

Positive effects of fire on birds may appear only under narrow combinations of fire severity and time-since-fire

Richard L. Hutto^{A,C} and David A. Patterson^B

^ADivision of Biological Sciences, 32 Campus Drive #4824, University of Montana, Missoula, MT 59812, USA.

^BDepartment of Mathematical Sciences, 32 Campus Drive #0864, University of Montana, Missoula, MT 59812, USA.

^CCorresponding author. Email: hutto@mso.umt.edu

Abstract. We conducted bird surveys in 10 of the first 11 years following a mixed-severity fire in a dry, low-elevation mixed-conifer forest in western Montana, United States. By defining fire in terms of fire severity and time-since-fire, and then comparing detection rates for species inside 15 combinations of fire severity and time-since-fire, with their rates of detection in unburned (but otherwise similar) forest outside the burn perimeter, we were able to assess more nuanced effects of fire on 50 bird species. A majority of species (60%) was detected significantly more frequently inside than outside the burn. It is likely that the beneficial effects of fire for some species can be detected only under relatively narrow combinations of fire severity and time-since-fire. Because most species responded positively and uniquely to some combination of fire severity and time-since-fire, these results carry important management implications. Specifically, the variety of burned-forest conditions required by fire-dependent bird species cannot be created through the application of relatively uniform low-severity prescribed fires, through land management practices that serve to reduce fire severity or through post-fire salvage logging, which removes the dead trees required by most disturbance-dependent bird species.

Additional keywords: Black-backed Woodpecker, conifer forest, ecological integrity, fire severity, mixed-severity fire, restoration, salvage logging, wildfire.

Received 22 July 2015, accepted 26 May 2016, published online 11 July 2016

Introduction

The earliest synthesis of fire effects on birds (Kotliar *et al.* 2002) revealed that many species respond positively, others negatively and still others in a mixed fashion to burned forest conditions. Perhaps the most important pattern that emerged from this synthesis is that some species (the more extreme including the American Three-toed Woodpecker (*Picoides dorsalis*), Black-backed Woodpecker (*Picoides arcticus*), Mountain Bluebird (*Sialia currucoides*) and Tree Swallow (*Ichthyophaga bicolor*)) are relatively abundant in burned forest conditions. One (the Black-backed woodpecker) is even relatively restricted in its distribution to such conditions. For example, Hutto (1995) reported that 15 species were more abundant in burned forests than they were in any of the other 14 vegetation types included in his meta-analysis. This carries important management implications because those species may depend to a large extent on fire to create the habitat conditions they need for persistence – habitat conditions that are severely compromised by fire prevention, fire suppression, and post-fire salvage logging, seeding, tree planting and removal of native shrubs (Saab and Dudley 1998; Kotliar *et al.* 2002; DellaSala *et al.* 2006; Hutto and Gallo 2006; Hutto 2008; Saab *et al.* 2009; Swanson *et al.* 2011; DellaSala *et al.* 2014; Tingley *et al.* 2014).

Until very recently, studies of fire effects did not distinguish the effects of low-severity, mixed-severity and high-severity fires. Therefore, reported responses of species were oftentimes different from one study to the next, and terms like ‘mixed responder’ were included in tables generated from synthetic work on fire effects (Kotliar *et al.* 2002). Kotliar *et al.* (2005) noted that fire severity, time-since-fire, vegetation type and other considerations could probably explain some of the variation among studies, but it was not until Smucker *et al.* (2005) characterised the severity of the fire surrounding each of a series of survey points that bird responses to fire became much less ambiguous and remarkably consistent. Smucker *et al.* (2005) proposed that most bird species respond predictably to fire, but that the type of response (positive or negative) depends strongly on fire severity. Subsequently, numerous studies (e.g. Covert-Bratland *et al.* 2006; Kirkpatrick *et al.* 2006; Conway and Kirkpatrick 2007; Koivula and Schmiegelow 2007; Kotliar *et al.* 2007; Hanson and North 2008; Kotliar *et al.* 2008; Vierling and Lentile 2008; Nappi *et al.* 2010; Nappi and Drapeau 2011; Dudley *et al.* 2012; Fontaine and Kennedy 2012; Lee *et al.* 2012; Lindenmayer *et al.* 2014; Rush *et al.* 2012; Hutto *et al.* 2015; Stephens *et al.* 2015) have demonstrated a marked effect of fire severity on either the occurrence or breeding success of selected

bird species. In addition to fire severity, the number of years following a fire event (time-since-fire) can have significant influence on bird response. Again, there are some important studies that have included early vs later stages of succession after fire in their analyses of bird occurrence patterns (Taylor 1973, 1979; Taylor and Barmore 1980; Raphael *et al.* 1987; Breininger and Smith 1992; Hutto *et al.* 1995; Pyke *et al.* 1995; Ganey *et al.* 1996; Woinarski *et al.* 1999; Bechtoldt and Stouffer 2005; Covert-Bratland *et al.* 2006; Saab *et al.* 2007; Vierling and Gentry 2008; Brown *et al.* 2009; Chalmandrier *et al.* 2013; Holmes *et al.* 2013; Hutto *et al.* 2015). Taken together, results from these two kinds of studies suggest that the simultaneous consideration of severity and time-since-fire might allow us to detect fire effects that are even more nuanced.

The purpose of this study was to document the response of native bird species to the Black Mountain fire, a 3500-ha, lightning-caused, mixed-severity fire that burned through a lower-elevation dry, mixed-conifer forest immediately west of Missoula, Montana, in 2003. Using point-count data from each of 10 years following the fire, we compared the occurrence rates of bird species in a variety of burned forest conditions across a space-time continuum with their occurrence rates in surrounding unburned forest of the same vegetation type. This study was designed to test whether a combination of fire severity and time-since-fire is necessary to expose some positive effects of fire on birds in dry, mixed-conifer forest, which is common across the mountainous West.

Methods

Study area

Situated at the south-west edge of the city of Missoula, Montana, United States, the 2003 Black Mountain fire started in mature, low-elevation, mixed-conifer forest dominated by Ponderosa Pine (*Pinus ponderosa*), Western Larch (*Larix occidentalis*), Lodgepole Pine (*Pinus contorta*), and Douglas-fir (*Pseudotsuga menziesii*) on 8 August as the result of a lightning strike. The fire burned slowly until it grew rapidly on 16 August when it spread across 1500 ha in 2 h and prompted the evacuation of 130 homes; it eventually burned ~3500 ha. The spatio-temporal effects of the Black Mountain fire and their relationship with wildland fire hazard and risk were discussed by Hardy (2005), the fire was also the subject of several studies that were designed to measure the effectiveness of the severity classifications associated with the Burned Area Reflectance Classification (BARC) map that was generated following the fire (Hudak *et al.* 2004; Hudak *et al.* 2007; Lentile *et al.* 2007).

Overall design

There are limits to case history studies of single fire events due to the lack of treatment replication, but it is nearly impossible to attain true treatment-level replication of severe-fire events in either an experimental or natural fashion; case studies are *sine qua non* in fire ecology (Hargrove and Pickering 1992). Therefore, fire ecologists must take advantage of individual opportunities that arise, and then rely on meta-analyses at some point in the future to understand the extent to which results can be safely generalised more broadly beyond any single event.

To assess fire effects, we sought to compare bird occurrence rates in the burned forest to those we would have expected to observe in the absence of fire. As is true with most unplanned natural disturbance events, no bird surveys had been conducted within the burned area before the fire, so we estimated what the occurrence rates of bird species in the study area were likely to have been before the fire by drawing samples from a subset of the Northern Region Landbird Monitoring Program database (Hutto and Young 2002). Point-count locations were positioned in unburned but otherwise similar (dry, low-elevation, mixed-conifer) forest within a 100-km² block centred on the fire using methods identical to those used in this study (Fig. 1). We used data from the most recent year sampled at each point, which yielded 717 points that were surveyed sometime between 1992 and 2009. Although bird occurrence rates certainly vary across space and time, that variation is very small relative to variation among vegetation types. Therefore, the large number of points drawn from a variety of locations and years should serve to swamp outlier places or years that might otherwise bias an estimate of the 'average' occurrence rate for each species in a typical unburned mixed-conifer forest.

We used a digital orthophoto of the fire perimeter to initially position 279 bird survey points throughout the burned area, spacing points no closer than ~200 m from any other point. Beginning 9 months after the fire and for 10 of the first 11 years following the fire, one of the authors (RLH) visited an average of 100 (range = 77–127) points every post-fire year except 2008 within a 6 × 2 km rectangle that covered the south-east portion of the fire (Fig. 1). The survey locations were well distributed across the study area in each year, although the precise locations varied somewhat from year to year because of variation in survey routes taken by the observer. A given point may or may not have been visited in more than one year; specifically, the numbers of points visited from 1 to 10 times across years were 80, 37, 29, 14, 17, 41, 39, 12, 9 and 1, respectively. In most instances, points were visited on a single occasion in any given year (of 1087 point visits across all years, only 29 were visited multiple times in a given year). In instances where points were visited more than once in a given year, we randomly selected one of the visits for analysis. Thus, data associated with each point are represented by a single visit in each year. A summary of survey effort (numbers of independent survey points) across the combinations of fire severity and time-since-fire are presented in Table 1.

