ABSTRACT

TAILLIE, PAUL J. Using Distribution and Abundance of Birds to Guide Management of Fire-maintained Forest Ecosystems. (Under the direction of Chris Moorman and Nils Peterson).

Over the past century, the widespread suppression of fire has dramatically altered the structure and composition of forests previously maintained by fire. As a result, wildlife species associated with fire-maintained ecosystems have drastically declined. In an effort to mitigate this decline, forest managers use fire to restore these communities in a variety of ecological and geographical contexts. To aid restoration goals, the natural history of certain wildlife species can be used to infer ecosystem processes. We used species of birds associated with two distinct habitat types, to guide the management and restoration of fire-maintained ecosystems. In the Atlantic Coastal Plain, longleaf pine historically dominated the landscape but is now limited to isolated patches. We investigated the distribution of Bachman's sparrow to illustrate the implications of this shift in landscape context. Our results suggest focusing restoration efforts on large areas of high connectivity will facilitate the dispersal and occurrence of longleaf pine-associated species. In the mountains of the western United States, the varied topography and weather patterns result in high variation in fire frequency and severity, both locally and regionally. We investigated how the abundance of early successional species changed with time and across different burn severities following wildfire. These species responded primarily to moderate and high severities, on both short and long time scales. Establishing and maintaining early successional vegetation by reincorporating high severity fire in shrub-dominated habitats will help to mitigate declines of early successional birds that are otherwise rare or absent in the montane West. In both

cases, mimicking the historical disturbance regime helps to establish and conserve the habitat conditions required by bird species of concern.

Using Distribution and Abundance of Birds to Guide Management of Fire-maintained Forest Ecosystems

by
Paul J. Taillie

A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Master of Science

Fisheries, Wildlife, and Conservation Biology

Raleigh, North Carolina

2013

APPROVED BY:

Chris Moorman
Committee Co-Chair

M. Nils Peterson
Committee Co-Chair

Jaime Collazo

Peter Campbell

DEDICATION

To my parents.

BIOGRAPHY

Paul grew up in Upstate NY. Though he has always had a passion for the outdoors, it was not until he went to college at Cornell University in Ithaca, NY that he became seriously interested in ecology and wildlife as a career. After receiving his Bachelors' degree in May of 2006, he immediately flew to Colorado for his first field job surveying birds for Rocky Mountain Bird Observatory. After several years, working various field jobs across several states, he moved to North Carolina at the end of 2010 to begin his graduate education at North Carolina State University.

ACKNOWLEDGMENTS

This thesis would not be possible without the help of many people. Foremost, I would thank my committee for their invaluable advice, prompt reviews, and continuous patience. Also, I greatly appreciate funding for this project from Marine Corps Installations East, without which this project would not be possible. Beth Gardner and Nick Flanders provided substantial assistance with statistical concepts and analysis. Biologists Ed Corey, Jeff Marcus, John Carpenter, and others assisted with obtaining access to properties and offered their knowledge of the local ecology. Amanda Dube assisted with GIS and spatial analysis. Ryan Burnett and Nat Seavy provided field resources in CA and several manuscript reviews. Lastly, I would like to thank Winter Wren for her continued encouragement and support. She always seems to know when I need a break, but more often when I need to stay motivated.

TABLE OF CONTENTS

LIST OF TABLES

Using Occupancy of a Dispersal Limited, Longleaf Pine Specialist to Guide Restoration

Using Distance Sampling to Measure the Response of Early Successional Birds to Wildfire

LIST OF FIGURES

Using Occupancy of a Dispersal Limited, Longleaf Pine Specialist to Guide Restoration

Using Distance Sampling to Measure the Response of Early Successional Birds to Wildfire

