figure 3). Although body condition was included in our top models for post-fledging survival (Table 4) we did not detect a measurable effect of body condition (β = 5.91 [95% CI: −12.42, 24.24], hazard ratio = 368.39 [95% CI: 0.00, 1.80 × 10¹²], χ^2 = 0.70, *P* = 0.40) on post-fledging survival.

DISCUSSION

In our study, we did not detect differences in either daily nest survival rate or reproductive output between Black-backed Woodpeckers nesting in green and burned forests. Nest survival was high, as is generally true for woodpeckers in temperate regions (Li and Martin 1991), and most of the nest failures we documented were due to predation with no clear patterns regarding the timing of failure. Of note, the breeding pairs in our study that used green forests were almost exclusively restricted to nesting in lodgepole pine stands, as was the case for birds breeding in green forest in California (Fogg et al. 2014) and in a nearby population in central Oregon (Goggans et al. 1989). Black-backed Woodpeckers nesting in green forest in the western part of their range therefore appear to be limited to areas dominated by lodgepole pine. Thus, additional work that investigates the potential constraints on Black-backed Woodpecker breeding activity, including what factor(s) may constrain breeding activity to lodgepole pine stands, will be a fruitful avenue for future research.

Our estimates of nest survival rates in green forest are similar to those from Black-backed Woodpecker nests in undisturbed green boreal forests in Canada (Tremblay et al. 2015b) and greater than those of individuals nesting in green forest following mountain pine beetle outbreak in the Black Hills (Rota et al. 2014); additionally, reproductive output in our study was slightly higher than both of those prior investigations (Rota et al. 2014, Tremblay et al. 2015b). Thus, our findings regarding nest survival and reproductive output in

TABLE 4. A comparison of candidate models used to evaluate factors influencing Black-backed Woodpecker post-fledging survival, with top models including body condition and forest type when comparing among the candidate models. See Supplementary Material Table 4 for an explanation of the biological significance of covariates include in candidate models.

Model	K^a	ΔAIC_c	W_i^b	ER^c
Body condition + forest type [d]	2	0	0.34	–
Body condition + initiation date + forest type	3	0.18	0.31	1.09
Number fledge + body condition + forest type	3	0.73	0.24	1.44
Sex + number fledge + body condition	6	2.49	0.01	3.47
Initiation date + forest type	2	12.30	0.00	469.8
Intercept only	0	12.42	0.00	498.92
Forest type	1	14.49	0.00	1,398.85
Number fledge + forest type	2	15.04	0.00	1,841.04
Year + forest type	3	16.98	0.00	4,877.38
Sex + number fledge + initiation date + forest type	6	17.23	0.00	5,523.44
Sex + number fledge + forest type	5	17.90	0.00	7,714.71
Sex + forest type	4	17.91	0.00	7,754.1

[a]Denotes number of parameters in model.
[b]Relative likelihood of model (*i*) based on AIC_c value.
[c]Evidence ratio.
[d]AIC_c value for the top model = 133.12.

southern Oregon green forests more closely paralleled nest survival and reproductive output from studies conducted in burned forests of Quebec (Nappi and Drapeau 2011), California (Stillman et al. 2019a), and the Black Hills area (Rota et al. 2014). This also indicates that food resources in the green forests we studied support Black-backed Woodpecker breeding activity, as offspring production differed little relative to populations using burned forests elsewhere in their range (Nappi and Drapeau 2011, Rota et al. 2014, Stillman et al. 2019a).

We found that nest initiation date was an important predictor of Black-backed Woodpecker nest success, which is concordant with previous studies in both green forest recently disturbed by mountain pine beetle (Bonnot et al. 2008) and in areas impacted by wildfire (Stillman et al. 2019a). We also found that individuals breeding in green forest consistently initiated nests later in the season than individuals that used burned forests 2–4 yr post-wildfire, which may be due differences in bioclimatic phenology and food availability. Bark and wood-boring beetles, the primary food items of Black-backed Woodpeckers (Tremblay et al. 2020, Stillman et al. 2022a) become active earlier in the season when spring temperatures are warmer (Chinellato et al. 2014, Galko et al. 2018). If green forest is characterized by cooler spring temperatures that results in beetle activity starting later in the season, it may explain the differences in nest initiation dates we observed. Whether this explanation or others are the basis for this difference remains unknown, so additional research investigating the links between nest initiation, food availability, and microclimatic factors in green forests will be useful for understanding temporal variation in breeding activity, as well as the role food resources play in promoting breeding success across different forest types.

