Title: Chaparral bird community responses to prescribed fire and shrub removal in three management seasons

Running headline: Fire management and chaparral birds

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Abstract

1. Chaparral, a type of shrubland common throughout the California Floristic Province, is subject to management and removal in regions where wildfire threatens human lives and property. Management practices include conducting prescribed burns outside of the historical fire season and employing mechanical fuel reduction (mastication). As the wildland-urban interface grows, particularly in coastal California, more of this ecosystem is subject to active management.
2. To understand the ecological implications of current California chaparral fire management practices, we studied bird species composition, abundance, and foraging guilds in managed and unmanaged chaparral over five years. Study areas were located in Mendocino County in the Coast Ranges of northern California. We contrast six chaparral removal or “fuels manipulation” treatments: 1) fall fire, 2) winter fire, 3) spring fire, 4) fall mastication, 5) spring mastication and 6) untreated control. Treatment and control were implemented in ~2 hectare plots and replicated four times each.
3. We find that species richness in prescribed fire treatments reaches comparable levels to controls in the first 3 years following treatment, whereas masticated units always have lower species richness. Generalized linear mixed models additionally confirm that mastication has highly negative effects on observed abundances of birds compared to controls and to prescribed fire.
4. The season in which fuels reduction occurred was less important to species richness, although fall fire was more beneficial to bird abundance than spring or winter fire. Fire treatments in all seasons maintain the same general bird community structure as controls,

while mastication results in strongly differentiated assemblages, increasing granivores while nearly excluding foliage-gleaners.

5. *Synthesis and applications.* We conclude that prescribed fire and mastication are not interchangeable management techniques, and that mastication can negatively impact bird communities, reducing both diversity and abundance.

Key words: bird communities, chaparral, California Floristic Province, Fire and Fire Surrogates, fire management, fuels manipulations, mastication, prescribed fire, shrublands

Introduction

California chaparral, a unique and diverse set of Mediterranean-climate shrub communities restricted to the California Floristic Province (CFP), is one of the most fire-prone ecosystems in North America. California chaparral extends over much of California, extreme southwestern Oregon, and northwestern Baja California, and is characterized by sclerophyllous vegetation, high local and regional species diversity, and high levels of endemism among both plants and animals. Chaparral harbours a major fraction of the biodiversity of the CFP (identified as a biodiversity hotspot; Conservation International 2011, Myers *et al.* 2000). Of the 4846 native species of vascular plants in the CFP, 24% (or 1177) are present in chaparral (Halsey and Keeley 2016), and of these, 44% are considered rare (Keeley 2005).

Chaparral is also the most suburbanized habitat in California (with the possible exception of coastal scrub); the wildland-urban interface in California currently contains over 5 million housing units (Radeloff *et al.* 2005), with development pressures in chaparral and areas of very high fire risk predicted to only increase (Hammer *et al.* 2009; Mann *et al.* 2014). While fire

67 poses a threat to human lives and property, too-frequent fire and degradation of chaparral
68 ecosystems for agriculture and fire management are causing extreme losses of biodiversity in this
69 ecosystem (Stylinski & Allen 1999; Keeley 2002, 2006). These factors combined pose major
70 challenges for fire managers. Balancing conservation priorities with human health and safety
71 requires targeted studies evaluating both the efficacy of vegetation management techniques in
72 reducing fire risk, and their effects on biodiversity. These challenges are not unique to
73 California; similar issues exist for ecological consequences of fuel management in other xeric or
74 Mediterranean sclerophyll scrublands elsewhere in the world, such as in Europe and Australia
75 (Brotons *et al.* 2005; Herrando *et al.* 2002; Woinarski 1999).

76 In California today, chaparral fire management practices do not reproduce historical fire
77 regime norms. Wildfire risk, concerns about smoke and public health, political and economic
78 pressures, and regulations at many levels often force land managers who use prescribed burns to
79 conduct them outside of the historical fire season (Knapp *et al.* 2009). In California and
80 elsewhere, managers increasingly replace prescribed fire with mechanical crushing of vegetation,
81 known as “mastication.” Although both prescribed fire and mastication are used widely
82 throughout the range of California chaparral, there are few studies focusing on prescribed fire
83 effects in this habitat (Lawrence 1966; Beyers & Wakeman 2000; Potts & Stephens 2009, Potts
84 *et al.* 2010). Targeted studies on the effects of mastication on chaparral communities indicate
85 that exotic invasives and annual grasses are more prevalent after treatment (Bradley *et al.* 2006,
86 Potts and Stephens 2009, and see Coulter *et al.* 2010 for work outside California in the CFP),
87 reducing native diversity (Stylinski & Allen 1999) and, counter to the intention, increasing fire
88 frequency (D’Antonio 2000).

Of the fire characteristics that have been evaluated, prescribed fire (Beyers & Wakeman 2000) and season of burn (Knapp *et al.* 2009, Potts & Stephens 2009, Coulter *et al.* 2010) are known to produce significant changes to the vegetation community, but there is a complete absence of comparative effects of season of prescribed fires on chaparral birds (Knapp *et al.* 2009). Research from southern California shows that wildfire in chaparral can alter bird community composition by changing habitat structure, food availability, and predator movement (Lawrence 1966; Wirtz 1979, 1982, Mendelsohn *et al.* 2008), but such studies are limited. Studies of vertebrates in post-conversion chaparral (as by mastication) are similarly limited (Lilywhite 1977), although recent work has shown strong negative effects of medium to large-scale mastication projects on shrub-associated bird diversity (Seavy *et al.* 2008).

This study was conducted part of a unique, controlled and replicated experiment conducted in 2001-2005 in northern California. Our project represents the first controlled experiment with replication comparing the effects of prescribed fire and mastication treatments in multiple seasons on the chaparral bird community. We contrast the effects on bird diversity and abundance of two chaparral fuels reduction treatments (prescribed fire and mastication) in three seasons (fall, winter and spring), and a comparison control. We expected bird diversity to recover to control-like assemblages in prescribed fire units, with fall fire (occurring in the historic wildfire season) recovering with the highest degree of similarity within the first few years post-treatment compared to other treatment seasons. Although the two chaparral treatments have not been directly compared previously, we expected differences in vegetation species composition and structure between treatment types, affecting what bird species use them (Supporting Information (SI): Appendix 1). We therefore expected masticated plots to have

lower bird abundance and species richness compared to prescribed fire plots, and that treatment type would have larger effects than seasonality on bird biodiversity metrics and guild structure.

Materials and Methods

The Fire and Fire Surrogates Model

The Fire and Fire Surrogates Network is a group of large-scale studies across the United States in seasonally dry ecosystems, implemented to create a scientific basis for evaluating tradeoffs between fuels management by prescribed fire and mechanical thinning, measuring fire behaviour during treatment, and assessing effects on native and non-native biodiversity (McIver *et al.* 2009; Schwilk *et al.* 2009; Youngblood *et al.* 2005). Following this model, this California chaparral fuels manipulation experiment took place over 2001-2005 at the Hopland Research and Extension Center (HREC, managed by the University of California, Berkeley) and the nearby Red Mountain and Cow Mountain Recreation Area (both managed by the Bureau of Land Management) in the North Coast Ranges of Mendocino County, California. All study plots are located within the northern California chaparral vegetation community, situated ~50 km from the Pacific coast and 180 km north of San Francisco (Fig. 1).

This experiment began in 2001 with pre-treatment monitoring. Fire and mechanical treatments were conducted in 2002 and 2003. Post-treatment monitoring was conducted from 2002-2005. Project findings synthesize five years of replicated data on fuel recovery (Potts *et al.* 2010), nonnative plant invasion and plant diversity (Potts & Stephens 2009; Wilkin *et al.* 2014), and bird community response (this study) (SI: Appendix 1). Implementation of this project, including provision of research sites, permits, and fire crews, was accomplished through collaboration between HREC, the Bureau of Land Management Ukiah Field Office (BLM), and

the California Department of Forestry and Fire Protection (CALFIRE) Mendocino and Lake County Units.

