



RESEARCH ARTICLE

Age structure of Black-backed Woodpecker populations in burned forests

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ABSTRACT

Population age structure is important for understanding population dynamics, but can be difficult to resolve in landbirds due to the limited number of age classes discernible by examining plumage. In forests of western North America, Black-backed Woodpeckers (*Picoides articus*) typically colonize burned areas shortly after fire, but densities decline within 6–10 yr. This pattern is often assumed to result from adult Black-backed Woodpeckers abandoning territories when food resources wane, yet long-distance breeding dispersal is relatively rare in birds, whereas long-distance natal dispersal is more common. To determine whether colonization of newly burned areas is driven primarily by breeding dispersal of adults or natal dispersal by young birds, we captured 57 adult Black-backed Woodpeckers in 6 burned areas in California between 1 and 8 yr after fire. We used patterns of multiple feather generations retained among primary coverts, secondaries, and secondary coverts to assign birds to 1 of 5 age classes (second-, third-, and fourth-calendar-year; after-third-calendar-year; and after-fourth-calendar-year). Population age structure varied dramatically across burned areas, with a preponderance of second-calendar-year birds in the 1 yr and 2 yr postfire areas, and a preponderance of birds at least 3 yr old in the older postfire areas. Poisson generalized linear mixed models (GLMMs) revealed that the effect of years since fire on woodpecker age was highly significant ($z = 3.575$, $P < 0.001$). Our results indicate that natal dispersal is the primary means by which Black-backed Woodpeckers colonize recently burned areas in western forests, and that breeding dispersal is uncommon. The decline of Black-backed Woodpecker populations 6–10 yr after fire likely reflects the lifespan of individual birds that colonized the burned area, or of offspring that they produced in the early postfire years. Our discrimination of Black-backed Woodpeckers into 5 age classes confirms previous suppositions about plumage-based age determination in woodpeckers, and is likely applicable to other woodpecker species.

Keywords: Black-backed Woodpecker, *Picoides articus*, natal dispersal, breeding dispersal, population age structure, molt

Estructura de Edad de Poblaciones de *Picoides articus* en Bosques Quemados

RESUMEN

La estructura de edad de una población es importante para entender la dinámica poblacional, pero puede ser difícil de averiguar en las aves terrestres debido al limitado número de clases de edad discernibles mediante el examen del plumaje. En los bosques del oeste, la especie *Picoides articus* típicamente coloniza áreas incendiadas poco después de un fuego, pero las densidades disminuyen dentro de los 6 a los 10 años. Se asume frecuentemente que este patrón es el resultado del abandono de los territorios por parte de *P. articus* cuando escasean los recursos alimenticios, aunque la dispersión reproductiva de larga distancia es relativamente rara en las aves, mientras que la dispersión natal de larga distancia es más común. Para determinar si la colonización de nuevas áreas incendiadas está ocasionada principalmente por la dispersión reproductiva de adultos o la dispersión natal de aves jóvenes, capturamos 57 individuos adultos de *P. articus* a lo largo de seis áreas incendiadas en California entre 1 y 8 años luego del fuego. Usamos patrones de múltiples generaciones de plumas retenidas entre coberteras primarias, secundarias y coberteras secundarias para asignar a las aves a una de cinco clases de edad (segundo, tercero y cuarto año calendario; luego del tercer año calendario; y luego del cuarto año calendario). La estructura de edad poblacional varió dramáticamente a través de las áreas incendiadas, con una preponderancia de aves del segundo año calendario en las áreas incendiadas de uno y dos años, y una preponderancia de aves de al menos tres años de edad en los incendios más viejos. Los análisis de modelos mixtos lineales generalizados de Poisson revelaron que el efecto del año desde el fuego en la edad de los carpinteros fue altamente significativo ($z = 3.575$, $P < 0.001$). Nuestros resultados indican que la dispersión natal es la manera principal en que *P. articus* coloniza nuevas áreas incendiadas en los bosques del oeste y que la dispersión

reproductiva es poco común. La disminución de las poblaciones de *P. articus* luego de seis a diez años del fuego probablemente refleja la longevidad de las aves individuales que colonizan el área incendiada, o los pichones que producen en los primeros años posteriores al fuego. Nuestra separación de los individuos de *P. articus* en cinco clases de edad confirma las suposiciones previas basadas en la determinación de la edad de los carpinteros usando el plumaje y probablemente se aplica a otras especies de carpinteros.