Bird surveys

Point counts were conducted during the height of the breeding season every year (last week of May to the first week of July) and lower elevations were visited earlier in the season than higher elevations. On a given visit to each point, we used standard 10-min point-count methodology (Hutto *et al.* 1986; Ralph *et al.* 1995) to record the distance to and identity of each bird detected by either sight or sound between 0630 and 1130 hours. We also recorded an on-the-ground visual estimate of tree mortality percentage (1–20%, 21–40%, 41–60%, 61–80% and >80%) within 100 m of each survey point during each of the first 2 years after the 2003 fire and used the mean value as an index of fire severity surrounding the point.

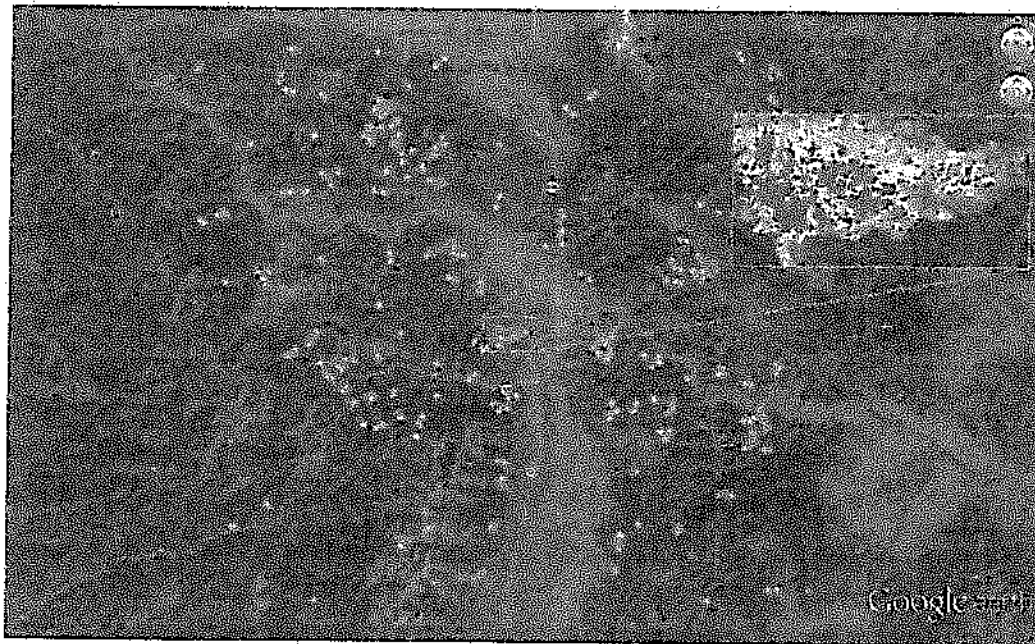


Fig. 1. The small rectangle encloses the bird survey points that were positioned within the 2003 Black Mountain fire perimeter, 5 km west of Missoula, Montana. The larger 100-km² area surrounding the rectangle shows the locations of the 717 unburned-forest bird survey points outside the fire perimeter. Source: Google Earth.

Table 1. The number of independent surveys (point-counts) that were conducted in each combination of time-since-fire and fire severity within the Black Mountain fire near Missoula, Montana, USA

Fire severity (tree mortality)	Two-year interval				
	2004–2005	2006–2007	2009–2010	2011–2012	2013–2014
1–40%	35	36	40	59	57
41–80%	47	51	65	85	97
>80%	100	97	84	108	126

Statistical analyses

Because the numbers of individuals of any one species are notoriously difficult to estimate during a 10-min count, the most reliable information that can be obtained from a point count is the presence or absence of a species (Hutto 2016). Therefore, we recorded the species detected within a fixed, 100-m radius surrounding each survey point and used the proportion of points at which a species was detected (naïve occupancy) as a response variable to reflect bird abundance. We did not employ occupancy modelling (MacKenzie *et al.* 2006) or distance sampling to estimate bird density (Buckland *et al.* 2001) because points were visited only once in a given year, sample sizes for most species were too small to estimate reliable detection functions and mean detection distances to all bird species in the unburned and burned forest types (the most important potential source of detectability bias) were not significantly different (46.6 m vs 47.1 m; $t = -1.14$, d.f. = 15 810, $P = 0.26$). In addition, several fundamental assumptions associated with distance sampling

could not be met; these include the assumptions that (1) there is no bird movement in response to the observer, (2) changes in vegetation with distance from the observer do not confound the effect of distance alone, (3) observers can obtain accurate estimates of the number of individuals of each species surrounding a point and (4) observers can obtain accurate estimates of distances to birds that were heard but not seen (90% of all detections). Welsh *et al.* (2013) discussed why these and other problems can lead to biases that are as bad as or worse than those that might be present in unadjusted data. Johnson (2003) also discussed instances where simple indices, such as percentage occurrence, are likely to be more reliable than distance-adjusted density estimates and a multi-species survey is one of those instances. To confirm that the patterns we describe are not artefacts of detection bias, we conducted an additional analysis based on data drawn from a very limited 50-m radius, where detections can be assumed to be very near 100% for most species, none of the bird distribution patterns was affected by the

use of this more restricted dataset. Analyses were conducted on 50 species that were detected on at least 10 point-counts (either inside or outside the fire perimeter), were not wide-ranging large raptors and were not restricted to riparian or wetland habitats embedded within the mixed-conifer forest.

We started with a traditional analytical approach, where we used Chi-square test analyses to investigate whether the probability of occurrence of any given bird species differed significantly between burned and unburned points. We then conducted a more refined analysis to assess whether there were differences in percentage occurrence between the surrounding unburned mature forest and any combination of fire severity and time-since-fire. To smooth out smaller-scale variability and to achieve adequate sample sizes in each combination of fire severity and time-since-fire, we first aggregated the counts for each species into 3 fire-severity levels (1–40%, 41–80% and 81–100% tree mortality) and 5 2-year periods (2004–2005, 2006–2007, 2009–2010, 2011–2012 and 2013–2014), which produced counts for 15 combinations of fire severity and time-since-fire. We then computed the odds ratio of seeing a species in each of the 15 combinations relative to the surrounding unburned (equivalent to pre-fire) forest. Since there were some 0 counts, we added 0.5 to all counts for all species (Agresti 2002). The odds ratio for fire severity level i and time period j for a given species is:

$$\hat{\theta}_{ij} = \frac{(x_{ij1} + 0.5)/(x_{ij0} + 0.5)}{(x_{b1} + 0.5)/(x_{b0} + 0.5)}$$

where x_{ij1} and x_{ij0} are the numbers of points where the species was and was not detected, in fire severity level i during time period j , and x_{b1} and x_{b0} are the analogous counts for the outside-fire base (labelled 2003 along the year axis, but representing data from outside the burn, regardless of year that the data were collected). An approximate standard error for $\log \hat{\theta}_{ij}$ is (Agresti 2002):

$$SE(\log \hat{\theta}_{ij}) = \left(\frac{1}{x_{ij1} + 0.5} + \frac{1}{x_{ij0} + 0.5} + \frac{1}{x_{b1} + 0.5} + \frac{1}{x_{b0} + 0.5} \right)^{1/2}$$

To assess the statistical significance of the odds ratio we computed $z_{ij} = \log \hat{\theta}_{ij} / SE(\log \hat{\theta}_{ij})$ (the expected value of the log-odds ratio is 0 when the true-odds ratio is 1). Because we ran over 700 comparisons in total, we calculated Bonferroni-adjusted P -values to provide an estimate of the statistical significance associated with each odds ratio. All data manipulation and plots were conducted in R (R Core Team 2014) using packages dplyr (Wickham and François 2015), tidyr (Wickham 2014) and ggplot2 (Wickham 2009).

Results

We detected a total of 107 bird species in the combined dataset drawn from burned and unburned forests, and 50 of those species met target requirements for inclusion in analyses as described in the methods (Table 2). By grouping points into two categories (burned-forest and unburned-forest points) and then calculating the percentage occurrence rates of each species inside and

outside the burned forest (Table 2), we found 25 species to be more abundant in the burned forest (23 significantly so; $P < 0.05$), and 25 to be more abundant outside the burned forest perimeter (21 significantly so; $P < 0.05$). In contrast, a majority of species (60%) was significantly more likely to be detected in at least one category representing a particular combination of fire severity and time-since-fire within the burned forest than within mature, unburned, green-tree forests of the same type (Fig. 2). Although most species responded positively at 1 or more combinations of fire severity and time-since-fire, not all species responded positively in the same way. To help visualise the positive and negative responses to fire and the differences in patterns of response among species, we colour-coded the odds ratios associated with a comparison of the occurrence rates for a species in each combination of fire severity and time-since-fire and its occurrence rate in unburned forest outside the fire perimeter (Fig. 2).