Mastication and prescribed fires created a homogeneous treatment, which removed or reduced 95-100% of standing aboveground biomass without damaging subsurface soil and root systems. Whereas the masticator shredded vegetation into a <5 cm layer of small-diameter (<2.5 cm) woody debris, prescribed fire treatments left some “skeletons” of surface-killed plants, maintaining some vertical structure (Fig. 2). Treatments and controls were replicated four times for a total of 24 experimental units, each larger than 2 ha (details, dates of implementation, and site descriptions are available in SI: Appendix 2). Effects of management on bird communities may depend on the scale of treatment area, and we note that while 2 ha might be similar to area managed near houses, other management areas in California are much larger.

Bird counts

Bird surveys were conducted in most of the vegetation management units and one additional control unit (5 control, 4 spring fire, 4 winter fire, 4 fall fire, 3 spring mastication and 3 fall mastication units) for a total of 23 units. Two masticated units were not surveyed for birds due to accessibility issues. Bird community composition and abundance was estimated using a double-observer point count method (Nichols *et al.* 2000) with a detection cut-off of 50m. This technique reduces observer bias: one observer stands at a fixed point for 10 minutes noting every bird detection (visual, call and song) as well as its distance from the observer, while the second observer records and adds missed detections. Two point counts were conducted in each treatment unit, sequentially (for >46 points, due to opportunistic sampling in control areas), with a distance of at least 100 m separating the points. Points placed at this distance within chaparral stands can

be considered independent due to the extreme density of vegetation leading to low detection radii. For consistency, only two observers (Vaughn and Potts) performed the point counts over the entire study period.

Point counts were conducted 4-7 times per year in each experimental unit, with scheduled visits distributed throughout the year: once in winter, each month in spring/early summer, and once in fall (SI: Appendix 3). All counts were conducted within the first four hours of daylight, with all sites visited over a several-day period within each seasonal sampling window. Experimental units were visited in a random order to reduce time-of-day bias. No counts were performed in heavy rain, fog or windy conditions. Because fuel reduction treatments were implemented over two years, we collected bird point count data in each experimental unit for between 1.5 and >3.5 years.

Data analysis

Species richness and similarity comparisons

Species richness is the count of all species present within an experimental unit, and is a reliable metric for comparing biodiversity between the treatment types and seasons. We employed rarefaction methods to correct for sampling bias introduced by uneven sampling effort. Rarefaction and species richness estimations were performed 200 replicates, and without replacement to create meaningful variance estimates. Each point count was considered one data point. Time since treatment was not considered. Sample-based rarefaction and estimation of variance was performed first, followed by replotting on an x -axis of individual abundances instead of number of samples (Gotelli & Colwell 2001; 2011). This method allows direct

comparison of species richness between sample sets with very different abundances (Gotelli & Colwell 2011).

Mean species richness resulting from rarefaction was then compared between treatment-seasons with unpaired 2-tailed Welch's t-tests, with a null hypothesis that management does not change mean species richness compared to the control, and the alternative hypothesis that management changes the mean. Welch's t-tests assess statistical significance when variances between samples are unequal. These tests were standardized by applying them at comparable numbers of individuals between control and treatment, at the number of individuals associated with extrapolated rarefaction estimates on twice the number of surveys performed (Hsieh *et al.* 2016), and were then followed by Bonferroni corrections to conservatively assess the true statistical significance levels of the multiple comparisons performed.

We calculated an abundance-based dissimilarity metric, the Morisita-Horn index (C_{mH}), for all pair-wise comparisons of experimental units by treatment type and season. The Morisita-Horn index ranges from 0 (no overlap in communities) to 1 (full overlap of communities) and is relatively unaffected by sample size and diversity (Wolda 1981).

Guild analyses

We classified bird species into five functional guilds (De Graaf *et al.* 1985): feeding guilds by main source of calories (nectarivores, insectivores, granivores, bird predators, and "multiple", comprising omnivores and birds that switch dietary preferences seasonally); preferred feeding substrate (ground, foliage gleaning, aerial, bark, and "aerial," comprising hovering, true aerial, and flycatching); resident status (summer breeding, year-round, migration, and winter non-breeding); breeding status (breeding and non-breeding); and nesting guilds among birds that

breed in this area (tree, shrub, ground, and cavity) for analysis (guild designations from Birds of North America Online, <http://bna.birds.cornell.edu/bna/>; the Cornell Lab of Ornithology online bird guide, <http://www.allaboutbirds.org/guide>); and breeding observations recorded at HREC, Vaughn & Kieffer 2007), (SI: Appendix 4).

Count data for bird individuals were aggregated across years, and analysed as the by-guild response in the immediate post-treatment timeframe. For each of the five categories, the proportions of bird individuals in each guild were compared between treatment-season experimental units using Pearson's Chi-squared test for count data with Yeats' continuity correction, or Fisher's exact test for small sample sizes, with the hypothesis that proportions of individuals in each guild do not differ between control and treated units.

Modelling observed bird abundances

We constructed a Poisson-distributed generalized linear mixed model (GLMM; Bolker *et al.* 2009) to analyse total bird detections per survey within our experimental design. We tested three fixed effects central to our hypotheses: (1) treatment type (prescribed fire, mastication, control), (2) treatment season (fall, winter, spring, or "none" corresponding to the control), and (3) growth period, *i.e.*, an index of the number of years (turning over in January) since treatment or first surveys in the case of controls. For example, a plot that was treated in September would be surveyed in growth period 0 until January of the following year (4 months total), at which point surveys are considered to be in growth period 1.

Three interactions among fixed effects were also included: (1) fire*fall, an interaction to test whether or not fall surveys were different between fire and mastication treatments; (2) fire*grow, an interaction to see if the effects of growth season differed between fire and control;

and (3) mast*grow, an interaction to test if the effects of growth season differed between mastication and control. Non-nested random effects measured during the study were included: (1) location (Cow Mountain, Red Mountain, or Hopland), (2) count season (“ctseason,” winter, spring, summer, or fall) and (3) calendar year in which the survey occurred (as a proxy for interannual variation in climate conditions). Vegetation surveys occurred too infrequently to include variables related to shrub cover and height; however, an interaction between growth period and treatment type was included to serve as a proxy for vegetation regrowth (details in SI: Appendix 5).

Data were analysed and manipulated in R (version 3.2.1) using the packages “stats” (R Core Team, 2015), “pscl” (Jackman 2015; Zeileis *et al.* 2008), and “MASS” (Venables & Ripley 2002). Rarefaction and Morisita-Horn analyses were then carried out in EstimateS version 9.0 (Colwell 2013). GLMM analysis was conducted in R using the package ‘lme4’ (Bates *et al.* 2014).

Results

Bird survey results

A total of 49 bird species and 2529 total bird individual detections were made in 354 point-count surveys (SI: Appendix 6, Table S1). Survey effort differed greatly between masticated plots and other types of plots. Fall mastication sites were visited far fewer times than prescribed fire and control units because of accessibility issues (Table 1). Control plots were surveyed for an additional year prior to vegetation management activity, and visited 123 times in total. The vast majority (99%) of detections recorded during point counts were $\leq 10\text{m}$ from observers, which supports the independence of point counts separated by 100 m in dense shrub

(SI: Appendix 7). Raw counts of abundances per survey show generally increasing numbers of birds detected in prescribed fire units in all seasons, while masticated units show relatively low observed abundance in all post-treatment growth periods for both treatment seasons (Fig. 3).

Treatments differed strongly by their most abundant species detected (SI: Appendix 6, Table S1). In control units, the most detected birds were Wrentit (*Chamaea fasciata*), California Scrub-Jay (*Aphelocoma californica*), and Lesser Goldfinch (*Spinus psaltria*), followed by Spotted Towhee (*Pipilo maculatus*). Fire-treated plots show high similarity to controls in all seasons, with Wrentit, California Scrub-Jay, and Spotted Towhee also ranking among the most observed (SI: Appendix 6, Table S2). Fall and spring fire also contained high numbers of Bewick's Wrens (*Thryomanes bewickii*), while control and winter fire plots shared high numbers of Bell's Sparrows (*Artemisiospiza belli*). In contrast, masticated plots had Bewick's Wrens, Dark-eyed Juncos (*Junco hyemalis*), and Western Bluebird (*Sialia mexicana*) as the most commonly detected species, with fall mastication additionally having high numbers of California Quail (*Callipepla californica*). Ranked abundance comparisons (SI: Appendix 6, Table S3) show that prescribed fire maintains the same dominant species as controls, and mastication does not. This conclusion is further supported by calculations of the Morisita-Horn index (Table 2), comparing similarity among bird communities in all experimental units.