Palabras clave: dispersión natal, dispersión reproductiva, estructura de edad de la población, muda, *Picoides arcticus*

INTRODUCTION

Knowledge of the age structure of populations is critical for developing population models based on the demographic rates of long-lived species (Caswell 1989, Holmes and York 2003). Age structure can change across space and time due to differential effects of biotic and abiotic factors on age-specific vital rates. Consequently, investigations of age structure provide a snapshot of how populations are growing or shrinking, and can be critical for understanding natural history and informing conservation and management. In birds, a major challenge to resolving population age structure is our limited ability (relative to other taxa) to discern the ages of individuals. Age determination is primarily accomplished through examination of plumage and molt limits (Ricklefs and Rohwer 2005), but these clues are fixed for most landbird species after the second year of life (Pyle 1997). The close inspection of plumage and molt limits to expand available age classes may lead to advances in the population ecology and conservation of species.

More so than any other bird species in North America, Black-backed Woodpeckers (*Picoides arcticus*) are strongly associated with recently burned conifer forests (Hutto 1995, Dixon and Saab 2000, Kotliar et al. 2002, Smucker et al. 2005), which they commonly colonize within 1 yr after fire and then occupy at much higher densities than are observed in unburned forests (Hoyt and Hannon 2002, Hutto 2008, Fogg et al. 2014). In western forests, density typically peaks by 4 or 5 yr after fire (Saab et al. 2007) and then declines rapidly over the next 3–5 yr (Saab et al. 2007, Saracco et al. 2011). This boom-and-bust cycle appears to be correlated with the population dynamics of the woodpeckers' preferred food source, the larvae of wood-boring beetles (especially Cerambycidae), which also temporarily colonize recently burned forest in high densities (Villard and Beninger 1993, Murphy and Lehnhausen 1998).

The rapid decline in Black-backed Woodpeckers coincident with the decline of wood-boring beetle larvae has led to the hypothesis that relatively long-distance breeding dispersal must be common in the species (e.g., Hutto 1995, Murphy and Lehnhausen 1998, Pierson et al. 2010). Long-distance dispersal is defined by Clobert et al. (2001) as the movement of individuals who have already bred or

attempted to breed in one location moving to a new location where they attempt to breed again. Under this scenario, adult birds that occupy territories in aging postfire forests eventually abandon their territories when food resources wane and relocate to more recently burned areas or other habitat patches with more abundant food.

Although difficult to study, long-distance breeding dispersal in most bird species is uncommon and may impose substantial fitness costs (Danchin and Cam 2002), whereas long-distance natal dispersal of young birds is believed to be far more common (Greenwood and Harvey 1982, Paradis et al. 1998). Genetic studies of Black-backed Woodpeckers (Pierson et al. 2010, 2013) and observations of frequent population irruptions in eastern portions of their range (Yunick 1985) make clear that the species is capable of long-distance movement and dispersal, but it remains unknown whether newly burned areas in western forests are generally colonized by young birds (i.e. natal dispersers) or adult birds that previously attempted reproduction elsewhere (i.e. breeding dispersers). The answer to this question may have important implications for the population dynamics and conservation of Black-backed Woodpeckers in western forests, as the Oregon–California segment of the population is currently being reviewed for candidacy as Threatened or Endangered under the federal Endangered Species Act. Although Black-backed Woodpeckers in western forests are not restricted to burned areas (Fogg et al. 2014), their strong association with ephemeral patches of complex early seral forest (DellaSala et al. 2014) suggests some degree of metapopulation structure. Understanding the demography and dispersal of the species within and among burned forest patches could be an important first step toward modeling metapopulation dynamics.

Dale et al. (2004) predicted that, unlike the majority of bird species, relatively rare and patchily distributed bird species would be more likely to exhibit longer breeding dispersal than natal dispersal distances. Black-backed Woodpeckers in western forests are both relatively uncommon and patchily distributed, and also rely on an inherently ephemeral habitat, which could be an additional factor favoring long-distance breeding dispersal. However, an alternative hypothesis is that long-distance breeding dispersal by Black-backed Woodpeckers is rare, and that natal dispersal is the primary colonization mechanism of

newly burned areas. The typical postfire occupancy period of 6–10 yr for Black-backed Woodpeckers is roughly equivalent to the lifespan recorded for other medium-sized woodpeckers (Kennard 1975, Clapp et al. 1983, Rowan et al. 2014). This suggests that, although food resources in a burned area diminish, adult birds that initially colonized the area—or offspring that they produced in the early postfire years—are likely to remain in the area for the rest of their lives, whereas young birds produced in the later postfire years may become increasingly likely to disperse out of their natal area.