USING BACHMAN’S SPARROW OCCUPANCY TO GUIDE RESTORATION OF THE LONGLEAF PINE ECOSYSTEM AT MULTIPLE SCALES

ABSTRACT

As the longleaf pine ecosystem has declined to just 3% of its historical extent and persists mostly as isolated patches across its former range, species associated with this system are of conservation priority. Though the vegetation composition and structure of remnant patches influence habitat quality for these species, the distribution of habitat across a larger scale likely also contributes to habitat suitability. We used Bachman’s Sparrow (*Peucaea aestivalis*) as a surrogate species to measure the relative importance of local vegetation and landscape connectivity to restoration of the longleaf pine ecosystem. We surveyed sparrows using repeated point counts at 232 points within 111 habitat patches in the Onslow Bight region of North Carolina between 10 April and 20 July, 2011. We then fit a series of single-season occupancy models, including both local and landscape-level predictors, to identify those that best explained the distribution of Bachman’s Sparrows. We documented a strong response to vegetation characteristics best maintained via prescribed fire, namely intermediate grass volume and low shrub height, which matches findings from other studies of Bachman’s Sparrow habitat selection. However, we determined the most influential predictor of Bachman’s Sparrow occupancy was the amount of open-canopy pine forest within 3 km. Specifically, the probability of sparrow occurrence was close to 0 in landscapes comprised of <10% open-canopy pine forest, regardless of local vegetation conditions. As such, efforts to restore longleaf pine ecosystems should be focused in areas of

high connectivity to accommodate species sensitive to habitat loss and fragmentation such as Bachman's Sparrow.

INTRODUCTION

The flora and fauna associated with longleaf pine (*Pinus palustris*) forests comprise one of the most diverse communities in North America (Peet & Allard 1993; Simberloff 1993; Van Lear et al. 2005). Currently, this ecosystem is one of the most endangered, occupying a mere 3-5% of its historical range (Frost 1993; Landers et al. 1995; Frost 2006). In addition to the loss in total area, the distribution of this ecosystem across its range has fundamentally changed. Historically, longleaf pine forests dominated the Atlantic and Gulf Coastal Plains in the Southeast, interrupted only by rivers and scattered swamps, whereas today, these forests persist as isolated patches within a matrix of row crop agriculture, fire-suppressed pine plantations, and increasing urban development. This fundamental shift in landscape context likely has important implications for the many, associated plant and animal species that evolved in a landscape comprised of vast, contiguous tracts of longleaf pine forest.

In recent years, attempts to restore functioning landscapes of longleaf pine forest have gained momentum. The Range-wide Conservation Plan for Longleaf Pine was developed by a variety of federal, state, and private organizations and calls for the restoration of 4.6 million acres of longleaf pine forest (America's Longleaf 2009). However, information on how site-level factors, landscape characteristics, and land-use history interact to influence restoration outcomes is limited (Brudvig & Damschen 2011). To inform decisions of where to focus restoration efforts or acquire new properties to restore, a better understanding of how species of interest respond to landscape conditions is needed.

We used Bachman’s Sparrow (*Peucaea aestivalis*) as a surrogate species to quantify the influence of habitat distribution across various spatial scales on wildlife species associated with longleaf pine forests. Bachman’s Sparrow is appropriate for this purpose because it has specific local habitat associations that reflect the conditions of quality longleaf pine forests, particularly the presence of a diverse herbaceous groundcover. Their window of habitat suitability is so narrow that sparrows abandon habitat patches after as little as 3 years without fire when grasses begin to form a dense thatch and restrict movement along the ground and less fire-tolerant woody species begin to replace existing herbaceous vegetation (Engstrom et al. 1984; Dunning & Watts 1990; Rutledge & Conner 2002; Tucker et al. 2004). Upon abandoning the unsuitable territory, individuals are tasked with dispersing to other more suitable habitat patches. Successful dispersal to a new territory will likely be facilitated by a more connected landscape (Dunning et al. 1995). As such, we expected Bachman's Sparrow occupancy to depend on landscape connectivity even when local habitat conditions were ideal.

Our study expands on previous research which has suggested patch isolation affects colonization of new habitat patches by Bachman’s Sparrow, possibly due to poor dispersal through the matrix of non-longleaf pine landcover types (Dunning et al. 1995; Dunning & Kilgo 2000). By modeling Bachman’s Sparrow occupancy across a variety of local vegetation characteristics, patch sizes, and degrees of connectivity, we quantitatively describe the relative effects of patch-level conditions and larger scale characteristics on patch occupancy. Our results, along with studies on other species of concern, should help guide restoration efforts for longleaf pine forests and other rare and declining ecosystems.