Our study failed to demonstrate meaningful differences in post-fledging survival of Black-backed Woodpeckers originating from green and burned forest, and we failed to detect a measurable effect of nestling body condition on post-

fledging survival. Both green and burned forests appear to provide key resources for Black-backed Woodpeckers during the post-fledging period, but for different reasons: green forest provides more vegetative cover to hide from predators (Stillman et al. 2019b) whereas burned forest is thought to provide a greater density of food resources (Rota et al. 2015, Stillman et al. 2019b). Thus, having both burned and green forest available to juvenile Black-backed Woodpeckers in a fire mosaic landscape would appear to confer increased benefits relative to conspecifics that can only access a single forest type (Stillman et al. 2019b, 2021). In our study, we found that radio-tagged fledglings originating in green forest had greater survival rates than either those in green forest subjected to a mountain pine beetle outbreak (Rota et al. 2014) or those originating in burned areas that subsequently used a mosaic of green and low-moderate severity burned forests in California and Washington (Stillman et al. 2021). Additionally, survival was markedly reduced for recently fledged Black-backed Woodpeckers in California that remained exclusively within high severity burn patches (Stillman et al. 2021), highlighting the importance of green forest to recently fledged young. Taken together with previous studies, our findings indicate that in the western part of its range the Black-backed Woodpecker—despite being considered a burned forest obligate species (Hutto 2008)—can benefit from green forest embedded within a pyrodiverse landscape (Fogg et al. 2014, Stillman et al. 2019b, 2022b; Tingley et al. 2020, Verschuyl et al. 2021).

Despite the limited differences in the vital rates we measured, we did observe that nesting pairs of Black-backed Woodpeckers within green forests occurred in lower densities than in nearby areas that had recently been subjected to high-severity wildfire (authors, personal observation. This pattern is similar to studies of unburned forest in the Sierra Nevada (Fogg et al. 2014, Tingley et al. 2020) and indicates that although vital rates in green and burned forest are similar, these two forest types are not functionally equivalent. Although the differences in nesting pair density that we observed may have been due in

part to differences in detection probability of breeders in the 2 forest types, the strong response of Black-backed Woodpeckers to playback in both forest types that we have observed (authors personal observations) suggests that these differences are due to biological, not methodological differences. Based on prior research with several woodpecker species, including the Black-backed Woodpecker, multiple drivers may be responsible for the lower nest densities in green forest, including reduced food availability (Tremblay et al. 2016, Linden et al. 2011), nest-site availability (Heppell et al. 1994, Fogg et al. 2014, Lorenz et al. 2015), and mate availability (Carrie et al. 1999, Daniels and Walters 2000). Additional work is currently being undertaken to differentiate which driver(s) limit Black-backed Woodpecker nest densities in green forests, which may allow for targeted management actions to enhance breeding populations in unburned conifer forest.

In contrast to recently burned areas, which provide large pulses of food and nesting resources to woodpeckers for a relatively short period of time after high-severity wildfire (Saab et al. 2007, Nappi and Drapeau 2009, Tremblay et al. 2015b), green forests with complex structure (i.e., dead and downed wood, old and senescing trees, multi-layered canopies) may provide more stable food availability for long-term population persistence (Powell 2000, Ray et al. 2019). We found nestling body condition was slightly improved in green forest in this study, and our related work has found that juveniles from green forests can colonize newly burned areas and successfully breed in their first adult year (authors personal observation). In addition, recent findings from other areas indicate that juveniles with improved body condition can travel further during natal dispersal (Stillman et al. 2022b). These observations, coupled with recent work that has demonstrated that Black-backed Woodpeckers avoid nesting in the interior of high severity megafires (White et al. 2019) and that fledglings require adjacent green forest (Stillman et al. 2019b), highlight the value green forests play to support successful nesting. Because recently burned forest occupies a relatively small proportion of the landscape at any one time (Fogg et al. 2014, Tremblay et al. 2015b)—for example, only ~2.1% of forests in Oregon burned annually from 2010 to 2020 (OFRI 2021)—green forests may play an even larger role than expected in supporting breeding Black-backed Woodpeckers across broad spatial scales in the western United States.