Existing evidence for whether Black-backed Woodpecker colonization of recently burned forests occurs primarily through natal dispersal or breeding dispersal is equivocal. Huot and Ibarzabal (2006) reported that 95% of migrating Black-backed Woodpeckers caught at a banding station in Québec, Canada, in the autumn were juveniles, and thus predicted that dispersing juveniles in the fall were likely the primary colonizers of newly burned forest. However, in the same study, the authors tested this prediction by comparing the prevalence of second-year woodpeckers in populations in 1-yr-old postfire and unburned forests, and found little difference. In western forests, limited data suggest that breeding-site fidelity is high (Dixon and Saab 2000), as is the case for other *Picoides* species (Huot and Ibarzabal 2006). Genetic evidence that male Black-backed Woodpeckers may sometimes cross large patches of unforested habitat, whereas females will not (Pierson et al. 2010), raises the question of whether the propensity to disperse and colonize newly burned areas is a function not only of age class, but also of sex. Concerns about the effects of postfire salvage logging on Black-backed Woodpecker populations (Koivula and Schmiegelow 2007, Hanson and North 2008, Tingley et al. 2014) exacerbate the need to better understand the species' colonization dynamics for effective landscape-scale conservation planning (Bond et al. 2012).

One obstacle to developing detailed age structures of bird populations is the practical difficulty of assessing the ages of living birds. Plumage characteristics can reliably categorize adult woodpeckers into at least 3 age classes: second-calendar-year (SY), third-calendar-year (TY), and after-third-calendar-year (ATY; Pyle and Howell 1995, Pyle 1997). Here, we describe methods for further discriminating ATY Black-backed Woodpeckers into fourth-calendar-year (4Y) and after-fourth-calendar-year (A4Y) birds, providing an opportunity to assess the age structure of populations among 5 age classifications in a cross-sectional study. Our objective was to utilize individual age class determinations to test for differences in the age structures of Black-backed Woodpecker populations across burned forests of different ages. A prevalence of SY birds in recently burned areas would indicate that newly burned forests are colonized primarily by natal

dispersers, whereas a similar population age structure in forests of different ages postfire or a prevalence of older birds in more recently burned areas would suggest that breeding dispersal of adult birds plays a larger role in the colonization of new burns.

METHODS

Between 2011 and 2015, we captured Black-backed Woodpeckers in 6 recently burned areas distributed across much of the species' range in California, USA: the 2009 Barry Point fire in Modoc National Forest; the 2009 Sugarloaf fire in Lassen National Forest; the 2008 Peterson Complex fire in Lassen National Forest; the 2007 Wheeler fire in Plumas National Forest; the 2013 Rim fire in Stanislaus National Forest; and the 2007 Moonlight fire in Plumas National Forest (Figure 1). Prior to the fires, all 6 burned areas were dominated by Sierra Mixed Conifer or Eastside Pine forest (California Department of Fish and Game 2005), at least in the areas where we captured woodpeckers. The 6 fires ranged in size from 1,161 ha (Peterson Complex fire) to 104,131 ha (Rim fire), and resulted in a mosaic of burn severities that in all 6 cases included substantial areas of vegetation affected at medium and high severity.

Birds were captured for numerous purposes, including radio-tagging for studies of home-range size and habitat selection (Siegel et al. 2014, Tingley et al. 2014). In all cases, sampling was essentially random from local populations of adult Black-backed Woodpeckers. We located birds by broadcasting recordings of vocalizations and drumming across large portions of the burned areas, targeting primarily areas that had burned at high or mixed severity and were proximal to roads. When birds responded, we attempted to lure them into a mist net with continued broadcasts and a wooden decoy of a Black-backed Woodpecker placed near the net. In a few instances, we caught birds in a hoop net as they exited their nest cavity. To avoid causing nest abandonment, we used hoop nets only after confirming that eggs had already hatched and that nestlings were at least several days old.

We captured, photographed, and determined the age of 57 adult Black-backed Woodpeckers (40 males and 17 females) during the nesting season in the 6 areas, which had burned between 1 and 8 yr prior to sampling (Table 1). One area (Wheeler) was sampled in 2 successive years (5 and 6 yr postfire, respectively). Three individuals were caught at this site in both years; we included them in the dataset for each respective year, yielding 60 total age determinations, to maintain a random sampling of the birds present in each year.