Species richness and similarity comparisons

Species richness varied greatly among treatment types, with prescribed fire units showing much higher richness than masticated units, and masticated units falling well below control levels of richness (Fig. 4). Welch's unpaired t-tests were applied to estimates of species richness generated by rarefaction methods for each management scenario, while controlling for similar

number of individuals (this is equivalent to assessing differences in species richness between controls and treatments at vertical lines drawn at maximum number of individuals plotted for each management case on Fig. 4). *Post hoc* comparisons using Bonferroni corrections (with $P=0.05$ significance level and $n=5$ comparisons, $P_{corr}=0.01$) indicated that the mean species richness for each treatment season was highly statistically different from the control in each case (SI: Appendix 8). Prescribed fire units recovered richness comparable to control units within three years, with winter fire treatments having the highest diversity of birds in plots and exceeding species richness in controls. Fall fire had 91% of control-level species richness (Welch's $t(2174) = 25.75$, $P < 0.0001$), spring fire had 89% of the species richness of controls (Welch's $t(1133) = 17.95$, $P < 0.0001$), and winter fire had 140% (Welch's $t(1117) = 49.04$, $P < 0.0001$). In contrast, masticated units had much lower richness than controls, with fall mastication having much lower richness than spring mastication. Fall mastication produced 43% of control-level species richness (Welch's $t(82)=31.15$, $P < 0.0001$) and spring mastication resulted in 75% of species richness compared to controls (Welch's $t(273) = 16.37$, $P < 0.0001$).

Comparisons of abundance structure of bird communities between experimental treatments and seasons with the Morisita-Horn index show highest similarity between control and winter fire units ($C_{mH}=0.923$), with control and spring fire then fall fire being next most similar ($C_{mH}=0.873$ and $C_{mH}=0.87$, respectively). Both spring and fall mastication showed very low similarity to controls ($C_{mH}=0.293$ and $C_{mH}=0.175$, respectively), with fall mastication and control representing the lowest similarity values across all treatment-season combinations (Table 2).

Guild analyses

All five categories of bird guilds studied were found to be differentially impacted by treatment types and seasons (Fig. 5). Compared to controls, masticated units attracted granivores over insectivores, and reduced the proportions of omnivores and birds that utilize multiple food sources (χ^2 test of proportions, $P < 0.0001$ for spring and fall). Spring masticated units attracted higher proportions of non-breeding birds than controls ($P < 0.0001$). Masticated units in both seasons were used by higher proportions of ground-nesting and ground-foraging birds, and correspondingly lower proportions of tree-nesting and foliage-gleaning birds ($P < 0.0001$ spring, $P < 0.0001$ fall). In almost every test, masticated plots had statistically significantly different guild structure compared to control plots (Fig. 5; SI: Appendix 4, Table S2).

In contrast, prescribed fire treatments did not differ as sharply from controls in guild composition, and season was more important in structuring the guilds than was the case for masticated plots (Fig. 5). Fall fire had more differences from controls, including feeding and foraging guild structure (compared to controls: more granivores, fewer insectivores; more ground feeders and fewer foliage gleaners, similar to mastication treatment plots; $P = 0.003$), and differences in nesting guilds, including fewer tree-nesters than controls ($P < 0.0001$). Winter fire treatments were the most similar to controls, while spring fire treatments resulted in differences in all categories examined. Compared to controls, spring fire had more birds that feed on multiple food sources, more ground feeders and fewer foliage gleaners ($P < 0.0001$), more visitations by year-round residents ($P = 0.0002$), more breeding birds ($P = 0.003$), and fewer tree-nesters ($P < 0.090$).

Modelling observed bird abundances

Observed bird abundances per survey varied substantially between experimental unit types (Fig. 3). GLMM analysis (Table 3) showed that (1) fire-treated units had fewer birds than controls ($P<0.001$); (2) masticated units had fewer birds than either controls ($P<0.001$) or fire-treated units ($P<0.001$); (3) when fire was applied in the fall, it led to higher bird abundance ($P=0.033$); (4) when fire was done in the winter, it may have led to higher bird abundance ($P=0.057$); (5) bird abundance increased with the number of growth seasons for fire ($P<0.001$), while the number of growth seasons had no effect on control ($P=0.393$) or masticated ($P=0.502$) plots; and finally, (6) year-to-year variation was about twice as great as either site-to-site or season-to-season variation ($\sigma_{\text{year}}^2=0.076$, $\sigma_{\text{site}}^2=0.030$, $\sigma_{\text{season}}^2=0.026$).

Discussion

Effects of management on chaparral bird communities

Our results provide the first direct comparison of the effects of two fuels manipulation treatments, prescribed fire and mastication, on California chaparral bird communities. Our primary finding is that mastication has very different effects on bird communities compared to prescribed fire and relative to controls. We found that prescribed fire treatments were more similar to controls in terms of species richness, abundance, community similarity, and guild structure than masticated treatments were. In contrast, mastication, compared to controls, lowers richness and overall abundances of bird species, changes the dominant species of birds, and alters guild structure by excluding insectivores, migratory and breeding birds. Whereas prescribed fire units had increasing bird abundances over successive seasons, masticated units did not show similar increases over time. Bird communities recover to control-like assemblages within 3-4 years after prescribed fire in any season, but do not recover in masticated units. These

effects on the bird community are likely mediated by the structure and species composition of the treated vegetation. Our results support our earlier hypothesis that the bird community is affected by the structure of vegetation resulting (and recovering) from treatment; however, further studies relating the bird and vegetation communities would be required to establish that this hypothesis is correct.

Secondarily (and consistent with plant community studies at these sites), we expected and found that treatment type would have a stronger effect on structuring the bird community than season of treatment. Season of treatment does appear to have a limited affect, particularly for prescribed fire. In terms of total avian abundance, fall fire had the highest abundance compared to all other treatments, but winter fire had both the highest community similarity to controls and had greater estimated species richness.

For every metric evaluated, masticated units in both seasons were the most different from controls. Mastication affects bird communities in very different, and generally negative ways compared to prescribed fire. Mastication is therefore not a substitute for prescribed fire as ecological management in chaparral. This finding differs from similar studies in other types of seasonally dry forests, where mastication may be a useful substitute for prescribed fire (with regards to bird communities) given management constraints (Fontaine & Kennedy 2012). However, our results strongly support similar findings of negative impacts on shrubland-associated birds in chaparral by Seavy *et al.* (2008), and may be consistent with Alexander *et al.* (2007)'s finding that hand-pile and burn practices impact bird communities less than mastication. We also note that bird species' responses may differ on landscapes with larger treatment patches than we were capable of experimentally manipulating.

Generalizability of the California chaparral fuels manipulation study

Previous work in California chaparral has been restricted to wildfire effects in southern California. Evidence suggests that wildfire and prescribed fire effects are not interchangeable (Alba *et al.* 2015), so the evaluation of prescribed fire as a management tool should not solely rely on studies following wildfire. Whereas the exact role of fire in chaparral likely varies across the region, it is clear that understanding its ecological effects throughout the entire range of chaparral and for taxa in addition to plants will be critically important to conservation efforts, as wildfire in California chaparral is predicted to increase with climate change (Batllori *et al.* 2013). An increase in fire sizes will likely affect the wildlife metacommunities, limiting refugia in wildfires (Mendelsohn *et al.* 2008), and affecting dispersal into and recolonization of burned areas (Brotons *et al.* 2005; van Mantgem *et al.* 2015). Management in California chaparral may also lead to the replacement of shrubland-associated birds with common suburban birds capable of transmitting Lyme disease bacteria, with consequences for disease ecology in California (Newman *et al.* 2015). More studies on chaparral wildlife and their interactions with a variety of fire characteristics and post-fire landscapes in California and elsewhere (Tingley *et al.* 2016) are needed to assess consequences of management for conservation and public health.

California chaparral has many similarities with Mediterranean scrublands elsewhere in the world and often shares their management challenges. The Fire and Fire Surrogates model employed here might productively be adapted to other systems where prescribed fire management and mechanical fuels treatments affect wildlife habitat, or where less is known about the interaction of the fire regime with wildlife (Woinarski 1999). However, we caution against interpreting these results as directly applicable to such scrublands due to the many differences among them in human land-use history, fire ecology, and avifaunas (*e.g.* Herrando *et*

385 *al.* 2002). Although controlled ecological experiments are expensive and logistically challenging,
386 the Fire and Fire Surrogates model is a strong inferential framework which would provide much
387 knowledge if replicated in other shrubland ecosystems around the world.