In addition to providing habitat, mature unburned conifer forests also play a key role in supporting breeding Black-backed Woodpeckers in post-fire settings via their biological legacies. Legacies that are required for successful nesting in post-fire areas, such as medium- to large-diameter trees (Saab et al. 2011, Seavy et al. 2012, Stillman et al. 2019a), typically require decades to grow to a suitable size before they can be used by woodpeckers. Therefore, how green forests are managed within fire-prone landscapes has strong potential to influence the extent to which these forests, after experiencing wildfire, will support Black-backed Woodpeckers populations (Hutto 1995, Nappi and Drapeau 2011). Management practices that are implemented after wildfire occurs, such as post-fire salvage logging, can have negative consequences for a range of cavity-nesting species, including the Black-backed Woodpecker, by reducing foraging and nesting resources (Nappi et al. 2004, Saab et al. 2007, Lindenmayer et al. 2008). Additionally, the frequency and intensity of wildfire is expected to increase with anthropogenic-induced climate change (Westerling et al. 2006, Yue et al. 2013, Abatzoglou and Williams 2016), with potential to convert forests to non-forest ecosystems (Coop et al. 2020). Therefore, broadscale management actions that promote large, live trees within unburned forest, retain adequate nesting and foraging resources in post-fire areas, and promote resilience of contemporary forests to increased wildfire risk will provide the greatest benefits to Black-backed Woodpeckers in the western part of their range (Tremblay et al. 2009, Saab et al. 2011, Stillman et al. 2019a, Coop et al. 2020), as well as the many other species that depend upon them (Tarbill et al. 2015, Tremblay et al. 2020). Although our findings demonstrate that green forests, such as mature stands dominated by lodgepole pine, can play an important role in supporting Black-backed Woodpecker populations, many questions remain about when and how this species uses green forests. In particular, we lack an understanding of the underlying mechanisms that limit nesting densities in green forests, and the factors that influence connectivity between green forests and burned forest, particularly during the natal dispersal period. Therefore, such topics will be important avenues for future investigation and will provide a more comprehensive understanding of how green and burned forests work in concert to support Black-backed Woodpecker populations within fire-prone landscapes.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Funding statement

Ethics statement

All capture, handling, and tagging procedures used in the collection of data were approved by the U.S. Fish and Wildlife Service, the U.S. Geological Survey, the Oregon Department

of Fish and Wildlife, and the Institutional Animal Care and Use Committee at Oregon State University.

Author contributions

J.W.R conceived of the idea and designed the methods. M.E.K conducted the research, analyzed the data, and drafted the initial version of the manuscript. Both authors contributed extensively to the review and editing of the final manuscript.

Data availability

Analyses reported in this article can be reproduced using the data provided by Kerstens and Rivers (2023).

LITERATURE CITED

Abatzoglou, J. T., and A. P. Williams (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences USA* 113:11770–11775.

Abatzoglou, J. T., D. S. Battisti, P. A. Williams, W. D. Hansen, B. J. Harvey, and C. A. Kolden (2021). Projected increases in western US forest fire despite growing fuel constraints. *Communications Earth and Environment* 2:27.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management* 74:1175–1178.

Bonnot, T. W., M. A. Rumble, and J. J. Millspaugh (2008). Nest success of Black-backed Woodpeckers in forests with mountain pine beetle outbreaks in the Black Hills, South Dakota. *The Condor* 110:450–457.

Bunnell, F. L. (2013). Sustaining cavity-using species: Patterns of cavity use and implications to forest management. *ISRN Forestry* 2013:1–33.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY, USA.

Carrie, N. R., R. N. Conner, D. C. Rudolph, and D. K. Carrie (1999). Reintroduction and postrelease movements of Red-cockaded Woodpecker groups in eastern Texas. *The Journal of Wildlife Management* 63:824–832.

Charnley, S., T. A. Spies, A. M. G. Barros, E. M. White, and K. A. Olsen (2017). Diversity in forest management to reduce wildfire losses: Implications for resilience. *Ecology and Society* 22:22.