We aged each woodpecker according to previous molt patterns, which resulted in 1 or more generations of feathers among primary coverts, secondaries, and second-

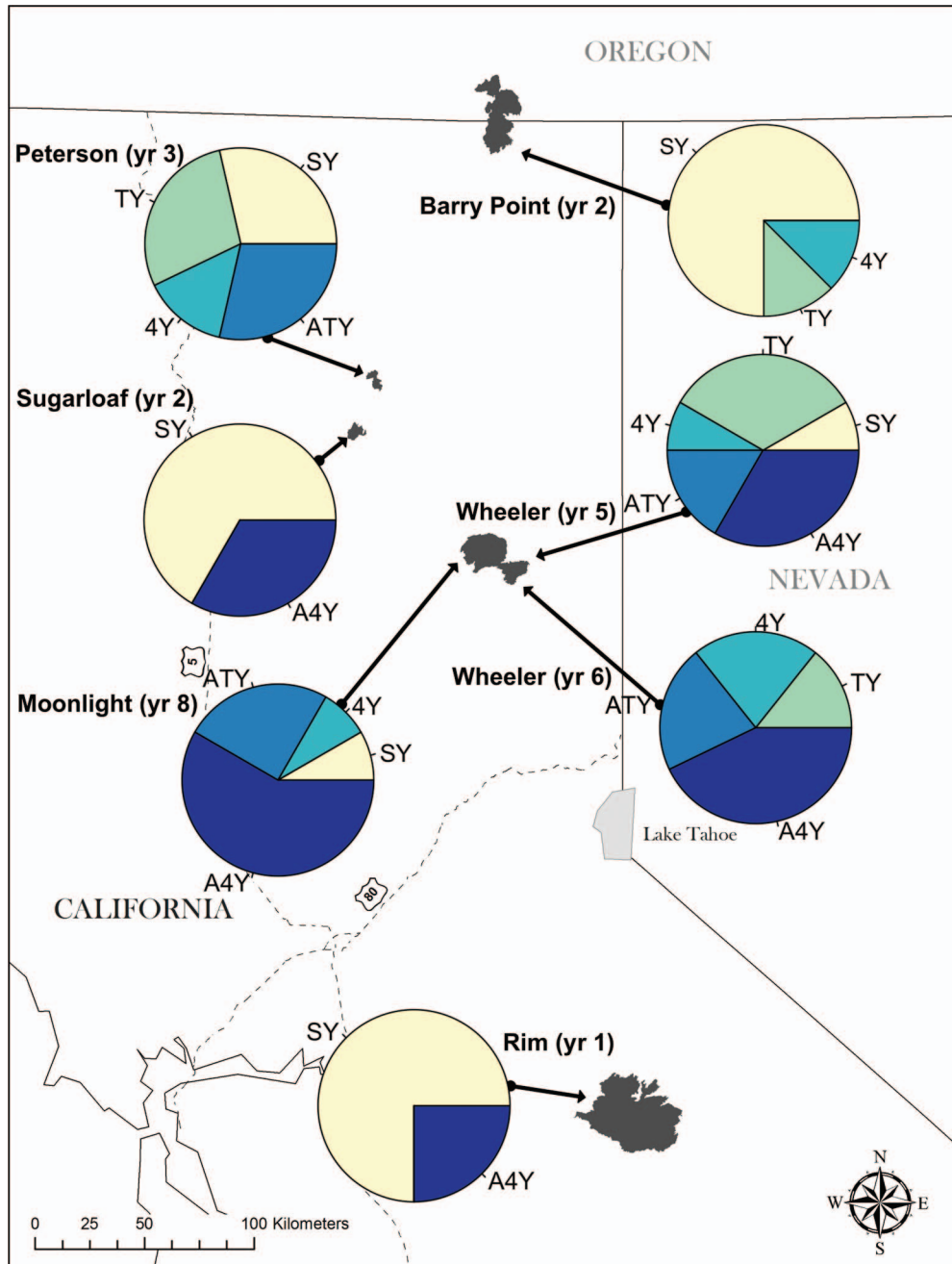


FIGURE 1. Locations of 6 fire areas in California where adult Black-backed Woodpeckers were sampled between 1 and 8 yr postfire. Pie charts indicate the proportion of individual birds classified as second-calendar-year (SY), third-calendar-year (TY), fourth-calendar-year (4Y), after-third-calendar-year (ATY; likely includes a mix of 4Y and A4Y individuals), or after-fourth-calendar-year (A4Y) at each fire area.

ary coverts (Pyle and Howell 1995, Pyle 1997; Figure 2). During each capture, we photographed each of these feather tracts on the dorsal surface of the wing. One of us (P. Pyle), who did not participate in capturing the birds and did not know the ages of the burns, then inspected the photographs and determined the age class of each captured bird. We initially identified our 60 captures into

15 second-calendar-year (SY), 9 third-calendar-year (TY), and 36 birds older than third-calendar-year (ATY) based on the criteria presented in Pyle and Howell (1995) and Pyle (1997), as illustrated in Figures 2A–2C.