Fourteen (28%) of the 50 species revealed significantly greater abundances within than outside the burned forest within 2 years following fire, most commonly in the moderate or severely burned forest patches (Fig. 2). These included four woodpecker species (Black-backed Woodpecker, Hairy Woodpecker (*Picoides villosus*), American Three-toed Woodpecker and Northern Flicker (*Colaptes auratus*)) several thrush species (Western Bluebird (*Sialia mexicana*), Mountain Bluebird, Townsend's Solitaire (*Myadestes townsendi*)), two flycatcher species (Western Wood-Pewee (*Contopus sordidulus*) and Dusky Flycatcher (*Empidonax oberholseri*)), and two seed-eating specialists (Cassin's Finch (*Haemorhous cassinii*), Pine Siskin (*Spinus pinus*)), among others (e.g. Rock Wren (*Salpinctes obsoletus*), Lazuli Bunting (*Passerina amoena*), Chipping Sparrow and (*Spizella passerina*)).

Several additional species exhibited significant but delayed increases in abundance within the burned forest (e.g. Tree Swallow, Lewis's Woodpecker (*Melanerpes lewis*), Pygmy Nuthatch (*Sitta pygmaea*), Dusky Grouse (*Dendragapus obscurus*), Vesper Sparrow (*Pooecetes gramineus*), White-breasted Nuthatch (*Sitta carolinensis*), Calliope Hummingbird (*Selasphorus calliope*) and Williamson's Sapsucker (*Sphyrapicus thyroideus*); Fig. 2).

The significantly positive response to fire was, for several species (e.g. Pygmy Nuthatch, Calliope Hummingbird, Cassin's Finch, Brown-headed Cowbird (*Molothrus ater*), Red Crossbill (*Loxia curvirostra*), Pine Siskin, Red-breasted Nuthatch (*Sitta canadensis*), Hammond's Flycatcher (*Empidonax hammondi*) and Hermit Thrush (*Catharus guttatus*)), relatively restricted to the lowest fire severity category (Fig. 2). A relatively large number of additional species (MacGillivray's Warbler (*Geothlypis tolmiei*), Common Raven (*Corvus corax*), Pileated Woodpecker (*Dryocopus pileatus*), Western Tanager (*Piranga ludoviciana*), Evening Grosbeak (*Coccothraustes vespertinus*), Yellow-rumped Warbler (*Setophaga coronata*), Mountain Chickadee (*Parus gambeli*), Cassin's Vireo (*Vireo cassinii*) and Ruby-crowned Kinglet (*Regulus calendula*)) showed a similar but non-significant response to fire.

Only six (12%) of the 50 species (Steller's Jay (*Cyanocitta stelleri*), Black-capped Chickadee (*Parus atricapillus*), Gray Jay (*Perisoreus canadensis*), Townsend's Warbler (*Setophaga townsendi*), Swainson's Thrush (*Catharus ustulatus*) and

Table 2. Bird species detected at survey points within burned or surrounding unburned mixed-conifer forest

The list excludes species detected on fewer than 11 points, riparian specialists, and raptors. The location where a species was more frequently detected is shown in bold. The last column shows the level of significance of any difference based on a Chi-square test. The four-letter mnemonic code for each species is provided in parentheses after the Latin binomial. Statistically significant differences are based on Chi-square likelihood ratio ($P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$)

Species	Burned ($n = 1087$)		Unburned ($n = 717$)		P^A
	Hits	%	Hits	%	
Dusky Grouse, <i>Dendragapus obscurus</i> (DUGR)	46	4.23	2	0.28	***
Calliope Hummingbird, <i>Selasphorus calliope</i> (CAHU)	75	6.90	14	1.95	**
Lewis's Woodpecker, <i>Melanerpes lewis</i> (LEWO)	15	1.38	0	0	***
Williamson's Sapsucker, <i>Sphyrapicus thyroideus</i> (WISA)	58	5.34	14	1.95	***
Hairy Woodpecker, <i>Picoides villosus</i> (HAWO)	244	22.45	21	2.93	***
American Three-toed Woodpecker, <i>Picoides dorsalis</i> (ATTW)	38	3.50	4	0.56	***
Black-backed Woodpecker, <i>Picoides arcticus</i> (BBWO)	76	6.99	0	0	***
Northern Flicker, <i>Colaptes auratus</i> (NOFL)	275	25.3	35	4.88	***
Pileated Woodpecker, <i>Dryocopus pileatus</i> (PIWO)	10	0.92	20	2.79	**
Olive-sided Flycatcher, <i>Contopus cooperi</i> (OSFL)	33	3.04	30	4.18	ns
Western Wood-Pewee, <i>Contopus sordidulus</i> (WEWP)	209	19.23	2	0.28	***
Hammond's Flycatcher, <i>Empidonax hammondi</i> (HAFH)	100	9.20	131	18.27	***
Dusky Flycatcher, <i>Empidonax oberholseri</i> (DUFL)	285	26.22	102	14.23	***
Cassin's Vireo, <i>Vireo cassinii</i> (CAVI)	94	8.65	195	27.20	***
Warbling Vireo, <i>Vireo gilvus</i> (WAVI)	96	8.83	142	19.8	***
Gray Jay, <i>Perisoreus canadensis</i> (GRAJ)	8	0.74	64	8.93	***
Steller's Jay, <i>Cyanocitta stelleri</i> (STJA)	2	0.18	19	2.65	***
Clark's Nutcracker, <i>Nucifraga columbiana</i> (CLNU)	43	3.96	15	2.09	*
Common Raven, <i>Corvus corax</i> (CORA)	16	1.47	22	3.07	ns
Tree Swallow, <i>Ichtyophaga bicolor</i> (TRES)	22	2.02	0	0	***
Black-capped Chickadee, <i>Parus atricapillus</i> (BCCH)	10	0.92	57	7.95	***
Mountain Chickadee, <i>Parus gambeli</i> (MOCH)	108	9.94	189	26.36	***
Red-breasted Nuthatch, <i>Sitta canadensis</i> (RBNU)	341	31.37	386	53.84	***
White-breasted Nuthatch, <i>Sitta carolinensis</i> (WBNU)	79	7.27	10	1.39	***
Pygmy Nuthatch, <i>Sitta pygmaea</i> (PYNU)	22	2.02	1	0.14	***
Brown Creeper, <i>Certhia americana</i> (BRCR)	12	1.10	17	2.37	*
Rock Wren, <i>Salpinctes obsoletus</i> (ROWR)	41	3.77	2	0.28	***
House Wren, <i>Troglodytes aedon</i> (HOWR)	384	35.33	0	0	***
Golden-crowned Kinglet, <i>Regulus satrapa</i> (GCKI)	2	0.18	120	16.74	***
Ruby-crowned Kinglet, <i>Regulus calendula</i> (RCKI)	152	13.98	321	44.77	***
Western Bluebird, <i>Sialia mexicana</i> (WEBL)	123	11.32	0	0	***
Mountain Bluebird, <i>Sialia currucoides</i> (MOBL)	403	37.07	8	1.12	***
Townsend's Solitaire, <i>Myadestes townsendi</i> (TOSO)	194	17.85	116	16.18	ns
Swainson's Thrush, <i>Catharus ustulatus</i> (SWTH)	48	4.42	280	39.05	***
Hermit Thrush, <i>Catharus guttatus</i> (HETH)	38	3.50	58	8.09	***
American Robin, <i>Turdus migratorius</i> (AMRO)	241	22.17	164	22.87	ns
Orange-crowned Warbler, <i>Oreothlypis celata</i> (OCWA)	118	10.86	115	16.04	***
MacGillivray's Warbler, <i>Geothlypis trichas</i> (MGWA)	151	13.89	151	21.06	***
Yellow-rumped Warbler, <i>Setophaga coronata</i> (YRWA)	394	36.25	462	64.44	***
Townsend's Warbler, <i>Setophaga townsendi</i> (TOWA)	55	5.06	281	39.19	***
Chipping Sparrow, <i>Spizella passerina</i> (CHSP)	676	62.19	319	44.49	***
Vesper Sparrow, <i>Poocetes gramineus</i> (VESP)	14	1.29	1	0.14	**
Dark-eyed Junco, <i>Junco hyemalis</i> (DEJU)	441	40.57	390	54.39	***
Western Tanager, <i>Piranga ludoviciana</i> (WETA)	295	27.14	372	51.88	***
Lazuli Bunting, <i>Passerina amoena</i> (LAZB)	163	15.00	11	1.53	***
Brown-headed Cowbird, <i>Molothrus ater</i> (BHCO)	164	15.09	74	10.32	**
Cassin's Finch, <i>Haemorrhous cassinii</i> (CAFI)	93	8.56	20	2.79	***
Red Crossbill, <i>Loxia curvirostris</i> (RECR)	77	7.08	39	5.44	ns
Pine Siskin, <i>Spinus pinus</i> (PISI)	184	16.93	131	18.27	ns
Evening Grosbeak, <i>Coccothraustes vespertinus</i> (EVGR)	3	0.28	16	2.23	***