Chinellato, F., M. Faccoli, L. Marini, and A. Battisti (2014). Distribution of Norway spruce bark and wood-boring beetles along alpine elevational gradients. *Agricultural and Forest Entomology* 16:111–118.

Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, S. D. Crausbay, P. E. Higuera, M. D. Hurteau, A. Tepley, E. Whitman, T. Assal, B. M. Collins, K. T. Davis, et al. (2020). Wildfire-driven forest conversion in western North American landscapes. *Bioscience* 70:659–673.

Daniels, S. J., and J. R. Walters (2000). Between-year breeding dispersal in Red-cockaded Woodpeckers: Multiple causes and estimated cost. *Ecology* 81:2473–2484.

Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz (2014). Large wildfire trends in the western United States, 1984–2011. *Geophysical Research Letters* 41:2928–2933.

Drever, M. C., K. E. H. Aitken, A. R. Norris, and K. Martin (2008). Woodpeckers as reliable indicators of bird richness, forest health and harvest. *Biological Conservation* 141:624–634.

Drever, M. C., and K. Martin (2010). Response of woodpeckers to changes in forest health and harvest: Implications for conservation of avian biodiversity. *Forest Ecology and Management* 259:958–966.

Flannigan, M., A. S. Cantin, W. J. De Groot, M. Wotton, A. Newbery, and L. M. Gowman (2013). Global wildland fire season severity in the 21st century. *Forest Ecology and Management* 294:54–61.

Fogg, A. M., L. J. Roberts, and R. D. Burnett (2014). Occurrence patterns of Black-backed Woodpeckers in green forest of the Sierra Nevada Mountains, California, USA. *Avian Conservation and Ecology* 9:3.

Fox, J., and S. Weisberg (2018). Cox Proportional-Hazards Regression for Survival Data in R. https://socialsciences.mcmaster.ca/jfox/Books/Companion/appendices/Appendix-Cox-Regression.pdf

Gaines, W. L., M. Haggard, J. F. Lehmkuhl, A. L. Lyons, and R. J. Harrod (2007). Short-term response of land birds to ponderosa pine restoration. *Restoration Ecology* 15:670–678.

Galko, J., B. Økland, T. Kimoto, S. Rell, M. Zúbrik, A. Kunca, J. Vakula, A. Gubka, and C. Nikolov (2018). Testing temperature effects on woodboring beetles associated with oak dieback. *Biologia* (Poland) 73:361–370.

Goggans, R., R. D. Dixon, and L. C. Seminara (1989). *Habitat use by Three-toed and Black-backed Woodpeckers*. Technical Report 87-3-02, USDA Deschutes National Forest, Portland, OR, USA.

Hagmann, R. K., A. G. Merschel, and M. J. Reilly (2019). Historical patterns of fire severity and forest structure and composition in a landscape structured by frequent large fires: Pumice Plateau eco-region, Oregon, USA. *Landscape Ecology* 34:551–568.

Hanson, C. T., and M. P. North (2008). Postfire woodpecker foraging in salvage-logged and unlogged forests of the Sierra Nevada. *The Condor* 110:777–782.

Heppell, S. S., J. R. Walters, and L. B. Crowder (1994). Management alternatives for Red-cockaded Woodpeckers: A modeling approach. *The Journal of Wildlife Management* 58:479–487.

van der Hoek, Y., G. V. Gaona, and K. Martin (2017). The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world. *Diversity and Distributions* 23:1120–1131.

Hutto, R. L. (1995). Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* 9:1041–1058.

Hutto, R. L. (2008). The ecological importance of severe wildfires: Some like it hot. *Ecological Applications* 18:1827–1834.

Ibarzabal, J., and J. A. Tremblay (2006). The hole saw method for accessing woodpecker nestlings during developmental studies. *Annales Zoologici Fennici* 43:235–238.

Jakob, E. M., S. D. Marshall, and G. W. Uetz (1996). Estimating fitness: A comparison of body condition indices. *Oikos* 77:61–67.

Jones, G. M., and M. W. Tingley (2021). Pyrodiversity and biodiversity: A history, synthesis, and outlook. *Diversity and Distributions* 28:386–403.