During careful analysis of the images, we gained confidence that we could age some of the ATY birds to either fourth-calendar-year (4Y) or older than fourth-

TABLE 1. Summary of Black-backed Woodpecker captures in 6 burned areas across the species' range in California, USA, between 2011 and 2015. Note that the Wheeler fire was sampled in 2 successive years.

Fire name	Year of fire	Years since fire when sampled	No. of birds captured
Rim	2013	1	4
Barry Point	2012	2	8
Sugarloaf	2009	2	3
Peterson	2008	3	7
Wheeler	2007	5	12 ^a
Wheeler	2007	6	14 ^a
Moonlight	2007	8	12
TOTAL			60

^a Includes 3 individuals captured in both 2012 and 2013.

calendar-year (A4Y) based on precise positions and generations of replaced and retained primary coverts (Figure 3). Among 36 woodpeckers initially aged as ATY, we assigned 7 birds to 4Y according to patterns in the primary coverts shown in figure 5F of Pyle and Howell (1995) and figure 122F of Pyle (1997), in which 1 or 2 worn juvenile coverts were retained among the 4th to 6th feathers from the outside and 2 generations of basic coverts were located distal to this (Figure 2D). These criteria were confirmed in 1 individual banded in 2012 as TY and recaptured in 2013 as 4Y (Figures 3A, 3B); however, we did not assume that all 4Y birds had retained juvenile coverts. By carefully analyzing the placement and age of retained and replaced basic coverts, we were able to separate the remaining 29 birds initially aged as ATY into 10 birds that could have been either 4Y or A4Y (retained as ATY; Figure 2C) and 19 birds showing patterns that we considered not attainable following the third prebasic molt of TY birds, which we therefore aged as A4Y (Figure 2E). Two individuals aged in 2012 as A4Y were recaptured in 2013 (Figures 3C–3F). Based on the patterns of feather replacement described above, 1 of these could only be aged as ATY (Figure 3D) and the other as A4Y (Figure 3E), although we considered both A4Y in our dataset based on their known history.

Statistical Analyses

We used generalized linear mixed models (GLMMs; Zuur et al. 2009) to test for statistical relationships between the number of years postfire and the age of woodpeckers inhabiting burned areas of that age. We modeled the expected age of woodpeckers as a Poisson-distributed variable with a log-linear relationship to the number of years since fire. Because all woodpeckers were captured in 1 of 6 burned sites, we also included a random effect of site to account for pseudoreplication. In addition to this basic model, we also fit 2 additional models, 1 with an additive

effect and 1 with an interactive effect, evaluating the additional potential effect of the sex of woodpeckers on age class distributions within burned areas. The 3 nested models were compared with likelihood ratio tests. All models were analyzed using R 3.2.1 (R Development Core Team 2015) using the lme4 package (Bates et al. 2015).

Based on the previously described age classifications, we converted the ordinal sequence SY, TY, 4Y, ATY, A4Y to the numerical values of 2, 3, 4, 5, and 6, respectively, for the purpose of Poisson modeling of the age of captured individuals. We additionally tried 2 other numerical conversions of age classes. First, we used only the classes SY, TY, and ATY (including 4Y and A4Y in ATY). Secondly, we used the classes SY, TY, 4Y, and A4Y (combining ATY and 4Y). We found that both of these alternative classifications provided statistically and inferentially similar results, and thus present only results for the classification with the greatest information content (i.e. most detailed resolution of age).

RESULTS

Population age structure varied dramatically across burned areas, with a preponderance of SY birds in areas 1 yr and 2 yr postfire, and a preponderance of 4Y, ATY, and A4Y birds in older burns (Figure 1). Results indicated a clear shift in age structure over time, with younger birds in more recently burned sites and older birds in areas that were burned less recently (Figure 4). Poisson GLMMs revealed a highly significant effect of years since fire on woodpecker age ($z = 3.575$, $P < 0.001$), with each additional year postfire increasing the log(age class) of woodpeckers present in a burned site by 0.10 ± 0.03 . We found no difference in woodpecker age distribution between the sexes. GLMMs including additive and interactive relationships of sex had no significant ($P \gg 0.05$) effects of sex on age. Likelihood ratio tests for both additive ($\chi^2 = 0.01$, $P = 0.90$) and interactive ($\chi^2 = 0.80$, $P = 0.67$) models indicated that the simpler model that excluded sex was the better fit.