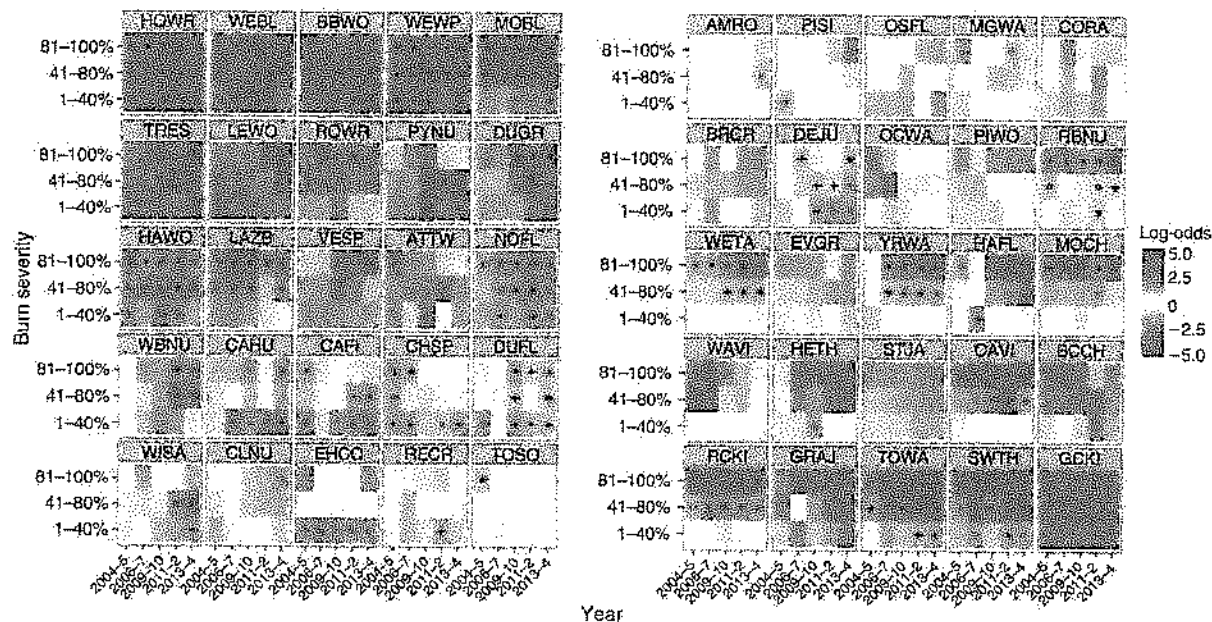


Fig. 2. Heat maps reflecting the log-odds ratio associated with the percentage occurrence in each combination fire severity and time-since-fire in comparison with the percentage occurrence in unburned forest outside the fire perimeter for each of 50 bird species (four-letter mnemonic codes provided in Table 2; species are organised by their average log-odds scores, from those that had a large average positive response to those that had a large average negative response to fire). Hotter (more red) blocks represent positive responses to fire and cooler (more blue) blocks represent negative responses to fire. The symbols correspond with Bonferroni adjusted P -values ($\diamond = 0.01 < P < 0.05$; $+$ $= 0.001 < P < 0.01$; $*$ $= P < 0.001$). Thirty of 50 species (60%) were significantly more abundant in burned forest at some combination of severity and time-since-fire than in unburned, mature green-tree forest.

Golden-crowned Kinglet (*Regulus satrapa*) were detected less frequently after fire, regardless of fire severity, and their detection rates generally continued to decrease over time (Fig. 2).

Discussion

Following the most common approach to assessing fire effects, we first looked at whether there were significant differences in bird abundances between the burned and surrounding unburned forest. The results from this analysis were consistent with those reported in many other studies of fire effects on birds (see Kotliar *et al.* 2002) – roughly half the bird species appeared to benefit and half did not (Table 2). Unfortunately, this kind of analysis hid positive responses that became apparent only after accounting for fire severity and time-since-fire. By dividing the burned-forest data into 15 combinations of fire severity and time-since-fire, we found results that were more nuanced than those obtained from a simple 'burned vs. unburned' analysis. Specifically, 30 of 50 (60%) of the bird species, considered were significantly more likely to occur inside the burned forest (at 1 or more combinations of fire severity and time-since-fire) than outside the burned forest. The distinct location of the greatest probability of detection for any 1 species across the 2-dimensional fire-severity and time-since-fire gradient, combined with differences in those locations among species (Fig. 2), suggests that the bird occurrence patterns are accurate reflections of bird abundance and not artefacts of some kind of sampling bias that might affect all species similarly. Other recent work (Stephens *et al.* 2015) has also revealed that the locations

of peak abundances across a fire-severity/time-since-fire gradient differ among species.

Many of these significantly positive responses would not have been evident without partitioning the data into multiple severity and time-since-fire categories. This kind of analysis is difficult to conduct with data from any one fire because sample sizes (the number of independent survey points in each severity-by-year category) are generally much smaller than what we were able to achieve here (Table 1). Even with the sample sizes we achieved, we were still forced to use fewer categories than the number used in the field to assess the statistical significance of fire effects. Although each bird species responded uniquely to the combination of fire severity and time-since-fire (Fig. 2), four general classes of response are worth noting, along with some of the most probable biological underpinnings behind each.

Response Pattern 1

This pattern is illustrated by species that showed an abrupt increase in abundance within the first few years following fire, and the elevated abundance persisted until the end of the 11-year study primarily (but not exclusively) in locations that burned at higher severities. Several woodpecker species (Black-backed Woodpecker, Hairy Woodpecker, American Three-toed Woodpecker and Northern Flicker) showed this response pattern (Fig. 2). The biological basis behind the abrupt increase in woodpecker populations is well established and unambiguous: bark and wood-boring beetle populations increase as individual beetles detect the newly created abundance of fire-killed trees.

In turn, developing larvae provide food for woodpeckers, which then respond numerically with an abrupt increase in abundance during the first year or two after fire. Relatively rare species like the American Three-toed and Black-backed woodpeckers are known to appear within months after fire (Blackford 1955; Villard and Beninger 1993; Villard and Schieck 1997). Their abundances then increase at a rate that is more rapid than expected if the increase were entirely the result of recruitment from inside the burn, so the increases are undoubtedly associated with colonisation by birds from outside the burned area, as others have noted (e.g. Van Tyne 1926; Koplin 1969; Yumick 1985; Hoyt and Hannon 2002; Huot and Ibarzabal 2006; Siegel *et al.* 2016). Perhaps the most iconic indicator of a severely burned mixed-conifer forest throughout the Sierra Nevadas of California, the Intermountain West and Canadian boreal forest is the Black-backed Woodpecker (Hutto 1995; Hanson and North 2008; Hutto 2008; Hutto *et al.* 2008; Nappi and Drapeau 2009; Swanson *et al.* 2011; Bond *et al.* 2012; Hutto *et al.* 2015). Although its pattern of response to fire is not much different than that of the American Three-toed Woodpecker, Hairy Woodpecker or Northern Flicker (Fig. 2), the key difference between this woodpecker and the others lies with the extent to which the species is restricted in its distribution to burned forest conditions. Other woodpecker species occur in green-tree forests to a much greater extent than the Black-backed Woodpecker; hence, the Black-backed Woodpecker is a better 'indicator' of severely burned forest conditions. The relatively high Black-backed Woodpecker occurrence rates across an 11-year period is somewhat surprising given the existing literature (Apfelbaum and Haney 1985; Hutto 1995; Murphy and Lehnhausen 1998; Hobson and Schieck 1999; Hoyt and Hannon 2002; Saab *et al.* 2007), which suggests that a 4–8-year window of opportunity is about all one can expect for this species before they begin to decline in abundance. It may very well be that the mixed-severity fire allowed this species to persist longer in this study than in most others because there was an abundance of weakened trees in the moderate- to low-severity border areas, which continued to provide adequate food resources after conditions in the more severely burned portions became less suitable. This mechanism of persistence beyond durations expected on the basis of averages gleaned from the literature has been suggested to operate elsewhere as well (Nappi *et al.* 2010; Dudley *et al.* 2012).

Other bird species (e.g. Cassin's Finch; Clark's Nutcracker, *Nucifraga columbiana*; Red Crossbill; Pine Siskin) that appear to respond abruptly and positively to more severe fire, do so for reasons that are most likely related to the abrupt increase in availability of seeds that are retained in cones that open in response to fire. Still other species in this group respond quickly to what is probably an increase in the availability of the combination of nest sites associated with standing-dead trees and open areas for foraging either on the ground (e.g. Western Bluebird and Mountain Bluebird) or in the air (e.g. Western Wood-Pewee) or to an increase in the availability of relatively predator-free nest sites at ground level from burned-out roots and root wads associated with wind-thrown trees (e.g. Rock Wren; Townsend's Solitaire; Dark-eyed Junco, *Junco hyemalis*). The Olive-sided Flycatcher (*Contopus cooperi*) makes special use of nest sites that are located in green-needled or

brown-needled trees on the edges of severely burned forest where they can sally into the openings created by crown fire.