METHODS

Study Area

Our study took place in the Onslow Bight region of southeastern North Carolina, which is identified as a "Significant Geographical Area" for longleaf pine conservation by the Longleaf Alliance (2009). Three large public properties contained the majority of fire-maintained longleaf pine forest in the region: Croatan National Forest, Marine Corps Base Camp Lejeune, and Holly Shelter Game Lands. In addition to other small public landholdings, a few scattered private properties were managed for longleaf pine ecosystem conservation. Otherwise, the landscape was dominated primarily by loblolly pine (*Pinus taeda*) plantation, row crop agriculture, and urban/suburban development.

Site Selection

We stratified the study area into two categories: 1) open-canopy, pine-dominated forest with a sparse middle-story (hereafter referred to simply as "habitat"), and 2) all other areas. To delineate patches of habitat, we combined remotely sensed data of vegetation cover-type and structure in a Geographical Information System (GIS) using ArcGIS v.10 (Environmental Systems Research Institute, Redlands, CA). Land cover data from the Southeast Gap Analysis Project (SEGAP 2008) and LANDFIRE (2006) were weighted according to Bachman's Sparrow habitat requirements in the current literature (Table 1). Areas that were suitable were reclassified with a value of 2, areas that were marginal were reclassified with a value of 1, and unsuitable areas were reclassified with a value of 0. We also derived vertical habitat structure layers using full-return Light Detection and Ranging (LiDAR) data collected for the North Carolina Floodplain Mapping Program (2001). Again, each layer was reclassified as habitat (2), marginal (1), or unsuitable (0; Table 1). We then conducted a series of summations of the layers and classified areas with sums of at least 75% of the total possible points ($\geq$ 9 out of 12) as habitat and areas with values < 9 as non-habitat. The resulting layer was a binary grid of 30-m x 30-m cells, where each cell had a value of either 1 (habitat) or 0 (non-habitat). We aggregated habitat cells into patches using 8-cell adjacency (i.e. if any of the four adjacent or four diagonal cells have the same value, they were considered part of the same patch). We attempted to access as many properties as possible to conduct sparrow and vegetation surveys. First, we contacted local experts to identify properties thought to support longleaf pine community types. We also identified the largest patches of habitat on private land using our GIS model and contacted landowners of the associated properties to solicit access. We were able to access 111 patches of various sizes and degrees of isolation.

Sparrow Surveys

We randomly selected the maximum number of survey points within each patch to survey sparrows, while maintaining a minimum of 250 m between survey points and 50 m from the patch boundary. After excluding 21 points due to inaccessibility, we surveyed 232 points (Fig. 1). Of those 232 points, 94 were visited 5 times, 89 were visited 4 times, 37 were visited 3 times, 11 were visited twice, and 1 was visited once. Some sites were sampled less because of limited access, especially during hunting seasons on private lands; however, by sharing the detection histories from all sites, our analysis accommodates an unbalanced sampling design (Fiske & Chandler 2011). Between 8 April and 25 July 2011, we randomly selected one of four observers to conduct each visit within 4 hours of sunrise. For the first 3 minutes of each survey, we recorded all visual and aural sparrow detections. We then broadcast a 30-second recording of a singing Bachman's Sparrow, followed by 5 seconds of call notes, using an mp3 player and portable speakers. Immediately following the broadcast, we surveyed sparrows for an additional 3 minutes. We recorded detections for all individuals during each 3-minute period separately.

Vegetation

We used an index of vegetation volume to quantify groundcover vegetation each visit by recording the number of 0.1-m intervals, or "hits," containing vegetation within 1 cm of a vertical 1-m pole (Mills et al. 1989; Dunning & Watts 1990; Plentovich et al. 1998; Moorman & Guynn 2001; Tucker et al. 2004). We categorized all hits as either: grass, forb/fern, woody/vine/shrub, switchcane (*Arundinaria gigantea*), or dead vegetation. We repeated this measurement every 10 m along a 100-m transect radiating away from the survey point at a random compass bearing. At successive visits, the procedure was repeated with a new random bearing. Vegetation height, also recorded by vegetation type, was obtained by recording the tallest "hit" on the 1-m pole, effectively rounding up to the nearest 0.1 m. Using a 10-factor prism, we measured basal area at the survey location during the first visit, and 50 m away from the survey point at a random bearing during successive visits.