DISCUSSION

Our ability to age some Black-backed Woodpeckers to 4Y and A4Y, based on positions of replaced and retained feathers, confirms previous suppositions that this may be possible (Pyle and Howell 1995, Pyle 1997). As most or all North American woodpeckers (Pyle 1997), and those worldwide for that matter (P. Pyle personal observation), generally show similar molt patterns, it is likely that determining age to 4Y and A4Y can also be accomplished for other woodpecker species. This may especially be the case for species that inhabit higher latitudes (e.g., American Three-toed Woodpecker [*Picoides dorsalis*]) and those that migrate (e.g., sapsuckers); both groups



FIGURE 2. Age-class determination of Black-backed Woodpeckers following Pyle and Howell (1995) and Pyle (1997): **(A)** second-calendar-year (SY) birds show uniformly juvenile primary coverts and secondaries and mixed formative secondary coverts; **(B)** third-calendar-year (TY) birds show 1–4 replaced outer primary coverts and 1–3 replaced inner coverts contrasting with at least 4 retained juvenile coverts in the center of the tract, usually show 1–5 retained juvenile secondaries in the middle of that tract, and show uniformly basic secondary coverts; and **(C)** after-third-calendar-year (ATY) birds show mixed generations of basic primary coverts, often mixed generations of basic secondaries, and uniformly basic secondary coverts. Further assignment of some ATY birds was made to **(D)** fourth-calendar-year (4Y) and **(E)** after-fourth-calendar-year (A4Y) based on the pattern of the primary coverts (see Figure 3).