Response Pattern 2

This pattern is illustrated by species that showed a slightly delayed increase in abundance, primarily (but not necessarily) in locations that burned at higher severities. If we had confined the study to the first year or two after fire, these positive responses to fire would have gone undetected. One of these species (Vesper Sparrow) appeared after a brief delay in the development of suitable grass-dominated patches, while several others (e.g. Dusky Grouse; Lazuli Bunting; Orange-crowned Warbler, *Oreothlypis celata*) were probably responding to the development of suitable shrub and seedling layers for foraging and nesting, which varied markedly from one place to another within the burn perimeter. Still other species (e.g. House Wren, *Troglodytes aedon*; Lewis's Woodpecker; Tree Swallow; Williamson's Sapsucker) were probably responding to a delayed increase in the availability of cavity nest sites that became available either after they were excavated by woodpeckers soon after fire or after the larger standing-dead trees began to soften with decay and break more easily in wind events. The House Wren clearly benefited from tree blowdown and breakage events that occurred in the first 6 years after fire; its abundance grew steadily to the point that it was the most abundant species in severely burned forest patches 6–11 years after fire.

Several authors (e.g. Hutto 1995; Gentry and Vierling 2007; Saab *et al.* 2007) have recognised a delayed increase in populations of Lewis's Woodpecker following severe fire, and it is clear that the benefit of severe fire to this woodpecker species would not have been detected in this study had the data collection period been restricted to the first few years after fire. The delayed positive responses of other species (e.g. Williamson's Sapsucker and White-breasted Nuthatch) have not been described previously and they are notable, as we discuss more fully below. Williamson's Sapsucker is noteworthy in that its distribution was nearly restricted to edge conditions between unburned forest patches (where it fed on sap of living trees) and adjacent burned forest patches (where it nested in relatively large, decayed or broken-topped trees that became abundant after wind events in severely burned patches created them a decade or so after fire). The delayed increase in White-breasted Nuthatch detections may be related to the increase in availability of insects beneath thick bark after the bark began to peel away from, or slough off, dead Ponderosa Pine, Western Larch, and Douglas-fir. Finally, the delayed increase by Western Bluebird represents a pattern that has received considerable attention (Duckworth and Badyaev 2007; Duckworth 2008, 2009, 2010, 2012, 2014); Western Bluebirds are not as well adapted as Mountain Bluebirds are to colonise burned forests early on after fire, but once they colonise, they are better suited to outcompete the Mountain Bluebird in severely burned hot spots.

The pattern of a rapid increase in abundance illustrated by species listed under the first response pattern is well described and well appreciated, but the second pattern of a delayed increase in severely burned forest patches is not widely appreciated because the use of a single 'after fire' category in many

previous fire effects analyses may have hidden the influence of a delayed response. For example, of the 11 published studies of bird communities in burned and unburned forests reviewed by Kotliar *et al.* (2002), none separated the effects of fire severity or time-since-fire. Since that time, numerous authors (Hannah and Hoyt 2004; Saab *et al.* 2004; Smucker *et al.* 2005; Kirkpatrick *et al.* 2006; Schieck and Song 2006; Kotliar *et al.* 2007; Saab *et al.* 2007; Hutto 2008; Kotliar *et al.* 2008; Pons and Clavero 2010; Nappi and Drapau 2011; Saracco *et al.* 2011; Stephens *et al.* 2015) have included either fire severity or time-since-fire in their analyses of fire effects, and all of these authors concluded that it is important to do so. This study serves to reinforce the idea that fire effects cannot be accurately assessed in the absence of knowledge about the context surrounding a particular sample location and that includes, but is not limited to, fire severity and time-since-fire.

Response Pattern 3

This pattern is illustrated by species that revealed a fairly abrupt or slightly delayed increase in abundance within the first year or two following fire, but the positive response is limited to locations that burned at lower severities. This group includes species that have previously been labelled as 'mixed' responders in meta-analyses of fire effects (e.g. Kotliar *et al.* 2002) because they respond positively to fire in some studies and negatively to fire in others. Our results suggest instead that these species do not respond to fire unpredictably; it is just that their response depends on fire severity. For example, some of these species maintained an elevated occurrence rate in locations that burned at a lower severity throughout the duration of the 11-year study (e.g. Brown-headed Cowbird, Red Crossbill, Red-breasted Nuthatch, Western Tanager and Ruby-crowned Kinglet), while others showed a positive but brief response to low-severity fire only for a brief period following fire (e.g. Common Raven, Brown Creeper, *Certhia americana*, Pileated Woodpecker, Evening Grosbeak, Yellow-rumped Warbler, Hammond's Flycatcher, Hermit Thrush). For those species that showed a sustained (albeit small) positive response to low-severity fire, a predominantly green-tree forest that burned recently at low severity might actually provide a forest condition that is more suitable than a long-unburned green-tree forest. The species that revealed a brief and limited increase in abundance only during the first year or two following fire may reflect an influx of individuals returning from wintering locations only to find many of their previously occupied locations too severely burned, so they then proceeded to squeeze into unburned or lightly burned forest near previously occupied forest patches. If true, their relatively high abundance in mildly burned forest may not reflect suitable conditions, but may be a reflection of birds making the best of a bad situation. A key question for future fire research would be to determine whether increases in numbers of detections after recent fire in mildly burned green-tree stands reflect conditions that are better in quality, even if only briefly, than long unburned green-tree stands for this group of species.

Response Pattern 4

This pattern is illustrated by the six species that were less abundant in burned than in unburned forest immediately

following fire and appeared to become even less abundant across the 11-year time span. For each of these species, there was no combination of fire severity and time-since-fire that resulted in detection rates that were as great as they were in unburned forest. Perhaps these species do not benefit in any way from fire. Indeed, many authors would be quick to classify the species associated with this group of six species as 'negative responders.' However, we know that the abundances of each of these six species will be lower in recently burned forests only in the short-term. This was only an 11-year study, and we know that these same species will reach their highest occurrence rates in the years to come. If those occurrence rates reach a peak at some point in the future before falling again when the forest reaches an even older age, then those species would also be more accurately classified as positive responders: it is just that the time required to show a relatively high abundance is longer than the length of the present study. Even a rudimentary knowledge of natural history suggests that many bird species (e.g. Orange-crowned Warbler, MacGillivray's Warbler, Calliope Hummingbird and Lazuli Bunting) benefit from high-severity fire, but the greatest positive response cannot usually be detected until somewhere between 10 and 30 years following severe fire when plant succession produces a high density of conifer seedlings and shrubs. Similarly, the six species in this last group could be said to benefit from fire if forest conditions associated with, hypothetically, a 300-year-old forest are not as good as forest conditions associated with a 100-year-old forest because the only way optimal conditions for these species could be 'restored' would be through a severe fire event that creates their preferred habitat 100 years later. Interestingly, Taylor and Barmore (1980; Table 2) showed precisely that pattern for Ruby-crowned Kinglet, Yellow-rumped Warbler and Hermit Thrush in Yellowstone and Grand Teton National Parks – those species that are more abundant in century-old than in either younger or older forests. Using the same logic, even a species that is more abundant at year 300 than at year 700 following fire would mean that severe disturbance (disturbance severe enough to trigger ecological succession) is necessary to 'restore' appropriate forest conditions for that species too (see also Imbeau *et al.* 1999, Schieck and Song 2006; Zhao *et al.* 2013). The important point is that we cannot assess the effects of fire without data on bird abundances from a more extended series of forest ages following fire.

Caveat and management implications

Because the bird occurrence rate at unburned points was based on a different set of years than the occurrence rate for any one of the two-year post-fire samples, it is possible that a significant difference in the abundance of any one species between the unburned and a particular fire severity/time-since-fire category resulted from a temporal change in abundance independent of fire effects. However, even though our results emerged from a single fire event that may be best considered a case study, a previous study of bird occurrence patterns across hundreds of fires over the past 30 years (see Hutto *et al.* 2015, and references therein) suggests that the individual species' responses make good biological sense and are not artefacts of unusual increases or declines in bird abundance independent of fire effects. Nonetheless, these findings should serve as hypotheses to be

tested through replication of independent samples drawn from different time-since-fire categories. Only through use of a chronosequence approach (Hutto and Belote 2013) will we be able to generate the replication of burned-forest conditions necessary to evaluate fire effects in a manner that will allow us to appreciate how both fire severity and time-since-fire create the conditions needed by birds that respond positively to fire.

The take-home lesson here is that we cannot rely on traditional 'burned vs unburned' comparisons presented in most published reports on fire effects to assess whether species respond positively or negatively to fire. Fire severity, time-since-fire and other forest conditions matter to organisms that respond positively to disturbance, therefore we will have to consider the kind of forest, tree sizes and densities, fire severity and time-since-fire if we want to investigate fire effects in a biologically meaningful way. By considering the effects of just two of those forest conditions here, it is clear that the majority of species increases in abundance during part or all of the first dozen years after fire, as evidenced by significant differences in rates of detection inside vs. outside burned forests. Thus, we cannot gain a thorough understanding of fire effects through results that emerge from short-term, before-and-after studies; we need to know more about the occurrence rates of species across very long time spans if we are to speak knowledgeably about the effects of fire on any particular species. Our finding that 60% of the bird species surveyed are most abundant in some stage of forest succession following fire than they are in mature forest is undoubtedly a conservative estimate of the proportion of species that benefit from fire because our data cover only a relatively short 11-year period following fire.