We averaged measurements of vegetation height, volume, and basal area across visits to obtain an average for each survey point.

Landscape

We calculated landscape metrics for the habitat patches delineated in our GIS analysis using the software package FRAGSTATS (MaGarigal et al. 2002). For each patch, we calculated the area of the patch and the proximity of neighboring patches (hereafter referred to as “proximity”), a commonly used metric of patch isolation (greater proximity = less isolated). This metric incorporates the distance and area of all neighboring patches within a specified search distance, or “neighborhood” (McGarigal & McComb 1995). To define this search distance, we used an estimated dispersal distance derived from the proportional relationship between territory size and juvenile dispersal described by (Bowman 2003). Using this relationship, the largest Bachman’s Sparrow home ranges reported by Cox and Jones (2006) correspond to an estimated dispersal distance of 3 km. As such, the calculation of proximity for each patch incorporated every other patch within 3 km.

We also calculated the percent of habitat within a given radius. This metric of landscape connectivity has been shown to be more reliable and consistent than more complicated metrics, and is more easily interpreted (Cunningham & Johnson 2011). We calculated the percent habitat within the estimated maximum dispersal distance discussed above, as well as the estimated median dispersal distance of 1 km (Sutherland et al. 2000). As such, our analysis incorporated variables at 4 scales, 1) within 100 m of the sampling location (vegetation characteristics), 2) the patch in which the sampling location was located (patch area), 3) the landscape within 1 km of the site (proportion of habitat), and 4) the landscape within 3 km (proximity and proportion of habitat).

Model Selection

Using the package “Unmarked” in R, we fit a set of single-season, single-species hierarchical occupancy models (Fiske & Chandler 2011). We incorporated both the passive and active survey data by including a binary covariate of survey type in all models. To further account for imperfect detection, we first fit a series of models containing all possible combinations of a linear effect of observer and both linear and quadratic effects of date as covariates on detection probability (p). In addition to these observation covariates, Unmarked allows for the incorporation of site covariates on detection. We anticipated vegetation conditions would impact detection, and thus included the site covariates of basal area and shrub height. We selected the best model according to lowest Akaike’s Information Criterion (Burnham & Anderson 2002), and used this model for the detection component of all successive occupancy models.

We then modeled site-level occupancy (ψ) at each site. We used grass volume as a site-level covariate for occupancy, as previous research has shown this to be an important predictor of Bachman’s Sparrow habitat selection (Plentovich et al. 1998). In addition, we added a quadratic effect of grass volume because we expected sparrow occurrence to increase with grass volume, but then decline as extreme values of grass density impeded sparrow movement, rendering the habitat patches less suitable (Cox & Jones 2009). We also included basal area and shrub height as site-level covariates because these are directly affected by management, particularly prescribed fire. For the larger scale effects, we included linear effects of all landscape metrics previously described. However, a preliminary analysis revealed that proportion of habitat at both 1 km and 3 km was correlated (R>.5) with both patch area and proximity, and thus all models containing proportion of habitat did not contain either patch area or proximity. We standardized all continuous covariates by subtracting the mean and dividing by the standard deviation. As with detection, we fit all possible models and selected the best model according to lowest AIC (Burnham & Anderson 2002). If more than one model had a ΔAIC less than 2 and differed only by non-informative parameters, we chose the more parsimonious model as the best model (Arnold 2010).

Model Inference

To further investigate the strength of covariate relationships, we refit the best model in a Bayesian framework using the “R2WinBUGS” Package. In addition to the inherent advantages of Bayesian inference regarding interpretation of uncertainty (Kéry 2012), this approach allowed us to incorporate random effects. Specifically, we included a random effect of the patch in which the site was located, because some patches contained more than one sampling location. This allowed us to separate variability in the response due to a site being in a different patch from the variability in the characteristics of that site (Saracco et al. 2011). To determine the relative strength of covariate relationships, we defined a significance threshold using the 95% credible interval (CRI). We further illustrated covariate relationships by predicting occupancy probability across the range of the covariates at each MCMC iteration, and plotting the means and 95% CRI’s of the posterior distributions.