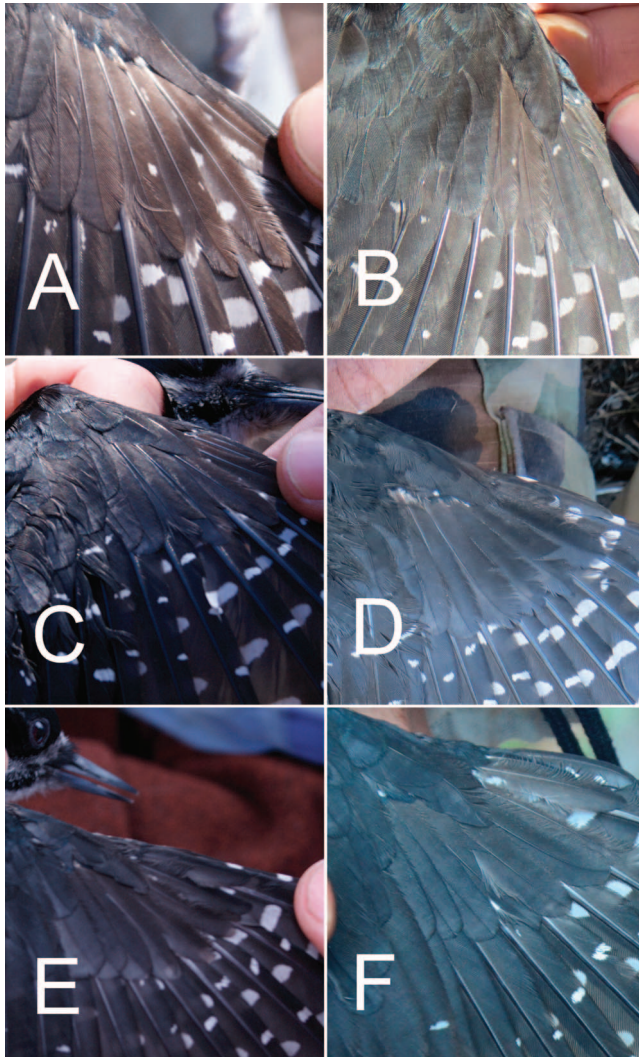


FIGURE 3. Replacement patterns among primary coverts of 3 Black-backed Woodpeckers captured in both 2012 and 2013, showing patterns enabling age determination of some birds to fourth-calendar-year (4Y) and after-fourth-calendar-year (A4Y). (A, B) A third-calendar-year (TY) bird captured in 2012 (A) with all but the outer 2 primary coverts juvenile; recaptured again in 2013 (B) showing the outer 2 coverts old basic, the next 2 and the inner 4 coverts replaced basic, and the 5th and 6th coverts from the outside still juvenile, a pattern indicating 4Y as indicated by Pyle and Howell (1995) and Pyle (1997). (C, D) A bird with a molt pattern not attainable by 4Y, i.e. retained basic feathers at the 3rd and 4th coverts from the outside, and thus aged A4Y in 2012 (C), but showing a pattern that may or may not indicate 4Y in 2013 (D), i.e. replaced basic coverts among the 4th–5th coverts from the outside, and thus aged ATY in 2013 based on molt patterns alone. (E, F) A bird aged A4Y in both 2012 (E) and 2013 (F), with molt patterns not attainable in a 4Y bird, including retained basic feathers at the 3rd–6th coverts from the outside in 2012 and again at the 3rd and 4th coverts from the outside in 2013.

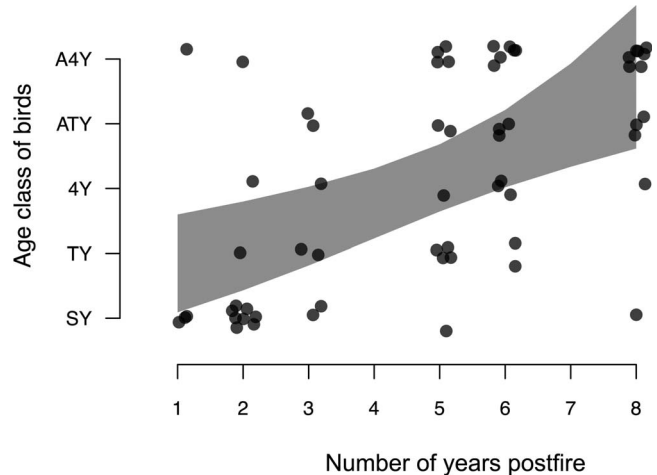


FIGURE 4. Relationship between the number of years since fire and the age of Black-backed Woodpeckers ($n = 60$ captures of 57 individuals) captured across 6 fire areas. Points are jittered slightly to reveal overlapping values in the number of birds of each age class captured at the indicated number of years after fire. No burned areas were sampled at 4 yr or 7 yr postfire. Gray area shows the 95% confidence interval around the generalized linear mixed model (GLMM) fitted relationship between years since fire and woodpecker age.

appear to average fewer feathers replaced, likely due to time constraints related to the onset of winter or the need to migrate, respectively.

SY birds predominated in burned areas sampled 1 or 2 yr postfire, and then became increasingly uncommon in older burns. Even with relatively small sample sizes in the younger burns, the relationship between woodpecker age class and years since fire was strong enough to indicate that natal dispersal by young birds, rather than breeding dispersal by older birds, was the primary means by which newly burned areas were colonized. Older birds were encountered in newly burned areas, but much less frequently than SY birds. One of the birds that we captured in the Rim fire area (1 yr after fire) was an A4Y female, and we captured 1 4Y female and 1 A4Y male in the Barry Point and Sugarloaf fire areas, respectively (both 2 yr after fire).

The occasional presence of older birds as apparent colonizers could be explained by several scenarios. Long-distance breeding dispersal appears to occur occasionally, even if it is far less important than natal dispersal for colonizing newly burned forest. Indeed, postfire population density has been reported to plummet as early as 3 (Québec; Nappi and Drapeau 2009) or 4 (Black Hills, South Dakota, USA; Vierling et al. 2008) yr after fire in other portions of the species' range. Such rapid declines in postfire Black-backed Woodpecker populations are unlikely to be related to senescence in the population; rather, they likely reflect a capacity for breeding dispersal. Evidence for early abandonment of burned areas, and

seasonal irruptions, comes primarily from eastern populations of the species. In western forests, neither seasonal irruptions nor early abandonment of occupied burned areas is generally observed (Saab et al. 2007, Saracco et al. 2011), suggesting that the propensity for long-distance movements in general, and dispersal dynamics in particular, may differ from that of eastern populations. The occasional presence of older birds as colonizers in western populations may also result from adults dispersing relatively short distances from nearby areas that burned in the recent past (i.e. within the lifespan of individual birds), or from adults that may have already been present within the area at low densities prior to fire (Fogg et al. 2014) and simply remained there after fire.

The increasing rarity of SY birds in older burned areas suggests that young birds become increasingly less likely to recruit into the adult population within their natal area as years pass, and presumably become more likely to disperse. Recruitment (whether local or long-distance) of young birds in the later postfire years is uncommon; nevertheless, some young birds are recruited into older burned areas, as evidenced by the fact that we encountered an SY female in the Moonlight fire site, which we sampled 8 yr postfire.