389 **Conclusions and Applications**

390 Comparative effects of fire management types and seasons on wildlife communities are
391 essential to understanding management tradeoffs. The information provided in this study is
392 important for chaparral managers who rarely have information about relative impacts of fuels
393 treatments on wildlife, but must consider the persistence of wildlife species to make science-
394 based management choices (Christensen *et al.* 1996).

395 Due to a lack of formal legal protections for chaparral in California, management
396 activities are often implemented without adequate knowledge of direct and indirect ecological
397 impacts to wildlife, and assessing the health of wildlife populations is in turn impeded by a lack
398 of management data. Our results indicate that where fuels treatment management in chaparral is
399 deemed necessary, prescribed fire will minimise diversity loss for bird communities compared to
400 mastication, with fall or winter fire likely having the lowest impacts. However, prescribed fire is
401 not necessary for the maintenance of chaparral biodiversity, and mastication may be more
402 effective for fuels reduction (Appendix 1). All fuels management in chaparral has the potential to
403 severely degrade habitat with repeated use. An ecologically conservative approach to lowering
404 fire management impacts on wildlife communities would therefore be to (1) limit fire
405 management to where there is a clear and demonstrated conflict with human habitation (this will
406 likely take the form of mastication for safety reasons), (2) plan development and manage risk to
407 human habitation rather than managing natural areas (Syphard *et al.* 2016), and (3) create a

chaparral management inventory system to allow scientists and managers to assess changes to the vegetation community due to management.

Authors' Contributions

SLS and JBP designed and implemented the original experiment. JBP and CV conducted all field surveys. EAN and MWT carried out all statistical analyses. EAN wrote the manuscript and supporting information. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

Data and metadata for this study are available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.mt3tr>

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635

Tables.

Table 1. Number of surveys conducted in each treatment type by season, followed by number of unique points surveyed in each combination [in brackets]. Exact coordinates of some control points were not recorded due to opportunistic sampling in these areas.

Treatment season	Treatment type			Totals
	CONTROL	FIRE	MASTICATION	
NONE	123 [20]	-	-	123 [20]
WINTER	-	69 [8]	-	69 [8]
SPRING	-	57 [8]	23 [6]	80 [14]
FALL	-	66 [8]	16 [6]	82 [14]
Totals	123 [20]	192 [24]	39 [12]	354 [56]

643 **Table 2.** Morisita-Horn indices of similarity of bird communities among experimental
 644 treatments. The Morisita-Horn index takes on values between 0 (no overlap) and 1 (full overlap
 645 of communities).

	CONTROL	FIRE: FALL	FIRE: WINTER	FIRE: SPRING	MASTICATION: FALL
FIRE: FALL	0.87	-	-	-	-
FIRE: WINTER	0.923	0.864	-	-	-
FIRE: SPRING	0.873	0.879	0.919	-	-
MASTICATION: FALL	0.175	0.339	0.139	0.223	-
MASTICATION: SPRING	0.293	0.514	0.273	0.308	0.651

648 **Table 3.** Fixed effect parameter estimates from GLMM analysis of observed bird abundances.

649 Significant parameters are printed in **bold**.

Parameter	Point Estimate	Standard error	<i>P</i> -value
Intercept	2.357	0.221	< 0.001
Fire	-0.811	0.136	< 0.001
Mastication	-1.116	0.232	< 0.001
Fall	-0.340	0.228	0.136
Winter	0.140	0.073	0.057
Growth Season	-0.051	0.060	0.393
Fire x Fall	0.537	0.252	0.033
Fire x Growth Period	0.175	0.041	< 0.001
Mastication x Growth Period	-0.071	0.106	0.502

650

651

Figures

Figure 1.

Locations of experimental units and coverage of California chaparral shrublands. Shrublands are represented in inset maps with wildlife habitat relationship data from the California GAP analysis project (USGS 2011), and include all GAP California chaparral classes. Shading in right panel represents north (light) /south (dark) aspect of topography.

661 Figure 2.
662 Prescribed fire (A) and mastication (B) treatments were carried out within 2 years. Aboveground
663 vegetation biomass was reduced by 95% in both types of treatments. Remaining fuel beds were
664 characterized by dead plant “skeletons” for prescribed fire (C), and ≤ 5 cm-length shredded,
665 woody debris for mastication treatments (D). A representative post-management fire (E) and
666 mastication (F) experimental unit are shown.

667

668

669

Figure 3.

Observed bird abundances per point count in all experimental units, by growth period. Error bars represent 1 standard error of the mean. No error bar could be calculated for winter fire treatments in growth period 5 due to low sample size.

Figure 4.

Species richness compared between controls and (A) prescribed fire and (B) mastication in all seasons. Prescribed fire treatments recovered to or exceeded control-like levels of species richness post-treatment, whereas masticated treatment areas always had lower species richness. Rarefaction was extrapolated to twice the number of surveys for all treatments, and rescaled to number of individuals to account for sample density. Shaded areas represent 95% confidence intervals around estimated species richness (solid lines).

Figure 5.

Proportions of birds in each guild by the following categories: (A) main food item, (B) foraging substrate, (C) resident status, (D) breeding status (whether or not a species breeds in the region), and (E) nesting substrate. Controls (CT) and treatments are prescribed fire in the fall, winter and spring (FF, FW and FS, respectively) and mastication in the fall and spring (MF, MS). Chi-squared tests for significance (followed by Fisher's exact test, where necessary) were performed on each group of proportions. Significance level codes are: ≤ 0.0001 '***'; ≤ 0.001 '**'; ≤ 0.01 '*'; ≤ 0.05 '.

SUPPORTING INFORMATION

For Newman et al., Chaparral bird community responses to prescribed fire and shrub removal in three management seasons.

Appendix 1: Summary of findings from other studies carried out in this California chaparral fuels manipulation experiment

Study	Findings
Stephens <i>et al.</i> Fire Ecology (2008)	Measurements from this experiment inform fire spread models useful to firefighting and wildfire/prescribed fire management
Potts & Stephens. Biological Conservation (2009)	Mastication has: <ul style="list-style-type: none">• highest number of non-natives• 34% more non-native annual grasses Winter and spring fire has: <ul style="list-style-type: none">• lowest non-native species and abundance
Potts, Marino & Stephens. Plant Ecology (2010)	By 3rd post-treatment year: <ul style="list-style-type: none">• Fire treatments have higher shrub cover: ($71 \pm 2\%$) compared to mastication ($43 \pm 4\%$)• No treatment effect on species diversity or composition
Wilkin <i>et al.</i> Final Report to the Joint Fire Sciences Program (2014) (non peer-reviewed technical report)	At 10th (and greater) post-treatment years: <ul style="list-style-type: none">• Persistent effect of shrub cover reduction in masticated units compared to prescribed fire units• Masticated unit have persistent higher cover in non-native plants and non-native annual grasses compared to prescribed fire units• Within prescribed fire treatments, season had no effect on vegetation height
Effects of chaparral management on birds	<i>This study</i>

Appendix 2: Site description and details of prescribed fire and mastication implementation

Site description

In California's Mediterranean-type climate, the growing season begins in fall and winter, and the climate is characterized by cool, rainy winters and hot, dry summers (Miller 1947, Keeley and Davis 2007). Average daily maximum temperatures range from 7°C in the winter to 34°C in the summer, with precipitation averaging 100 cm in per year (30-year average), mainly in the months of October through May. Precipitation measured during the study period ranged from 91-125 cm (Potts and Stephens 2009).

All the Hopland and Cow Mountain sites were within a ~2-km distance, and sites are positioned with similar south and west aspects and elevations (between 700-1000 m). This arrangement allows direct comparison between bird communities in the experimental units, which potentially vary in chaparral with elevation (Mendelsohn *et al.* 2008). Sites did not vary greatly in terms of vegetation community or distance from nearest water source; however, masticated plots had less steep slopes on average (up to 25-40%) than plots treated with prescribed fire (up to 35-55%), for equipment access. All sites were dominated (>65%) by chamise-type chaparral (*Adenostoma fasciculatum*), and also contained significant amounts of *Ceanothus cuneatis* and Manzanita (*Arctostaphylos spp.*) pre-treatment (Potts and Stephens 2009; Potts *et al.* 2010). Grasses and understory herbaceous plants were rare in all plots. Prior to treatment, all sites had ~100% cover and vegetation height measured between 1.5-2 m. All sites had not experienced fire or other management for 30+ years (although previous to that time, it had been common practice to burn areas after the end of deer hunt season in fall; R. Kieffer, *pers. comm.*).