RESULTS

We detected Bachman's Sparrows at 101 of the 232 total points, and at 48 of the 111 patches. The best model of detection included all the covariates we modeled (Table 2). The average probability of detection ranged from 0.40 to 0.68 for the 4 different observers across all surveys. Because we included data from both passive and active surveys in all models, we could not use model selection to evaluate the importance of this covariate. However, the 95% CRI of the posterior mean was positive and did not overlap 0, which suggests the use of playback significantly increased our detection probability (Table 3). All other covariates (date, shrub height, and basal area) had a negative relationship with detection, though the quadratic effect of date was positive, reflecting a slight increase in detection towards the end of the season.

The best occupancy model included effects of shrub height, percent cover within 3 km, and both linear and quadratic effects of grass volume (Table 2). The next-best model also was competitive (ΔAIC<2; Table 2), though differed from the top model only by the inclusion of basal area, which was non-informative. The top 7 models contained effects of both grass volume and percent habitat within 3 km, suggesting a strong relationship between these variables and Bachman's Sparrow occupancy probability. All models containing one of the three landscape variables were ranked higher than their analogous models without these variables. However, models containing proximity of neighboring patches or percent habitat within 1km all had a ΔAIC>10 (Table 2).

Analysis of the covariate relationships of the best model provided further support for the importance of both percent habitat within 3 km and grass volume, but also shrub height. Of these covariates, the posterior mean of percent habitat within 3 km was greatest, and thus had the strongest relationship with occupancy (Table 3). As more of the surrounding landscape was comprised of Bachman's Sparrow habitat, occupancy probability increased. Specifically, sites with open-canopy pine forest comprising at least 20% of the surrounding landscape had an occupancy probability greater than 0.75 (Fig. 2). Similarly, occupancy probability increased with increasing grass volume; however, the best model included a negative quadratic effect of grass volume as well. Thus, as the average number of hits exceeded 2.2, the occupancy probability began to decrease, though there was only weak statistical support for this trend as the 95% CRI slightly overlapped 0 (Table 3). Lastly, occupancy probability decreased sharply with increasing shrub height, such that the likelihood of sparrow occurrence at sites with shrubs taller than 0.5 m was close to 0 (Fig. 2).

DISCUSSION

Landscape-level habitat distribution plays an important role in the distribution of Bachman's Sparrow and likely other wildlife species in the longleaf pine ecosystem, even more so than the vegetative conditions and size of the habitat patch. Local vegetation conditions, particularly the herbaceous groundcover, often are emphasized as the most critical aspects of Bachman's Sparrow habitat (Dunning & Watts 1990; Haggerty 1998), yet we found sparrow occurrence was influenced more by the availability of habitat nearby. This relationship is likely related to dispersal, which was identified as one of the primary mechanisms explaining sensitivity to fragmentation among birds (Lampila et al. 2005). For Bachman's Sparrows, individuals will abandon a patch either because it burned recently (Seaman & Krementz 2001), or because the lack of fire permitted unsuitable vegetation conditions to develop (Engstrom et al. 1984; Tucker et al. 2004), requiring potentially multiple dispersal events in a lifetime. Isolation of a habitat patch then amplifies the challenges associated with each of these dispersal events, namely predation risk (Lampila et al. 2005). Thus, more connected landscapes will facilitate successful dispersal to previously unoccupied habitat (Dunning et al. 1995).

Dependence on landscape connectivity in longleaf pine ecosystems is not unique to Bachman’s Sparrows. For example, habitat fragmentation has been shown to negatively affect Red-cockaded Woodpeckers (*Picoides borealis*), possibly by limiting dispersal of juvenile birds (Rudolph & Conner 1994; Thomlinson 1995; Azevedo et al. 2000; Kesler & Walters 2012). More recently, research on gopher frogs (*Lithobates capito*) revealed that the amount of habitat required for population persistence is much greater than previously thought; individuals were observed traveling several km from breeding ponds to summer refugia (Humphries & Sisson 2012). This consistent pattern of connectivity dependence among longleaf pine-associated species likely reflects the historically contiguous distribution of this forest type. As such, restoration of isolated patches is unlikely to support the entire suite of animal species associated with the longleaf pine community, no matter if the vegetation conditions in the patches are ideal. Therefore, restoration efforts targeting areas with a high proportion of open-canopy pine forest will be most effective in accommodating these species dependent on landscape connectivity.