Kassambara, A., M. Kosinski, and P. Biecek (2021). Survminer: Drawing Survival Curves using "ggplot2." R package version 0.4.9. https://CRAN.R-project.org/package=survminer.

Key, C. H., and N. C. Benson (2006). FIREMON—Landscape Assessment. In *FIREMON: Fire Effects Monitoring and Inventory System* (D. C. Lutes, R. E. Keane II, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi, Editors). Technical Report RMRS-GTR-164-CD, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.

Kerstens, M. E., and J. W. Rivers (2023). Data from: Is green the new black? Black-backed Woodpecker vital rates do not differ between unburned and burned forests within a pyrodiverse landscape. *Ornithological Applications* 125:duad010. https://doi.org/10.5061/dryad.v9s4mw71b

Laake, J. L. (2013). Rmark: An R interface for analysis of capture-recapture data with MARK. FSC Processed Rep. 2013-01, Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, WA, USA. https://apps-afsc.fisheries.noaa.gov/Publications/ProcRpt/PR2013-01.pdf.

Labarbera, M. (1989). Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics* 20:97–117.

Li, P. and T. E. Martin (1991). Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. *The Auk* 108:405–518.

Linden, A., A. Lehikoinen, T. Hokkanen, and R. A. Vaisanen (2011). Modelling irruptions and population dynamics of the Great Spotted Woodpecker—joint effects of density and cone crops. *Oikos* 120:1065–1075.

Lindenmayer, D., R. J. Hobbs, R. Montague-Drake, J. Alexandra, A. Bennett, M. Burgman, P. Cale, A. Calhoun, V. Cramer, P. Cullen, D. Driscoll, et al. (2008). A checklist for ecological management of landscapes for conservation. *Ecology Letters* 11:78–91.

Lorenz, T. J., K. T. Vierling, T. R. Johnson, and P. C. Fischer (2015). The role of wood hardness in limiting nest site selection in avian cavity excavators. *Ecological Applications* 25:1016–1033.

Martin, K., and J. M. Eadie (1999). Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecology and Management* 115:243–257.

Matseur, E. A., F. R. Thompson, B. E. Dickerson, M. A. Rumble, and J. J. Millspaugh (2018). Black-backed Woodpecker abundance in the Black Hills. *The Journal of Wildlife Management* 82:1039–1048.

Maser, C., R. G. Anderson, and K. Cromack, Jr. (1979). Dead and down woody material. In *Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington* (J. W. Thomas, Editor). Agriculture Handbook No. 553. U.S. Department of Agriculture, Forest Service, Washington, DC, USA.

Mazerolle, M. J. (2020). Aiccmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. https://cran.r-project.org/package=aiccmodavg.

McCullough, M., R. A. Werner, and D. Neumann (1998). Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology* 43:107–127.

Mikusinski, G., M. Gromadzki, and P. Chylarecki (2001). Woodpeckers as indicators of forest bird diversity. *Conservation Biology* 15:208–217.

Nappi, A., P. Drapeau, and J. P. L. Savard (2004). Salvage logging after wildfire in the boreal forest: Is it becoming a hot issue for wildlife? *The Forestry Chronicle* 80:67–74.

Nappi, A., and P. Drapeau (2009). Reproductive success of the Black-backed Woodpecker (*Picoides arcticus*) in burned boreal forests: Are burns source habitats? *Biological Conservation* 142:1381–1391.

Nappi, A., P. Drapeau, M. Saint-Germain, and V. A. Angers (2010). Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood foraging birds. *International Journal of Wildland Fire* 19:500–511.

Nappi, A., and P. Drapeau (2011). Pre-fire forest conditions and fire severity as determinants of the quality of burned forests for deadwood-dependent species: The case of the Black-backed Woodpecker. *Canadian Journal of Forest Research* 41:994–1003.

Oregon Forest Resources Institute (OFRI) (2021). *Oregon Forest Facts: 2021-2022 Edition*. Oregon Forest Resources Institute, Portland, OR, USA.

Powell, H. D. (2000). Influence of prey density on post-fire habitat use of the Black-backed Woodpecker. Master's Thesis, University of Montana. Graduate Student Theses, Dissertations, and Professional Papers, Boise, MT, USA.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.