Not only are there unambiguous responses by the majority of bird species to fire, but the responses are also highly dependent on a spatial component associated with fire severity. As suggested by earlier work that included fire severity as an independent variable (e.g. Smucker *et al.* 2005; Kotliar *et al.* 2007, 2008; Vierling and Lentile 2008; Stephens *et al.* 2015), fire severity has a dramatic influence on the probability of occurrence of bird species. The same pattern was true here for nearly all species that were detected on at least 10 points. Some species are clearly most abundant in the less severely burned forest patches, while others are clearly most abundant in the more severely burned patches. This result is important because it implies that mixed-severity fire effects are necessary for the creation of conditions needed by the variety of bird species that respond positively to fire. Even more importantly, the variety of burned-forest conditions favoured by different bird species may be difficult to create through a prescription of low-severity understory fire applied outside the normal fire season, because such fires do not generate the higher-severity patches needed by the species that are relatively restricted to forests that have burned severely (Hutto 2008). In addition, land management practices designed to prevent or eliminate severe fire will also eliminate the very conditions required by many of the species highlighted here, as will post-fire salvage logging, which has been documented to have overwhelmingly negative effects on birds – effects that are among the strongest and most consistent scientific results ever published on any wildlife management issue (Hutto *et al.* 2015).

Ecologists have long known that severe, stand-replacement fires are characteristic of some (mostly subalpine) forest types

(Brown and Smith 2000), but many forest managers and most politicians along with the public at large are still remarkably uninformed about the naturalness and necessity of severe fire in vegetation types born of, and maintained by, severe fire (Hutto *et al.* 2016). Even more striking is the near absence of an appreciation for the naturalness and necessity of severe fire in the low- to mid-elevation mixed-conifer forest types, even though severe fire events that create patches of severely burned forest are a natural and important part of those forests too (Baker *et al.* 2007; Hessburg *et al.* 2007; Baker 2009; Margolis *et al.* 2011; Perry *et al.* 2011; Baker 2012; Heyerdahl *et al.* 2012; Marlon *et al.* 2012; Veblen *et al.* 2012; Williams and Baker 2012a, 2012b; Odion *et al.* 2014; Sherriff *et al.* 2014; Williams and Baker 2014; Baker 2015a, 2015b; Baker and Williams 2015; Yocom-Kent *et al.* 2015; Hutto *et al.* 2016). For the lower-elevation mixed-conifer forest types, such as the forest studied here, it is quite clear that some amount of severe fire is natural and that large numbers of bird species benefit from the severe-fire component. Given these results, the challenge is to educate land managers, politicians and the public at large about the importance of maintaining severe fire on the landscape and to design fire-safe communities that can withstand the effects of severe fire disturbance events (Hutto *et al.* 2016). Only then will we be in a position to manage for appropriate amounts and sizes of severely burned forest patches that occurred historically and to celebrate the creation of mosaics of different fire severities and post-fire ages that follow directly from severe fire as a natural disturbance process.

Acknowledgements

We thank Joran Elias for substantial help in creating the heat maps and thank Monica Bond, Chad Hanson, Sue Reel and anonymous reviewers for providing comments that helped improve the manuscript. The USFS Northern Region, Joint Fire Science Program, National Geographic Society and the University of Montana provided funding at various stages of this research. All data were collected in accordance with federal animal care and research permits (University of Montana, Missoula, IACUC AUP 058-13).

References

- Agresti A (2002) 'Categorical data analysis', 2nd edn. (John Wiley and Sons: Hoboken, NJ).
- Apfelbaum SI, Haney A (1985) Changes in bird populations during succession following fire in northern Great Lakes Wilderness. In 'Proceedings – National wilderness research conference: current research'. (Ed. RC Lucas) USDA General Technical Report INT-212, pp 10–16. (Ogden, UT)
- Baker WL (2009) 'Fire ecology in Rocky Mountain landscapes'. (Island Press: Washington, DC)
- Baker WL (2012) Implications of spatially extensive historical data from surveys for restoring dry forests of Oregon's eastern Cascades. *Ecosphere* 3, 23. doi:10.1890/ES11-00320.1
- Baker WL (2015a) Are high-severity fires burning at much higher rates recently than historically in dry-forest landscapes of the western USA? *PLoS One* 10(9), e0136147. doi:10.1371/JOURNAL.PONE.0136147
- Baker WL (2015b) Historical northern spotted owl habitat and old-growth dry forests maintained by mixed-severity wildfires. *Landscape Ecology* 30, 655–666. doi:10.1007/s10980-014-0144-6
- Baker WL, Williams MA (2015) Bet-hedging dry-forest resilience to climate-change threats in the western USA based on historical forest structure. *Frontiers in Ecology and Evolution* 2, art88. doi:10.3389/FEVO.2014.00088

- Baker WL, Veblen TT, Sherriff RL (2007) Fire, fuels and restoration of ponderosa pine-Douglas fir forests in the Rocky Mountains, USA. *Journal of Biogeography* 34, 251–269. doi:10.1111/j.1365-2699.2006.01592.X
- Bechtoldt CL, Stouffer PC (2005) Home-range size, response to fire, and habitat preferences of wintering Henslow's Sparrows. *The Wilson Bulletin* 117, 211–225. doi:10.1676/04-110.1
- Blackford JL (1955) Woodpecker concentration in burned forest. *The Condor* 57, 28–30. doi:10.2307/1364695
- Bond ML, Siegel RB, Hutto RL, Saab VA, Shunk SA (2012) A new forest fire paradigm: the need for high-severity fires. *The Wildlife Professional* 6, 46–49.
- Bräninger DR, Smith RB (1992) Relationships between fire and bird density in coastal scrub and slash pine flatwoods in Florida. *American Midland Naturalist* 127, 233–240.
- Brown S, Clarke M, Clarke R (2009) Fire is a key element in the landscape-scale habitat requirements and global population status of a threatened bird: the Mallee Emu-wren (*Stipiturus mallee*). *Biological Conservation* 142, 432–445. doi:10.1016/j.bioccon.2008.11.005
- Brown JK, Smith JK (2000) Wildland fire in ecosystems: effects of fire on flora. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-42-volume 2. (Ogden, UT).
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) 'Introduction to distance sampling: estimating abundance of animal populations.' (Oxford University Press: New York, NY.)
- Chalmandrier L, Midgley GF, Barnard P, Sirami C (2013) Effects of time since fire on birds in a plant diversity hotspot. *Acta Oecologica* 49, 99–106. doi:10.1016/j.actao.2013.03.008
- Conway CJ, Kirkpatrick C (2007) Effect of forest fire suppression on Buff-breasted Flycatchers. *Journal of Wildlife Management* 71, 445–457. doi:10.2193/2005-755
- Covert-Bradford KA, Block WM, Theimer TC (2006) Hairy woodpecker winter ecology in ponderosa pine forests representing different ages since wildfire. *Journal of Wildlife Management* 70, 1379–1392. doi:10.2193/0022-541X(2006)70[1379:HWWEIP]2.0.CO;2
- DellaSala DA, Karr JR, Schoennagel T, Perry D, Noss RF, Lindenmayer D, Beschta R, Hutto RL, Swanson ME, Evans J (2006) Postfire logging debate ignores many issues. *Science* 314, 51–52. doi:10.1126/SCIENCE.314.5796.51B
- DellaSala DA, Bond ML, Hanson CT, Hutto RL, Odion DC (2014) Complex early seral forests of the Sierra Nevada: what are they and how can they be managed for ecological integrity? *Natural Areas Journal* 34, 310–324. doi:10.3375/043.034.0317
- Duckworth RA (2008) Adaptive dispersal strategies and the dynamics of a range expansion. *American Naturalist* 172, S4–S17. doi:10.1086/588289
- Duckworth RA (2009) Maternal effects and range expansion: a key factor in a dynamic process? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364, 1075–1086. doi:10.1098/RSTB.2008.0294
- Duckworth RA (2010) Evolution of personality: developmental constraints on behavioral flexibility. *The Auk* 127, 752–758. doi:10.1525/AUK.2010.127.4.752
- Duckworth RA (2012) Evolution of genetically integrated dispersal strategies. In 'Dispersal Ecology and Evolution'. (Ed. J Clobert) pp 83–94. (Oxford University Press: Oxford, UK).
- Duckworth RA (2014) Human-induced changes in the dynamics of species coexistence. In 'Avian urban ecology: physiological and behavioural adaptations to the urban habitat'. (Eds D Gil, H Brumm) pp 181–191. (Oxford University Press: Oxford, UK).
- Duckworth RA, Badyaev AV (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America* 104, 15017–15022. doi:10.1073/PNAS.0706174104
- Dudley JG, Saab VA, Hollenbeck JP (2012) Foraging-habitat selection of Black-backed Woodpeckers in forest burns of southwestern Idaho. *The Condor* 114, 348–357. doi:10.1525/COND.2012.110020
- Fontaine JB, Kennedy PL (2012) Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. *Ecological Applications* 22, 1547–1561.
- Garney JL, Block WM, Boucher PF (1996) Effects of fire on birds in Madrean forests and woodlands. In 'Effects of fire on Madrean Province ecosystems'. (Eds PF Ffolliott, LF DeBano, MB Baker, GJ Gottfried, G Solis-Garza, CB Edminster, DG Neary, LS Allen, RH Hamre) USDA Forest Service General Technical Report RM-GTR-289, pp. 146–154. (Fort Collins, CO)
- Gentry DJ, Vierling KT (2007) Old burns as source habitats for Lewis's Woodpeckers breeding in the Black Hills of South Dakota. *The Condor* 109, 122–131. doi:10.1650/0010-5422(2007)109[122:OBASHF]2.0.CO;2
- Hannah KC, Hoyt JS (2004) Northern Hawk Owls and recent burns: does 'burn age matter? *The Condor* 106, 420–423. doi:10.1650/7342
- Hanson CT, North MP (2008) Postfire woodpecker foraging in salvage-logged and unlogged forests of the Sierra Nevada. *The Condor* 110, 777–782. doi:10.1525/COND.2008.8611
- Hardy CC (2005) Wildland fire hazard and risk: problems, definitions, and context. *Forest Ecology and Management* 211, 73–82. doi:10.1016/j.foreco.2005.01.029
- Hargrove WW, Pickering J (1992) Pseudoreplication: a sine qua non for regional ecology. *Landscape Ecology* 6, 251–258. doi:10.1007/BF00129703
- Hessburg PF, Salter RB, James KM (2007) Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. *Landscape Ecology* 22, 5–24. doi:10.1007/s10980-007-9098-2
- Heyerdahl EK, Lertzman K, Wong CM (2012) Mixed-severity fire regimes in dry forests of southern interior British Columbia, Canada. *Canadian Journal of Forest Research* 42, 88–98. doi:10.1139/X11-160
- Hobson KA, Schieck J (1999) Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. *Ecological Applications* 9, 849–863. doi:10.1890/1051-0761(1999)009[0849:CIB CIB]2.0.CO;2
- Holmes AL, Robinson WD (2013) Fire mediated patterns of population densities in mountain big sagebrush bird communities. *Journal of Wildlife Management* 77, 737–748. doi:10.1002/JWMG.540
- Hoyt JS, Hannon SJ (2002) Habitat associations of Black-backed and Three-toed woodpeckers in the boreal forest of Alberta. *Canadian Journal of Forest Research* 32, 1881–1888. doi:10.1139/X02-109
- Hudak AT, Robichaud PR, Evans JB, Clark J, Lannom K, Morgan P, Stone C (2004) Field validation of Burned Area Reflectance Classification (BARC) products for post fire assessment. In 'Remote sensing for field users; proceedings of the 10th Forest Service remote sensing applications conference'. 5–9 April 2004, Bethesda, MD. (Ed. JD Greer) American Society of Photogrammetry and Remote Sensing. (CD-ROM) (Salt Lake City, UT).
- Hudak AT, Morgan P, Bobbitt MJ, Smith AMS, Lewis SA, Lentile LB, Robichaud PR, Clark JT, McKinley RA (2007) The relationship of multispectral satellite imagery to immediate fire effects. *Fire Ecology* 3, 64–90. doi:10.4996/FIREECOLOGY.0301064
- Huot M, Ibarzabal J (2006) A comparison of the age-class structure of black-backed woodpeckers found in recently burned and unburned boreal coniferous forests in eastern Canada. *Annales Zoologici Fennici* 43, 131–136.
- Hutto RL (1995) Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* 9, 1041–1058. doi:10.1046/j.1523-1739.1995.9051033.x-11