Fire and mastication treatments

Prescribed fires were performed under the supervision of CALFIRE, BLM, and HREC and attended by hand crews and engines. Prescribed fires were lit with drip-torches and allowed to burn upslope, to create intense fire activity with a head fire. Mastication was carried out using by a steel-track tractor (Caterpillar D4) with a front-mounted, rotating, toothed drum. The mastication created a homogeneous treatment, which, like the prescribed fire treatments, removed or reduced 95-100% of standing aboveground biomass without damaging subsurface soil and root systems. Whereas the prescribed fire treatments left some “skeletons” of surface-killed plants, the masticator shredded vegetation into a <5 cm layer of small-diameter (<2.5 cm) woody debris (Fig. 2). Mastication and prescribed fire units were randomized between land ownership units (Hopland, Cow Mountain, Red Mountain), but were placed within those units non-randomly. Prescribed fire were placed in higher slope areas to encourage fire spread, but were surrounded by fire line to minimize risk of escape, and mastication was restricted to lower-grade slopes for stable machinery operation.

Prescribed fire treatments were carried out in fall, winter, and spring, and mastication was carried out in fall and spring during 2001-2003, with no winter treatment implemented because wet ground conditions prevented operation of mastication equipment. Treatment seasons were defined as: fall (3-20 November), winter (8-18 January), and spring (31 March-3 April for prescribed fire, and 23 April-2 June for mastication). Vegetation management treatments of the same type and season were planned to occur within the same season of a single year, but poor weather conditions shifted actual implementation of all treatments to being carried out over two years. Treatments were carried out under similar weather conditions, but fire behaviour was variable between plots. Treatments and controls were

replicated four times for a total of 24 experimental plots, each slightly larger than 2 ha. In some cases, units were contiguous, and in others, there was untreated area between treatment blocks. More details about dates and implementation of vegetation management are available in Potts and Stephens (2009).

Appendix 3: Details of point counts performed

Bird point counts were performed in 23 experimental units total; in 5 control units, in 4 units each of fall, winter and spring prescribed fire units, and 3 units each of fall and spring mastication. Point counts were performed at 2 fixed points in each unit, plus ~10 additional points in control areas, for a total of ~56 fixed point count locations.

A. Locations and plot designations of all experimental units surveyed during this study

Location	Plot	Treatment
Hopland - James II	1	MASTICATION: FALL
Hopland - James II	2	FIRE: SPRING
Hopland - James III	4	FIRE: FALL
Hopland - James II	5	FIRE: WINTER
Hopland - James I	6	CONTROL
Hopland - Orchard	GATE	CONTROL
Hopland	7	FIRE: FALL
Hopland	8	MASTICATION: SPRING
Red Mountain	A	MASTICATION: FALL
Red Mountain	B	MASTICATION: FALL
Red Mountain	C	FIRE: WINTER
Red Mountain	D	MASTICATION: SPRING
Red Mountain	E	FIRE: FALL
Red Mountain	F	MASTICATION: SPRING
Cow Mountain	G	FIRE: WINTER
Cow Mountain	H	FIRE: FALL
Red Mountain	J	FIRE: SPRING
Red Mountain	K	FIRE: SPRING
Red Mountain	L	FIRE: WINTER
Red Mountain	O	FIRE: SPRING
Red Mountain	HILL	CONTROL

Cow Mountain	14B	CONTROL
Cow Mountain	14G	CONTROL

B. Dates of surveys (point counts) performed in the experimental units by treatment type

(1) Control units

Treatment	Plot	Year surveyed	Calendar month	Calendar day
Control	6	2001	11	9
		2002	01	25
			03	08
				28
			04	12
				26
			05	23
			06	19
			10	02
			11	15
				21
		2003	02	21
			03	18
			04	30
			05	21
			06	05
			09	17
		2004	01	15
			03	04
			05	04
				28
			06	21
			10	06
		2005	01	19
			03	10
			04	25
			05	16
			06	09
	14B	2002	02	08
			03	15
				29

		05	03
			24
		06	12
		09	17
		11	15
			20
	2003	02	20
		04	10
		06	13
		09	23
	2004	03	17
		04	30
		05	25
		06	18
		09	30
	2005	01	21
		04	21
		05	12
		06	20
14G	2002	02	08
		03	15
			29
		05	03
			24
		06	12
		09	17
	2003	02	20
		03	19
		04	10
		06	13
		09	23
	2004	01	13
		03	17
		04	30
		05	25
		06	18
		09	30
	2005	01	21
		04	21
		05	12

		06	20
GATE	2001	11	09
	2002	01	25
		03	08
			28
		04	12
			26
		05	23
		06	19
		09	20
		11	15
			21
	2003	02	25
		03	11
		04	30
		05	21
		06	05
		09	17
	2004	01	15
		03	04
		05	04
			24
		06	14
		10	04
	2005	01	18
		03	14
		04	25
		05	23
		06	06
HILL	2002	02	28
		06	13
		10	01
		11	15
			20
	2003	01	15
		03	25
		04	09
		05	22
		06	25
		09	25

	11	01
2004	01	21
	03	18
	04	29
	05	18
	06	15
	09	29
2005	01	27
	03	17
	04	20
	05	11
	06	15

(2) Prescribed fire units

Treatment	Plot	Year surveyed	Calendar month	Calendar day
FIREFALL	4	2001	11	09
		2002	01	25
			04	26
			05	28
			06	20
			09	20
		2003	02	21
			03	11
			04	30
			05	21
			06	06
			09	18
		2004	01	20
			03	11
			05	05
				19
			06	11
			10	05
		2005	01	31
			03	15
			04	26
			05	13
			06	03

7	2002	11	22
	2003	02	21
		03	18
		05	01
			22
		06	26
		09	18
	2004	01	22
		03	11
		05	05
			19
		06	11
		10	05
	2005	01	31
		03	15
		04	26
		05	13
		06	03
E	2003	02	28
		06	20
		09	24
	2004	01	07
		03	12
		04	28
		05	20
		06	17
		10	01
	2005	01	20
		03	16
		04	19
		05	10
		06	14
H	2003	04	10
		09	23
	2004	03	17
		04	30
		05	25
		06	18
		09	30
	2005	04	21

			05	12
			06	20
FIRESRING	2	2002	04	12
				26
			05	28
			06	20
			10	02
		2003	03	11
			05	01
				23
			06	18
			09	18
		2004	03	11
			05	05
				19
			06	11
			10	04
		2005	01	19
			03	10
			04	25
			05	13
			06	09
J		2003	04	09
			05	22
			09	25
		2004	03	18
			04	29
			05	18
			06	15
			09	29
		2005	01	27
			03	17
			04	20
			05	11
			06	15
K		2003	09	25
		2004	01	21
			03	18
			04	29
			05	18

			06	15
			09	29
		2005	01	27
			03	17
			04	20
			05	11
			06	15
	O	2003	04	09
			06	25
			09	25
		2004	03	18
			05	18
			06	15
			09	29
		2005	01	27
			03	17
			04	20
			05	11
			06	15
FIREWINTER	5	2002	01	25
			04	26
			05	23
			06	20
			09	20
		2003	02	26
			03	11
			04	30
			05	21
			06	18
			09	18
		2004	01	22
			03	04
			05	04
				28
			06	21
			10	05
		2005	01	19
			03	10
			04	26
			05	13

		06	13
C	2003	01	15
		02	28
		03	25
		05	19
		06	20
		09	24
	2004	03	12
		04	28
		05	20
		06	17
		10	01
	2005	01	20
		03	16
		04	19
		05	10
		06	14
G	2002	03	15
		05	24
		06	12
	2003	02	20
		03	19
		06	13
		09	23
	2004	03	17
		04	30
		05	25
		06	18
		09	30
	2005	01	21
		04	21
		05	12
		06	20
L	2003	02	28
		04	09
		06	25
		09	25
	2004	01	21
		03	18
		04	29