Ray, C., D. R. Cluck, R. L. Wilkerson, R. B. Siegel, A. M. White, G. L. Tarbill, S. C. Sawyer, and C. A. Howell (2019). Patterns of woodboring beetle activity following fires and bark beetle outbreaks in montane forests of California, USA. *Fire Ecology* 15:1–20.

Rivers, J. W., J. Verschuyl, C. J. Schwarz, A. J. Kroll, and M. G. Betts (2019). No evidence of a demographic response to experimental herbicide treatments by the White-crowned Sparrow, an early successional forest songbird. *The Condor: Ornithological Applications* 121:duz004.

Rohwer, S. (1988). Guyed extension ladder for access to high nests. *Journal of Field Ornithology* 59:262–265.

Rota, C. T., J. J. Millspaugh, M. A. Rumble, C. P. Lehman, and D. C. Kesler (2014). The role of wildfire, prescribed fire, and mountain pine beetle infestations on the population dynamics of Black-Backed Woodpeckers in the Black Hills, South Dakota. *PLOS One* 9:e94700.

Rota, C. T., M. A. Rumble, C. P. Lehman, D. C. Kesler, and J. J. Millspaugh (2015). Apparent foraging success reflects habitat quality in an irruptive species, the Black-backed Woodpecker. *The Condor: Ornithological Applications* 117:178–191.

Saab, V. A., R. E. Russell, and J. G. Dudley (2007). Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. *The Condor* 109:97–108.

Saab, V. A., R. E. Russell, and J. G. Dudley (2009). Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. *Forest Ecology and Management* 257:151–159.

Saab, V. A., R. E. Russell, J. Rotella, and J. G. Dudley (2011). Modeling nest survival of cavity-nesting birds in relation to postfire salvage logging. *The Journal of Wildlife Management* 75:794–804.

Saint-Germain, M., P. Drapeau, and C. Hébert (2004). Xylophagous insect species composition and patterns of substratum use on fire-killed black spruce in central Quebec. *Canadian Journal of Forest Research* 34:677–685.

Sarà, M., D. Campobello, and L. Zanca (2012). Effects of nest and colony features on Lesser Kestrel (*Falco naumanni*) reproductive success. *Avian Biology Research* 5:209–217.

Schrader, M. S., E. L. Walters, F. C. James, and E. C. Greiner (2003). Seasonal prevalence of a hematozoan parasite of Red-Bellied Woodpeckers (*Melanerpes carolinus*) and its association with host condition and overwinter survival. *The Auk* 120:130–137.

Seavy, N. E., R. D. Burnett, and P. J. Taille (2012). Black-backed Woodpecker nest-tree preference in burned forests of the Sierra Nevada, California. *Wildlife Society Bulletin* 36:722–728.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. *The Auk* 121:526–540.

Squires, J. R., R. T. Reynolds, J. Orta, and J. S. Marks (2020). Northern Goshawk (*Accipiter gentilis*), version 1.0. In *Birds of the World* (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.norgos.01

Stillman, A. N., R. B. Siegel, R. L. Wilkerson, M. Johnson, C. A. Howell, and M. W. Tingley (2019a). Nest site selection and nest survival of Black-backed Woodpeckers after wildfire. *The Condor: Ornithological Applications* 121:duz039.

Stillman, A. N., R. B. Siegel, R. L. Wilkerson, M. Johnson, and M. W. Tingley (2019b). Age-dependent habitat relationships of a burned forest specialist emphasize the role of pyrodiversity in fire management. *Journal of Applied Ecology* 56:880–890.

Stillman, A. N., T. J. Lorenz, P. C. Fischer, R. B. Siegel, R. L. Wilkerson, M. Johnson, and M. W. Tingley (2021). Juvenile survival of a burned forest specialist in response to variation in fire characteristics. *Journal of Animal Ecology* 90:1317–1327.

Stillman, A. N., M. V. Caiafa, T. J. Lorenz, M. A. Jusino, and M. W. Tingley (2022a). DNA metabarcoding reveals broad woodpecker diets in fire-maintained forests. *Ornithology* 139:ukac009.