The establishment and maintenance of a diverse groundcover layer, primarily via prescribed fire, is fundamental to successful restoration of the longleaf pine ecosystem (Means et al. 2004; Van Lear et al. 2005). Though previous studies reported greater Bachman's Sparrow occupancy in areas with high grass density (Dunning & Watts 1990; Plentovich et al. 1998), we documented evidence of decreasing occupancy beyond a threshold of grass density, suggesting the dense grass thatch that forms in the absence of fire renders habitat less suitable, possibly by restricting movement. Additionally, less fire-tolerant woody species can out-compete herbaceous vegetation in the absence of frequent fire (Engstrom et al. 1984; Glitzenstein & Streng 2003). Though alternative methods are available to control fire-intolerant woody vegetation, such as mechanical thinning and the use of herbicides, prescribed fire best mimics the natural disturbance processes and maintains a diverse herbaceous community (Barnett 1999; Frost 2006). Furthermore, frequent fire, either used exclusively or in addition to other treatment methods, has been shown to be beneficial for a variety of wildlife in longleaf pine systems (Wilson et al. 1995; Russell et al. 1999; Litt et al. 2001; Karmacharya et al. 2012).

The successful restoration of the longleaf pine ecosystem should involve both efforts to establish and maintain local vegetation conditions that characterized historical longleaf pine forest, but also coordinated efforts that focus on landscapes comprised largely (>20%) of open-canopy pine forest. This is particularly important as restoration efforts continue to shift to private lands that are typically more fragmented than public lands (Riitters et al. 2012). Specifically, private lands adjacent to large extents of forest managed for longleaf pine, such as those on many public lands, should be targeted for restoration as such properties could still be functionally connected from the prospective of dispersing wildlife. Additionally, the use of prescribed fire should be promoted as an essential management tool for both public and private landowners (Heuberger & Putz 2003). Our data supports previous research that demonstrated frequent burning is necessary to maintain a diverse groundcover layer and prohibit the encroachment of woody vegetation (Glitzenstein & Streng 2003; Heuberger & Putz 2003). Unfortunately, the logistical and financial resources associated with prescribed fire currently restrict the widespread and frequent use of prescribed fire by private landowners across the historical range of the longleaf pine ecosystem (Alavalapati et al. 2002; Moorman et al. 2002). Overcoming these logistical hurdles will be essential for restoring functional longleaf pine ecosystems on private lands.

LITERATURE CITED

Alavalapati J.R.R., Stainback, G.A. and Carter, D.R. 2002. Restoration of the longleaf pine ecosystem on private lands in the US South: an ecological economic analysis. Ecol Econ **40**(3):411-419.

America's Longleaf. 2009. Range-wide conservation plan for longleaf pine. Report prepared for the Steering Committee of the Regional Working Group for America’s Longleaf.

Arnold T. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management **74**(6):1175-1178.

Azevedo J.C.M., Jack, S.B., Coulson, R.N. and Wunneburger, D.F. 2000. Functional heterogeneity of forest landscapes and the distribution and abundance of the red-cockaded woodpecker. For Ecol Manage **127**(1–3):271-283.

Barnett J.P. 1999. Longleaf pine ecosystem restoration. J Sustainable For **9**(1-2):89-96.

Bowman J. 2003. Is dispersal distance of birds proportional to territory size?. Can J Zool **81**(2):195.

Brudvig L.A. and Damschen, E.I. 2011. Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. Ecography **34**(2):257-266.

Burnham K.P. and D.R. Anderson. 2002. Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York.

Cox J.A. and Jones, C.D. 2009. Influence of prescribed fire on winter abundance of Bachman's sparrow. The Wilson Journal of Ornithology **121**(2):359-365.

Cunningham M.A. and Johnson, D.H. 2011. Seeking parsimony in landscape metrics. J Wildl Manage **75**(3):692-701.

Dunning J.B.,Jr., Borgella, R.,Jr., Clements, K. and Meffe, G.K. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. Conserv Biol **9**(3):pp. 542-550.