		05	18
		06	15
		09	29
	2005	01	27
		03	17
		04	20
		05	11
		06	15

(3) Masticated units

Treatment	Plot	Year surveyed	Calendar month	Calendar day
MASTFALL	8	2003	02	21
			04	30
			06	05
		2004	01	15
			06	21
	A	2004	04	28
			06	17
			10	01
		2005	04	19
			05	10
			06	14
	B	2004	04	28
			05	20
			06	17
		2005	01	20
			05	10
MASTSPRING	1	2002	04	26
			06	19
			10	02
		2003	05	23
		2004	01	22
			03	11
			05	05
				19
			06	11
		2005	03	10
				15

		04	25
			26
		05	13
		06	03
D	2003	04	08
		09	24
	2005	01	20
F	2003	06	20
		09	24
	2004	06	17
	2005	04	19
		05	10

Appendix 4: Categorization of bird species in this study for analysis by guilds

Bird species were classified into functional guilds for analyses of the effects of treatment type and season on bird guilds (De Graaf *et al.* 1985). Bird species were assigned to guilds based on information available from Birds of North America Online (<http://bna.birds.cornell.edu/bna/>), the Cornell Lab of Ornithology online bird guide (<http://www.allaboutbirds.org/guide>), breeding observations recorded at HREC (Vaughn and Kieffer 2007), and Sibley (2005). Bird common names and specific epithets follow Chesser *et al.* (2015).

Additional reference

Chesser, R.T., Banks, R.C., Burns, K.J., Cicero, C., Dunn, J.L., Kratter, A.W., Lovette, I.J., Navarro-Sigüenza, A.G., Rasmussen, P.C., Remsen Jr, J.V. and Rising, J.D., 2015. Fifty-sixth Supplement to the American Ornithologists' Union: Check-list of North American Birds. *The Auk*, 132(3), pp.748-764.

Sibley, D. 2005. *The Sibley field guide to birds of western North America*. Alfred A. Knopf, New York, New York, USA.

Table S1. Birds present in study, characterized into guilds

4-Letter Code	Common Name	Scientific Name	Main Food Item	Feeding Substrate	Resident Status	Breeding Status	Nesting Substrate
ACWO	Acorn Woodpecker	<i>Melanerpes formicivorus</i>	Insects	Bark	Year-round	Breeding	Cavity
AMRO	American Robin	<i>Turdus migratorius</i>	Insects	Ground	Year-round	Breeding	Tree
ANHU	Anna's Hummingbird	<i>Calypte anna</i>	Nectar	Aerial (Hovering)	Year-round	Breeding	Tree
ATFL	Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	Insects	Aerial (Hovering)	Summer (breeding)	Breeding	Cavity
BEWR	Bewick's Wren	<i>Thryomanes bewickii</i>	Insects	Foliage	Year-round	Breeding	Cavity
BESP	Bell's Sparrow	<i>Artemisiospiza belli</i>	Insects	Ground	Year-round	Breeding	Shrub
BGGN	Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	Insects	Foliage	Summer (breeding)	Breeding	Tree
BHGR	Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	Multiple (Insects/Fruit)	Foliage	Summer (breeding)	Breeding	Tree
BLPH	Black Phoebe	<i>Sayornis nigricans</i>	Insects	Aerial (Flycatching)	Year-round	Breeding	Cliff
BTYW	Black-throated Gray Warbler	<i>Setophaga nigrescens</i>	Insects	Foliage	Migration	Non-breeding	Non-breeding
BUSH	Bushtit	<i>Psaltiriparus minimus</i>	Insects	Foliage	Year-round	Breeding	Tree
CALT	California Towhee	<i>Melospiza crissalis</i>	Seeds	Ground	Year-round	Breeding	Shrub
CAQU	California Quail	<i>Callipepla californica</i>	Seeds	Ground	Year-round	Breeding	Ground
COHA	Cooper's Hawk	<i>Accipiter cooperii</i>	Birds	Aerial	Year-round	Breeding	Tree
CORA	Common Raven	<i>Corvus corax</i>	Multiple (Omnivore)	Ground	Year-round	Breeding	Cliff

4-Letter Code	Common Name	Scientific Name	Main Food Item	Feeding Substrate	Resident Status	Breeding Status	Nesting Substrate
CATH	California Thrasher	<i>Toxostoma redivivum</i>	Multiple (Insects/Fruit)	Ground	Year-round	Breeding	Shrub
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	Seeds	Ground	Winter (non-breeding)	Non-breeding	Non-breeding
FOSP	Fox Sparrow	<i>Passerella iliaca</i>	Insects	Ground	Winter (non-breeding)	Non-breeding	Non-breeding
GCSP	Golden-crowned Sparrow	<i>Zonotrichia atricapilla</i>	Insects	Ground	Winter (non-breeding)	Non-breeding	Non-breeding
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>	Insects	Bark	Year-round	Breeding	Cavity
HETH	Hermit Thrush	<i>Catharus guttatus</i>	Insects	Ground	Winter (non-breeding)	Non-breeding	Non-breeding
HUVI	Hutton's Vireo	<i>Vireo huttoni</i>	Insects	Foliage	Year-round	Breeding	Tree
LAGO	Lawrence's Goldfinch	<i>Spinus lawrencei</i>	Seeds	Foliage	Summer (breeding)	Breeding	Tree
LAZB	Lazuli Bunting	<i>Passerina amoena</i>	Insects	Ground	Summer (breeding)	Breeding	Shrub
LEGO	Lesser Goldfinch	<i>Spinus psaltria</i>	Seeds	Foliage	Year-round	Breeding	Tree
MODO	Mourning Dove	<i>Zenaida macroura</i>	Seeds	Ground	Year-round	Breeding	Tree
MOUQ	Mountain Quail	<i>Oreortyx pictus</i>	Seeds	Ground	Year-round	Breeding	Ground
NAWA	Nashville Warbler	<i>Oreothlypis ruficapilla</i>	Insects	Foliage	Migration	Non-breeding	Non-breeding
NOFL	Northern Flicker	<i>Colaptes auratus</i>	Insects	Ground	Year-round	Breeding	Cavity
OATI	Oak Titmouse	<i>Baeolophus inornatus</i>	Insects	Foliage	Year-round	Breeding	Cavity

4-Letter Code	Common Name	Scientific Name	Main Food Item	Feeding Substrate	Resident Status	Breeding Status	Nesting Substrate
OCWA	Orange-crowned Warbler	<i>Oreothlypis celata</i>	Insects	Foliage	Year-round	Breeding	Ground
OSFL	Olive-sided Flycatcher	<i>Contopus cooperi</i>	Insects	Aerial (Flycatching)	Summer (breeding)	Breeding	Tree
PISI	Pine Siskin	<i>Spinus pinus</i>	Seeds	Foliage	Year-round	Breeding	Tree
PSFL	Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	Insects	Aerial (Flycatching)	Migration	Non-breeding	Non-breeding
PUFI	Purple Finch	<i>Haemorhous purpureus</i>	Seeds	Foliage	Year-round	Breeding	Tree
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	Insects	Foliage	Winter (non-breeding)	Non-breeding	Non-breeding
RCSP	Rufous-crowned Sparrow	<i>Aimophila ruficeps</i>	Seeds	Ground	Year-round	Breeding	Ground
SAPH	Say's Phoebe	<i>Sayornis saya</i>	Insects	Aerial (Flycatching)	Winter (non-breeding)	Non-breeding	Non-breeding
SELHU	Selasphorus Hummingbird	<i>[Selasphorus spp. *]</i>	Nectar	Aerial (Hovering)	[multiple categories]	[multiple categories]	[excluded]
SPTO	Spotted Towhee	<i>Pipilo maculatus</i>	Multiple (Omnivore)	Ground	Year-round	Breeding	Ground
STJA	Steller's Jay	<i>Cyanocitta stelleri</i>	Multiple (Omnivore)	Ground	Year-round	Breeding	Tree
VATH	Varied Thrush	<i>Ixoreus naevius</i>	Insects	Ground	Winter (non-breeding)	Non-breeding	Non-breeding
WCSP	White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	Insects	Ground	Winter (non-breeding)	Non-breeding	Non-breeding

4-Letter Code	Common Name	Scientific Name	Main Food Item	Feeding Substrate	Resident Status	Breeding Status	Nesting Substrate
WEBL	Western Bluebird	<i>Sialia mexicana</i>	Insects	Aerial (Flycatching)	Year-round	Breeding	Cavity
WESJ	California Scrub-Jay	<i>Apelocoma californica</i>	Multiple (Omnivore)	Ground	Year-round	Breeding	Tree
WETA	Western Tanager	<i>Piranga ludoviciana</i>	Insects	Foliage	Migration	Non-breeding	Non-breeding
WIWA	Wilson's Warbler	<i>Cardellina pusilla</i>	Insects	Foliage	Migration	Non-breeding	Non-breeding
WREN	Wrentit	<i>Chamaea fasciata</i>	Insects	Foliage	Year-round	Breeding	Shrub
YRWA	Yellow-rumped Warbler	<i>Setophaga coronata</i>	Insects	Foliage	Year-round	Breeding	Tree

*Selasphorus Hummingbird comprises both Allen's and Rufous Hummingbirds, which are difficult to tell apart in field surveys; these two species may also hybridize in this region of California (J. McEntee, *personal communication*). "Selasphorus Hummingbird" is therefore treated as a single species for analyses throughout this study.