Stillman, A. N., T. J. Lorenz, R. B. Siegel, R. L. Wilkerson, M. Johnson, and M. W. Tingley (2022b). Conditional natal dispersal provides a mechanism for populations tracking resource pulses after fire. *Behavioral Ecology* 33:27–36.

Tarbill, G. L., P. N. Manley, and A. M. White (2015). Drill, baby, drill: The influence of woodpeckers on post-fire vertebrate communities through cavity excavation. *Journal of Zoology* 296:95–103.

Therneau, T. M. (2021). A Package for Survival Analysis in R. R package version 3.2-13, https://CRAN.R-project.org/package=survival.

Tingley, M. W., A. N. Stillman, R. L. Wilkerson, C. A. Howell, S. C. Sawyer, and R. B. Siegel (2018). Cross-scale occupancy dynamics of a postfire specialist in response to variation across a fire regime. *Journal of Animal Ecology* 87:1484–1496.

Tingley, M. W., A. N. Stillman, R. L. Wilkerson, S. C. Sawyer, and R. B. Siegel (2020). Black-backed Woodpecker occupancy in burned and beetle-killed forests: Disturbance agent matters. *Forest Ecology and Management* 455:117694.

Tremblay, J. A., J. Ibarzabal, and C. Dussault (2009). Habitat requirements of breeding Black-Backed Woodpeckers (*Picoides arcticus*) in managed, unburned boreal forest. *Avian Conservation and Ecology* 4:2.

Tremblay, J. A., J. Ibarzabal, J. P. L. Savard, and S. Wilson (2014). Influence of old coniferous habitat on nestling growth of Black-backed Woodpeckers *Picoides arcticus*. *Acta Ornithologica* 49:273–279.

Tremblay, J. A., J.-P. L. Savard, and J. Ibarzabal (2015a). Structural retention requirements for a key ecosystem engineer in conifer-dominated stands of a boreal managed landscape in eastern Canada. *Forest Ecology and Management* 357:220–227.

Tremblay, J. A., J. Ibarzabal, and J.-P. L. Savard (2015b). Contribution of unburned boreal forests to the population of Black-backed Woodpecker in eastern Canada. *Ecoscience* 22:145–155.

Tremblay, J. A., J. Ibarzabal, M.-C. Saulnier, and S. Wilson (2016). Parental care by Black-backed Woodpeckers in burned and unburned habitats of eastern Canada. *Ornis Hungarica* 24:69–80.

Tremblay, J. A., R. D. Dixon, V. A. Saab, P. Pyle, and M. A. Patten (2020). Black-backed Woodpecker (*Picoides arcticus*), version 1.0. In *Birds of the World* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.bkbwoo.01

U.S. Forest Service (USFS) (2022). RAVG Thematic Percent Change in Composite Burn Index (CBI-4). Raster Dataset. https://data.fs.usda.gov/geodata/rastergateway/ravg/index.php.

U.S. Fish and Wildlife Service (USFWS) (2017). Endangered and Threatened wildlife and plants; 12-month findings on petitions to list 25 Species as Endangered or Threatened Species. *Federal Register* 82:46618–46645.

Verschuyl, J., J. L. Stephens, A. J. Kroll, K. E. Halstead, and D. Rock (2021). Black-backed Woodpecker occupancy is extensive in green conifer forests of the southern cascade mountains, Oregon. *Avian Conservation and Ecology* 16:4.

Virkkala, R. (2006). Why study woodpeckers? The significance of woodpeckers in forest ecosystems. *Annales Zoologici Fennici* 43:82–85.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam (2006). Warming and earlier spring increase western U.S. Forest wildfire activity. *Science* 313:940–943.

White, A. M., G. L. Tarbill, R. L. Wilkerson, and R. B. Siegel (2019). Few detections of Black-backed Woodpeckers (*Picoides arcticus*) in extreme wildfires in the Sierra Nevada. *Avian Conservation and Ecology* 14:17.

Wiebe, K. L. (2001). Microclimate of tree cavity nests: Is it important for reproductive success in northern flickers? *The Auk* 118:412–421.

Yue, X., l. J. Mickley, J. A. Logan, and J. O. Kaplan (2013). Ensemble projections of wildfire activity and carbonaceous aerosol concentrations over the western united states in the mid-21st century. *Atmospheric Environment* 77:767–780.