Our results do not support the prediction of Dale et al. (2004) that inherently rare species with patchy distributions will tend to exhibit greater breeding dispersal distances compared with natal dispersal distances. Rather, our findings are consistent with the general pattern observed in birds of high adult breeding-site fidelity, lower natal philopatry, and greater natal dispersal distances compared with breeding dispersal distances (Greenwood 1980, Greenwood and Harvey 1982, Paradis et al. 1998). Breeding dispersal could permit a bird to breed at a higher-quality site or, during subsequent reproductive efforts, with a higher-quality mate. However, these potential advantages of dispersal are balanced by the risk that a dispersing bird may fail to find a new site, a new mate, or both, and may lose all reproductive potential, or that the new site or mate may be of lower quality. Furthermore, remaining or reuniting with a prior mate or retaining a territory across seasons may be beneficial because breeding at a familiar site or with a familiar mate may have reproductive advantages (Oring and Lank 1982, 1984, Schieck and Hannon 1989, Johnson and Walters 2008). For Black-backed Woodpeckers, even though beetle larvae abundance presumably declines in the later postfire years, these advantages may be strong enough to counterbalance the possible advantages of dispersing in search of areas with more food. The limited information available corroborates high site fidelity in Black-backed Woodpeckers in western forests (Dixon and Saab 2000) and in the Black Hills of South Dakota, at least among individuals that nested successfully in the prior year (Rota 2013).

Reproductive success improves with age during the first few years of reproductive life for the majority of bird species (Clutton-Brock 1988, Newton 1988, Sæther 1990), although information is lacking for Black-backed Woodpeckers specifically. Knowing the location of resources (food, potential nest sites) and predators makes a familiar site more valuable than an unfamiliar site (Pärt 1994). Older, more experienced, male Black-backed Woodpeckers that are site-faithful may occupy the highest quality sites in older burned areas and thus may attract older, more productive, site-faithful females. If Black-backed Woodpeckers have a good chance of occupying a sufficiently high-quality territory and acquiring or retaining a high-quality mate, the benefits of breeding-site fidelity may outweigh the risks of dispersal for birds in older burned areas, despite waning prey populations. Evidence that Black-backed Woodpecker home ranges enlarge with time since fire (Dudley and Saab 2007, Rota et al. 2014, but see Tingley et al. 2014) may indicate how older birds are able to cope with declining food abundance.

The increasingly large proportion of older birds in older burned areas, along with the evidence that we have presented that older birds rarely colonize newly burned areas, supports the hypothesis that the eventual postfire decline in Black-backed Woodpecker populations signifies not that adult birds commonly abandon their established breeding territories to emigrate to new areas, but rather that colonizers or their offspring in the early years after fire likely remain in the burned area for their entire lives. The observed declines and disappearances of Black-backed Woodpeckers from occupied burned areas in western forests between 6 and 10 yr postfire likely reflect attrition and the inherent lifespan of Black-backed Woodpeckers as much as the persistence of highly abundant insect prey in the postfire period.

Burned forests favored by Black-backed Woodpeckers are frequently targeted for salvage logging or other management activities that reduce habitat suitability or eliminate habitat altogether. The preponderance of young birds in more recently burned areas suggests that populations there have a greater potential for future reproductive output (because the birds presumably have more breeding years ahead of them) than older populations occupying areas that burned less recently. Any landscape-level conservation planning for Black-backed Woodpeckers should therefore prioritize newly burned areas for habitat retention rather than older burned areas, perhaps even when older burns are known to be occupied. Indeed, the tendency of older birds to not disperse out of a burned area once they have bred there provides a caution that occupancy of older burned sites may not be a particularly good indicator of habitat quality.

More generally, the age structure of populations is a key element necessary to understanding the population

dynamics of species. Age structure data can be combined with data on vital rates and occurrence (e.g., Saracco et al. 2011) to develop region-wide inference about the fundamental drivers of change in population size or demographic rates (Schaub and Abadi 2011). Such integrated population models have proven powerful for understanding long-term trends in long-lived species through the merging of multiple, independent sources of information on abundance, demography, and trends (Tempel et al. 2014). To this end, age structure information—as resolved through the determination of additional age classes from plumage characteristics—could be leveraged with other datasets on Black-backed Woodpeckers to better understand metapopulations and source–sink dynamics of this species.

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