Observed abundances were not augmented by modelling before statistical tests (see Appendix 8: *Bird detection and abundances within guilds*). For each of the five categories, the proportions of bird individuals in each guild were compared between treatment-season experimental units using Pearson's Chi-squared test for count data with Yeats' continuity correction, or Fisher's exact test for small sample sizes, with the hypothesis that proportions of individuals in each guild do not differ between control plots and treated plots (Table S2).

Table S2. Pairwise Chi-square and Fisher's exact test results demonstrate differences between bird guilds' use of experimental units. Chi-squared values are two-tailed, and calculated based on comparison to the expected control unit proportions. Where the Chi-squared statistic is approximate due to low sample numbers, Fisher's exact test was also performed (*P*-values in parentheses). Significant *P*-values are in **bold**.

Category	Experimental treatment	Chi-squared	Degrees of freedom	<i>P</i> -value
Main food item	FIRE: FALL	15.684	4	0.003 (0.003)
	FIRE: SPRING	21.788	4	0.0002 (0.0001)
	FIRE: WINTER	10.648	4	0.031 (0.020)
	MASTICATION: FALL	47.908	4	<0.0001 (<0.0001)
	MASTICATION: SPRING	50.646	4	<0.0001 (<0.0001)
Feeding substrate	FIRE: FALL	49.396	3	<0.0001 (<0.0001)
	FIRE: SPRING	22.212	3	<0.0001 (<0.0001)
	FIRE: WINTER	7.390	3	0.060 (0.092)
	MASTICATION: FALL	30.801	3	<0.0001 (<0.0001)
	MASTICATION: SPRING	55.028	3	<0.0001 (<0.0001)
Resident status	FIRE: FALL	1.2617	3	0.738 (0.795)
	FIRE: SPRING	18.454	3	0.0004 (0.0002)
	FIRE: WINTER	8.069	3	0.045 (0.046)
	MASTICATION: FALL	1.3395	3	0.720 (0.740)
	MASTICATION: SPRING	34.761	3	<0.0001 (<0.0001)
Breeding status	FIRE: FALL	0.012	1	0.912
	FIRE: SPRING	8.761	1	0.003
	FIRE: WINTER	2.836	1	0.092
	MASTICATION: FALL	0.277	1	0.598
	MASTICATION: SPRING	26.462	1	<0.0001
Nesting substrate	FIRE: FALL	55.954	4	<0.0001 (<0.0001)
	FIRE: SPRING	12.325	4	0.015 (0.090)
	FIRE: WINTER	12.911	4	0.012 (0.090)
	MASTICATION: FALL	35.171	4	<0.0001 (<0.0001)
	MASTICATION: SPRING	49.072	4	<0.0001 (<0.0001)

Appendix 5: Generalized linear mixed model specification

We constructed a Poisson-distributed generalized linear mixed model (GLMM; Bolker *et al.* 2009) to analyze total bird detections per survey within our experimental design. We tested three fixed effects that are central to our hypotheses: (1) treatment type (prescribed fire, mastication, control), (2) treatment season (fall, winter, spring, or “none” corresponding to the control), and (3) growth period (a positive, continuous variable marking number of years rolling over in January, when the growing season takes place). To deal with the mismatching contrasts, we created independent contrast variables for seasons and treatments. Specifically, we specified that fire = 1 if treatment was fire, 0 otherwise; mast = 1 if treatment was mastication, 0 otherwise; fall = 1 if treatment occurred in the fall, 0 otherwise; and winter = 1 if treatment occurred in the winter, 0 otherwise. The overall intercept for the model is for the control, and the treatment-level intercept is for the spring.

Three interactions among fixed effects were also included: (1) fire*fall, an interaction to test whether or not fall surveys were different between fire and mastication treatments; (2) fire*grow, an interaction to see if the effects of growth season differed between fire and control; and (3) mast*grow, an interaction to test if the effects of growth season differed between mastication and control.

Finally, non-nested random effects measured during the study were included: (1) location (Cow Mountain, Red Mountain, or Hopland), (2) count season (“ctseason,” winter, spring, summer, or fall) and (3) calendar year in which the survey occurred (as a proxy for interannual variation in climate conditions). Vegetation surveys occurred too infrequently to include variables related to shrub cover and height; however, an interaction between growth period and treatment type was included to serve as a proxy for vegetation regrowth.

GLMM analysis was conducted in R (R Core Team 2015) using the package ‘lme4’ (Bates *et al.* 2014). While predictive checks indicated that the total abundance data were slightly over-dispersed, a comparative model using a negative binomial distribution to account for overdispersion did not appreciably improve fit or change parameter values. Consequently, we report results from the simpler Poisson model.

Appendix 6: Bird species, their observed abundances and ranks within experimental treatments

Table S1: Bird species and their observed abundances listed alphabetically by common name

Columns denote presence within untreated control (CT), fall fire (FF), spring fire (FS), winter fire (FW), fall mastication (MF), and spring mastication (MS) experimental units. The most prevalent bird species by detections (comprising $\geq 10\%$ of total counts) are presented in **(bolded in parentheses)** for each experimental treatment type. (*Field detections of Rufous Hummingbird changed to Selasphorus hummingbird due to range overlap with Allen's Hummingbird in a likely hybridization zone).

Common Name	Scientific Name	CT	FF	FS	FW	MF	MS
Acorn Woodpecker	<i>Melanerpes formicivorus</i>				2		
American Robin	<i>Turdus migratorius</i>	6	3		18		
Anna's Hummingbird	<i>Calypte anna</i>	46	19	14	16		2
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	2	15	3	6		
Bewick's Wren	<i>Thryomanes bewickii</i>	52	(50)	(40)	14	(7)	(11)
Bell's Sparrow	<i>Artemisiospiza belli</i>	82	(57)	28	(50)		2
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	70	16	8	13		
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	1	2	1			
Black Phoebe	<i>Sayornis nigricans</i>			1			
Black-throated Gray Warbler	<i>Setophaga nigrescens</i>	4	1	1			
Bushtit	<i>Psaltirparus minimus</i>	45		17	25		
California Towhee	<i>Melospiza crissalis</i>	9	30	7	1		1
California Quail	<i>Callipepla californica</i>	7	22	1		(16)	8
Cooper's Hawk	<i>Accipiter cooperii</i>	1					
Common Raven	<i>Corvus corax</i>						2
California Thrasher	<i>Toxostoma redivivum</i>	37	12	8	4		