- Hutto RL (2008) The ecological importance of severe wildfires: some like it hot. *Ecological Applications* 18, 1827–1834. doi:10.1890/08-0895.1
- Hutto RL (2016) Should scientists be required to use a model-based solution to adjust for possible distance-based detectability bias? *Ecological Applications*. In press.
- Hutto RL, Belote RT (2013) Distinguishing four types of monitoring based on the questions they address. *Forest Ecology and Management* 289, 183–189. doi:10.1016/j.foreco.2012.10.005
- Hutto RL, Gallo SM (2006) The effects of postfire salvage logging on cavity-nesting birds. *The Condor* 108, 817–831. doi:10.1650/0010-5422(2006)108[817:TEOPSL]2.0.CO;2
- Hutto RL, Young JS (2002) Regional landbird monitoring: perspectives from the northern Rocky Mountains. *Wildlife Society Bulletin* 30, 738–750.
- Hutto RL, Pletscher SM, Hendricks P (1986) A fixed-radius point count method for nonbreeding and breeding season use. *The Auk* 103, 593–602.
- Hutto RL, Conway CJ, Saab VA, Walters JR (2008) What constitutes a natural fire regime? Insight from the ecology and distribution of coniferous forest birds in North America. *Fire Ecology* 4, 115–132. doi:10.4996/FIREECOLOGY.0402115
- Hutto RL, Bond ML, DellaSala DA (2015) Using bird ecology to learn about the benefits of severe fire. In 'The ecological importance of mixed-severity fires: nature's phoenix'. (Eds DA DellaSala, CT Hanson) pp 55–88. (Elsevier: New York, NY).
- Hutto RL, Keane RE, Sherriff RL, Rota CT, Eby LA, Saab VA (2016) Toward a more ecologically informed view of severe forest fires. *Ecosphere* 7, e01255.
- Imbeau L, Savard J-P, Gagnon R (1999) Comparing bird assemblages in successional black spruce stands originating from fire and logging. *Canadian Journal of Zoology* 77, 1850–1860. doi:10.1139/Z99-172
- Johnson DH (2008) In defense of indices: the case of bird surveys. *The Journal of Wildlife Management* 72, 857–868. doi:10.2193/2007-294
- Kirkpatrick C, Conway C, Jones PB (2006) Distribution and relative abundance of forest birds in relation to burn severity in southeastern Arizona. *The Journal of Wildlife Management* 70, 1005–1012. doi:10.2193/0022-541X(2006)70[1005:DARAOF]2.0.CO;2
- Koivula MJ, Schmiegelow FKA (2007) Boreal woodpecker assemblages in recently burned forested landscapes in Alberta, Canada: effects of post-fire harvesting and burn severity. *Forest Ecology and Management* 242, 606–618. doi:10.1016/j.foreco.2007.01.075
- Koplin JR (1969) The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. *The Condor* 71, 436–438. doi:10.2307/1365747
- Kotliar NB, Hejl SJ, Hutto RL, Saab VA, McFether CP, McFadden ME (2002) Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. *Studies in Avian Biology* 25, 49–64.
- Kotliar NB, Saab VA, Hutto RL (2005) Fire on the mountain: birds and burns in the Rocky Mountains. USDA Forest Service, General Technical Report PSW-GTR-191, pp 1090–1092. (Albany, CA)
- Kotliar NB, Kennedy PL, Petroc K (2007) Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. *Ecological Applications* 17, 491–507. doi:10.1890/06-0253
- Kotliar NB, Reynolds EW, Deutschman DH (2008) American three-toed woodpecker response to burn severity and prey availability at multiple spatial scales. *Fire Ecology* 4, 26–45. doi:10.4996/FIREECOLOGY.0402026
- Lee DE, Bond ML, Siegel RB (2012) Dynamics of breeding-season site occupancy of the California Spotted Owl in burned forests. *The Condor* 114, 792–802. doi:10.1525/COND.2012.110147
- Lentile LB, Morgan P, Hudak AT, Bobbitt MJ, Lewis SA, Smith AMS, Robichaud PR (2007) Post-fire burn severity and vegetation response following eight large wildfires across the western United States. *Fire Ecology* 3, 91–108. doi:10.4996/FIREECOLOGY.0301091
- Lindenmayer DB, Blanchard W, McBurney L, Blair D, Banks SC, Driscoll DA, Smith AL, Gill AM (2014) Complex responses of birds to landscape-level fire extent, fire severity and environmental drivers. *Diversity and Distributions* 20, 467–477. doi:10.1111/DDI.12172
- MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006) 'Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence'. (Elsevier Academic Press: Burlington, MA).
- Margolis EQ, Swetnam TW, Allen CD (2011) Historical stand-replacing fire in upper montane forests of the Madrean Sky Islands and Mogollon Plateau, southwestern USA. *Fire Ecology* 7, 88–107. doi:10.4996/FIRE ECOLOGY.0703088
- Marlon JR, Bartlein PJ, Gavin DG, Long CJ, Anderson RS, Briles CE, Brown KJ, Colombaroli D, Hallett DJ, Power MJ, Scharf EA, Walsh MK (2012) Long-term perspective on wildfires in the western USA. *Proceedings of the National Academy of Sciences of the United States of America* 109, E535–E543. doi:10.1073/PNAS.1112839109
- Murphy EG, Lehnhausen WH (1998) Density and foraging ecology of woodpeckers following a stand-replacement fire. *The Journal of Wildlife Management* 62, 1359–1372. doi:10.2307/3802002
- Nappi A, Drapeau P (2009) Reproductive success of the Black-backed Woodpecker (*Picoides arcticus*) in burned boreal forests: are burns source habitats? *Biological Conservation* 142, 1381–1391. doi:10.1016/j.biocon.2009.01.022
- Nappi A, Drapeau P (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. doi:10.1139/X11-028
- Nappi A, Drapeau P, Saint-Germain M, Angers VA (2010) Effect of fire severity on long-term occupancy of burned boreal conifer forests: saproxylic insects and wood-foraging birds. *International Journal of Wildland Fire* 19, 500–511. doi:10.1071/WF08109
- Odion DC, Hanson CT, Arseneault A, Baker WL, DellaSala DA, Hutto RL, Klénner W, Moritz MA, Sherriff RL, Veblen TT, Williams MA (2014) Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PLoS ONE* 9, e87852. doi:10.1371/JOURNAL.PONE.0087852
- Perry DA, Hessburg PF, Skinner CN, Spies TA, Stephens SL, Taylor AN, Franklin JF, McComb B, Riegel G (2011) The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. *Forest Ecology and Management* 262, 703–717. doi:10.1016/j.foreco.2011.05.004
- Pons P, Claytor M (2010) Bird responses to fire severity and time since fire in managed mountain rangelands. *Animal Conservation* 13, 294–305. doi:10.1111/j.1469-1795.2009.00337.x
- Pyke GH, Saillard R, Smith J (1995) Abundance of Eastern Bristlebirds in relation to habitat and fire history. *Emu* 95, 106–110. doi:10.1071/MU9950106
- R Core Team (2014) R: A language and environment for statistical computing. (R Foundation for Statistical Computing: Vienna, Austria). Available at <http://www.R-project.org/> [Verified 7 June 2016]
- Ralph CJ, Sauer JR, Droege S (1995) Monitoring bird populations by point counts. USDA Forest Service, General Technical Report PSW-GTR-149, pp 1–181. (Albany, CA)
- Raphael MG, Morrison ML, Yoder-Williams MP (1987) Breeding bird populations during twenty-five years of post-fire succession in the Sierra Nevada. *Condor* 89, 614–626. doi:10.2307/1368651
- Rush S, Klaus N, Keyes T, Petrick J, Cooper R (2012) Fire severity has mixed benefits to breeding bird species in the southern Appalachians. *Forest Ecology and Management* 263, 94–100. doi:10.1016/j.foreco.2011.09.005
- Saab VA, Dudley JG (1998) Responses of cavity-nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. USDA Forest Service, Research Paper RMRS-RP-11, pp 1–17. (Ogden, UT)