Dark-eyed Junco	<i>Junco hyemalis</i>	42	43	6	22	(5)	(22)
Fox Sparrow	<i>Passerella iliaca</i>	44	13	5	9	2	
Golden-crowned Sparrow	<i>Zonotrichia atricapilla</i>	12	11	11	5		4
Hairy Woodpecker	<i>Picoides villosus</i>		2		1		
Hermit Thrush	<i>Catharus guttatus</i>	29	4	2	6		
Hutton's Vireo	<i>Vireo huttoni</i>	1			2		
Lawrence's Goldfinch	<i>Spinus lawrencei</i>	4	1			2	
Lazuli Bunting	<i>Passerina amoena</i>	4	3		1		
Lesser Goldfinch	<i>Spinus psaltria</i>	(109)	22	4	12		2
Mourning Dove	<i>Zenaida macroura</i>		1				
Mountain Quail	<i>Oreortyx pictus</i>	2	10	12	6		2
Nashville Warbler	<i>Oreothlypis ruficapilla</i>				1		
Northern Flicker	<i>Colaptes auratus</i>	4	1		1		
Oak Titmouse	<i>Baeolophus inornatus</i>	18	8	7	13		
Orange-crowned Warbler	<i>Oreothlypis celata</i>	14	7	1	7		
Olive-sided Flycatcher	<i>Contopus cooperi</i>				2		
Pine Siskin	<i>Spinus pinus</i>	1					
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	1	1				
Purple Finch	<i>Haemorhous purpureus</i>	1	2		4		
Ruby-crowned Kinglet	<i>Regulus calendula</i>	7			1		
Rufous-crowned Sparrow	<i>Aimophila ruficeps</i>				1		
Say's Phoebe	<i>Sayornis saya</i>			1			
Selasphorus hummingbird	[<i>Selasphorus spp.*</i>]	2	1		1		
Spotted Towhee	<i>Pipilo maculatus</i>	100	(67)	(45)	(50)		3
Steller's Jay	<i>Cyanocitta stelleri</i>		2	4	1		
Varied Thrush	<i>Ixoreus naevius</i>	3			1		
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	1			1		
Western Bluebird	<i>Sialia mexicana</i>	7	8		1	(4)	(9)
California Scrub-Jay	<i>Aphelocoma californica</i>	(120)	(52)	(61)	(58)	3	2
Western Tanager	<i>Piranga ludoviciana</i>	2					
Wilson's Warbler	<i>Cardellina pusilla</i>	1					
Wrentit	<i>Chamaea fasciata</i>	(180)	(63)	(59)	(89)		
Yellow-rumped Warbler	<i>Setophaga coronata</i>				1		
Total Species		38	32	35	36	7	13

Table S2: Ranks and rank comparisons of the most common bird species in each experimental unit type. Bird species shown comprise >80% of birds detected in control units. Equal abundances within one treatment-season are assigned the same rank. “NP” indicates that a species was not present in surveys of that experimental unit type.

SPECIES	Abundance in CONTROL	Rank in CONTROL	Rank in FIREFALL	Rank in FIREWINTER	Rank in FIRESRING	Rank in MASTFALL	Rank in MASTSPRING
WREN	180	1	2	1	2	NP	NP
WESJ	120	2	4	2	1	5	7
LEGO	109	3	8	11	14	NP	7
SPTO	100	4	1	3	3	NP	6
BEWR	82	5	3	4	5	NP	7
BGGN	70	6	11	10	10	NP	NP
BESP	52	7	5	9	4	2	2
ANHU	46	8	9	8	7	NP	7
BUSH	45	9	NP	5	6	NP	NP
FOSP	44	10	12	12	13	6	NP
DEJU	42	11	6	6	12	3	1

Table S3. Rank comparisons between bird species in controls compared to other experimental units. Bird species shown comprise >80% of birds detected in control units. Equal abundances within one treatment-season are assigned the same rank. Positive numbers indicate a relative increase in rank, and negative numbers indicate a relative decrease. “N/A” indicates that no comparison could be made, because the species was absent from either the control units or the experimental unit being compared to it.

SPECIES	Rank in CONTROL	Rank in FIRE: FALL	Rank in FIRE: WINTER	Rank in FIRE: SPRING	Rank in MASTICATION: FALL	Rank in MASTICATION: SPRING
WREN	1	-1	0	-1	(N/A)	(N/A)
WESJ	2	-2	0	1	-3	-5
LEGO	3	-5	-8	-11	(N/A)	-4
SPTO	4	3	1	1	(N/A)	-2
BEWR	5	2	1	0	(N/A)	-2
BGGN	6	-5	-4	-4	(N/A)	(N/A)
BESP	7	2	-2	3	5	5
ANHU	8	-1	0	1	(N/A)	1
BUSH	9	(N/A)	4	3	(N/A)	(N/A)
FOSP	10	-2	-2	-3	4	(N/A)
DEJU	11	5	5	-1	8	10

Appendix 7. Bird detection and abundances within guilds

Without trapping, chaparral animals—including birds—are difficult to detect because of the structure of the vegetation, and baseline population statistics are therefore difficult to establish throughout this widespread and heterogeneous ecosystem. Generally, we attribute the higher observed abundance in post-fire plots to higher true abundances, which are driven by the more complex habitat structure provided by plant skeletons that remain after fire but are destroyed during mastication. Plant skeletons provide perching and nesting sites, protection from predators, foraging substrate, and potentially greater variation in post-treatment microclimates, and masticated plots lack these structures entirely. The common post-fire species also tend to be those that favour taller stand structure (*e.g.* California Scrub Jay, Spotted Towhee and Bewick's Wren) compared to post-mastication species, which typically forage and nest on or near the ground (*e.g.* California Quail, Dark-eyed Junco).

We were not able to use detection-corrected models (*e.g.* MacKenzie *et al.* 2002) given the structure of the experiment (implementation of treatments over multiple years, lack of secondary survey units); however, abundance-related conclusions about bird use of vegetation structure using detections as a proxy for true abundances are still valid (Hutto 2016). Although false absences might bias abundance estimates, we believe that the direction of bias here reinforces our conclusions about species richness and abundance structure. Control plots were the most densely vegetated treatment with the highest percent cover and tallest vegetation heights (Potts and Stephens 2009; Potts *et al.* 2010). Consequently, detection probability should be lowest for species within the control plots. Additionally, within treatment plots, given vegetation regrowth, we would expect detectability within plots

to decline over years, particularly for small birds with low-volume calls (*e.g.* Bushtits) or birds that feed on the ground (*e.g.* California Quail). Therefore, our finding that masticated units contained fewer individuals and species is robust to the expected higher detection probability that should accompany the vegetation characteristics of these plots. If imperfect detection biases our results, the bias is in the direction of further strengthening our main finding.

Additional references

MacKenzie, D.I., Nichols, J.D., Lachman, G.B. *et al.* 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology*. 83:2248–2255.

Hutto, R.L. 2016. Should scientists be required to use a model-based solution to adjust for possible distance-based detectability bias?. *Ecological Applications*. 26:1287–1294.

Appendix 8. Results of Welch's unpaired t-tests comparing species richness between treatment seasons and controls

Table S1. Welch's unpaired t-tests were used to assess differences between species richness of control and management plots. The tests were applied in each case at the maximum number of individuals considered in the rarefaction estimates, described in the main text. Results and details of these tests are presented below, along uncorrected p -values. Bonferroni corrections calculated for the $P = 0.05$ level and 5 comparisons yield a new threshold of $P_{corr} = 0.01$, but none of the results of statistical significance change after the correction is applied. The P -values presented in the table are for 2-tailed Welch's t-tests, with the null hypothesis that management does not change mean species richness compared to the control, and the alternative hypothesis that management changes the mean. Other abbreviations are: Mean = mean species richness; SD = standard deviation; N = number of individuals in the rarefaction analysis; df = degrees of freedom; SEM = standard error of the difference between means; 95% CI = 95% confidence interval of the difference between means.

Table S1. (continued)

	CONTROL	FIRE: FALL	Welch's t statistic	df	P-value	SEM	95% CI
MEAN	40.29	36.51	25.75	2174	<0.0001	0.147	3.49 to 4.07
SD	3.27	3.6					
N	1098	1098					
	CONTROL	FIRE: SPRING					
MEAN	35.03	31.06	17.95	1133	<0.0001	0.221	3.54 to 4.40
SD	3	5					
N	697	694					
	CONTROL	FIRE: WINTER					
MEAN	37.91	52.95	49.04	1117	<0.0001	0.307	-15.64 to -14.44
SD	3.11	8.62					
N	898	892					
	CONTROL	MASTICATION: FALL					
MEAN	16.47	7.16	31.15	82	<0.0001	0.299	8.72 to 9.90
SD	2.59	0.51					
N	78	78					
	CONTROL	MASTICATION: SPRING					
MEAN	20.64	15.39	16.37	273	<0.0001	0.321	4.619 to 5.88
SD	2.81	2.54					
N	139	140					