- Saab VA, Dudley J, Thompson WL (2004) Factors influencing occupancy of nest cavities in recently burned forests. *The Condor* 106, 20–36. doi:10.1650/7485
- Saab VA, Russell RE, Dudley J (2007) Nest densities of cavity-nesting birds in relation to post-fire salvage logging and time since wildfire. *Condor* 109, 97–108. doi:10.1650/0010-5422(2007)109[97:NDOCB]2.0.CO;2
- Saab VA, Russell RE, Dudley JG (2009) Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. *Forest Ecology and Management* 257, 151–159. doi:10.1016/j.foreco.2008.08.028
- Saracco JF, Siegel RB, Wilkerson RL (2011) Occupancy modeling of Black-backed Woodpeckers on burned Sierra Nevada forests. *Ecosphere* 2, art31. doi:10.1890/ES10-00132.1
- Schieck J, Song SJ (2006) Changes in bird communities throughout succession following fire and harvest in boreal forests of western North America: literature review and meta-analysis. *Canadian Journal of Forest Research* 36, 1299–1318. doi:10.1139/X06-017
- Sherriff RL, Platt RV, Vebien TT, Schoennagel TL, Gartner MH (2014) Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. *PLoS One* 9, e106971. doi:10.1371/JOURNAL.PONE.0106971
- Siegel RB, Tingley MW, Wilkerson RL, Howell CA, Johnson M, Pyle P (2016) Age structure of Black-backed Woodpecker populations in burned forests. *The Auk* 133, 69–78. doi:10.1642/AUK-15-137.1
- Smucker KM, Hutto RL, Steele BM (2005) Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* 15, 1535–1549. doi:10.1890/04-1353
- Stephens JL, Ausprey JJ, Seavy NE, Alexander JD (2015) Fire severity affects mixed broadleaf-conifer forest bird communities: results for 9 years following fire. *The Condor* 117, 430–446. doi:10.1650/CONDOR-14-58.1
- Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB, Swanson FJ (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9, 117–125. doi:10.1890/090157
- Taylor DL (1973) Some ecological implications of forest fire control in Yellowstone National Park, Wyoming. *Ecology* 54, 1394–1396. doi:10.2307/1934205
- Taylor DL (1979) Forest fires and the tree-hole nesting cycle in Grand Teton and Yellowstone National Park. In 'Proceedings of the First Conference on Scientific Research in the National Parks, vol. 1', 9–12 November 1976, New Orleans, LA. (Ed. RM Linn) USDI National Park Service Transactions Series 5, pp. 509–511. Available at <https://archive.org/details/proceedingsoffir00linn> [Verified 16 June 2016]
- Taylor DL, Barmore WJ (1980) Post-fire succession of avifauna in coniferous forests of Yellowstone and Grand Teton National Parks, Wyoming. In 'Workshop proceedings: management of western forests and grasslands for nongame birds'. (Ed. RM DeGraaf) USDA Forest Service, General Technical Report INT-86, pp. 130–145 (Ogden, UT).
- Tingley MW, Wilkerson RL, Bond ML, Howell CA, Siegel RB (2014) Variation in home-range size of Black-backed Woodpeckers. *The Condor* 116, 325–340. doi:10.1650/CONDOR-13-140.1
- Van Tyne J (1926) An unusual flight of Arctic Three-toed Woodpeckers. *The Auk* 43, 469–474. doi:10.2307/4075133
- Vebien TT, Romme WH, Regan C (2012) Regional application of historical ecology at ecologically defined scales: forest ecosystems in the Colorado front range. In 'Historical environmental variation in conservation and natural resource management'. (Eds JA Wiens, GD Hayward, HD Safford, CM Giffen) pp. 149–165. (John Wiley and Sons, Ltd.; Oxford, UK)
- Vierling KT, Gentry DJ (2008) Red-headed Woodpecker density and productivity in relation to time since fire in burned pine forests. *Fire Ecology* 4, 15–25. doi:10.4996/FIREECOLOGY.0402015
- Vierling K, Léntile L (2008) Indirect effects of fire severity on avian communities in ponderosa pine and aspen forests in western North America: a review. *Fire Ecology* 4, 133–149. doi:10.4996/FIREECOLOGY.0402133
- Villard P, Beninger CW (1993) Foraging behavior of male Black-backed and Hairy woodpeckers in a forest burn. *Journal of Field Ornithology* 64, 71–76.
- Villard MA, Schieck J (1997) Immediate post-fire nesting by Black-backed Woodpeckers, *Picoides arcticus*, in northern Alberta. *Canadian Field Naturalist* 111, 478–479.
- Welsh AH, Lindenmayer DB, Donnelly CF (2013) Fitting and interpreting occupancy models. *PLoS One* 8, e52615. doi:10.1371/JOURNAL.PONE.0052615
- Wickham H (2009) 'ggplot2: elegant graphics for data analysis.' (Springer: New York, NY).
- Wickham H (2014) 'tidyr: Easily tidy data with spread() and gather() functions. R package.' Version 0.2.0. Available at <http://CRAN.R-project.org/package=tidyr> [Verified 7 June 2016]
- Wickham H, François R (2015) 'dplyr: a grammar of data manipulation. R package.' Version 0.4.1. Available at <http://CRAN.R-project.org/package=dplyr> [Verified 7 June 2016]
- Williams MA, Baker WL (2012a) Comparison of the higher-severity fire regime in historical (A.D. 1800s) and modern (A.D. 1984–2009) montane forests across 624,136 ha of the Colorado Front Range. *Ecosystems* 15, 832–847. doi:10.1007/s10021-012-9549-8
- Williams MA, Baker WL (2012b) Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests. *Global Ecology and Biogeography* 21, 1042–1052. doi:10.1111/j.1466-8238.2011.00750.x
- Williams MA, Baker WL (2014) High-severity fire corroborated in historical dry forests of the western United States: response to Fulé et al. *Global Ecology and Biogeography* 23, 831–835. doi:10.1111/GEB.12152
- Woinarski JCZ, Brock C, Fisher A, Milne D, Oliver B (1999) Response of birds and reptiles to fire regimes on pastoral land in the Victoria River District, Northern Territory. *The Rangeland Journal* 21, 24–38. doi:10.1071/RJ9990024
- Yocom-Kent LL, Fulé PZ, Bunn WA, Gdula EG (2015) Historical high-severity fire patches in mixed-conifer forests. *Canadian Journal of Forest Research* 45, 1587–1596. doi:10.1139/CJFR-2015-0128
- Yunick RP (1985) A review of recent irruptions of the Black-backed Woodpecker and Three-toed Woodpecker in eastern North America. *Journal of Field Ornithology* 56, 138–152.
- Zhao Q, Azeria ET, LeBlanc M-L, Lemaître J, Fortin D (2013) Landscape-scale disturbances modified bird community dynamics in successional forest environment. *PLoS ONE* 8, e81358. doi:10.1371/JOURNAL.PONE.0081358