Dunning J.B.,Jr. and Watts, B.D. 1990. Regional differences in habitat occupancy by Bachman's sparrow. Auk **107**(3):pp. 463-472.

Dunning J.B. and Kilgo, J.C. 2000. Avian research at the Savannah River Site: A model for integrating basic research and long-term management. Studies in Avian Biology **21**.

Engstrom R.T., Crawford, R.L. and W. Wilson Baker. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: A 15-year study. The Wilson Bulletin **96**(3):pp. 437-450.

Fiske I. and Chandler, R. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software **43**(10):1548.

Frost C. C. 2006. History and future of the longleaf pine ecosystem. pages9-48 in S. Jose, E. J. Jokela, D. L. Miller, Alex and D. E. er, editors. The Longleaf Pine Ecosystem. Springer, New York.

Frost C.C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Tall Timbers Fire Ecology Conference Proceedings **18**:17.

Glitzenstein J.S. and Streng, D.R. 2003. Fire frequency effects on longleaf pine vegetation in South Carolina and northeast Florida, USA. Natural Areas Journal **23**(1):22.

Haggerty T.M. 1998. Vegetation structure of Bachman's sparrow breeding habitat and its relationship to home range. J Field Ornithol **69**(1):45-50.

Heuberger K.A. and Putz, F.E. 2003. Fire in the suburbs: Ecological impacts of prescribed fire in small remnants of longleaf pine (Pinus palustris) Sandhill. Restor Ecol **11**(1):72-81.

Humphries W.J. and Sisson, M.A. 2012. Long distance migrations, landscape use, and vulnerability to prescribed fire of the Gopher Frog (Lithobates capito). J Herpetol **46**(4):665-670.

Karmacharya B., Hostetler, J.A., Mike Conner, L., Morris, G. and Oli, M.K. 2012. Longleaf pine management practices and their impact on small mammal populations. For Ecol Manage **271**(0):140-146.

Kéry M. 2012. Bayesian population analysis using WinBUGS : a hierarchical perspective. Academic Press, Waltham, MA.

Kesler D.C. and Walters, J.R. 2012. Social composition of destination territories and matrix habitat affect red-cockaded woodpecker dispersal. The Journal of Wildlife Management **76**(5):1028-1035.

Lampila P., Mönkkönen, M. and Desrochers, A. 2005. Demographic responses by birds to forest fragmentation; Respuestas demográficas de aves a la fragmentación de bosques. Conserv Biol **19**(5):1537-1546.

Landers J.L., Van Lear, D.H. and Boyer, W.D. 1995. The longleaf pine forests of the Southeast: Requiem or renaissance?. J For **93**(11):38-44.

Litt A.R., Provencher, L., Tanner, G.W. and Franz, R. 2001. Herpetofaunal responses to restoration treatments of longleaf pine sandhills in Florida. Restor Ecol **9**(4):462-474.

FRAGSTATS: Spatial pattern analysis program for categorical maps, 2002. URL http://www.umass.edu/landeco/research/fragstats/fragstats.html [accessed on April/17].

McGarigal K. and McComb, W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol Monogr **65**(3):pp. 235-260.

Means D.B., Dodd, C.K., Johnson, S.A. and Palis, J.G. 2004. Amphibians and fire in longleaf pine ecosystems: Response to Schurbon and Fauth. Conserv Biol **18**(4):1149-1153.

Mills G.S., Dunning, J.B.,Jr. and Bates, J.M. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. The Condor **91**(2):416-428.

Moorman C. E., P.T. Bromley, M.A. Megalos and D. Drake. 2002. The role of non-industrial private forest lands in the conservation of southern fire-dependent wildlife. pages116-123 in M. W. Ford, K. R. Russell and C. E. Moorman, editors. Proceedings: the role of fire for nongame wildlife management and community restoration: traditional uses and new directions. USDA Forest Service GTR-NE-288.

Moorman C.E. and Guynn, D. 2001. Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. Ecol Appl **11**(6):1680-1691.

Peet R. K. and D.J. Allard. 1993. Longleaf pine-dominated vegetation of the southern Atlantic and eastern Gulf Coast region in Nature Conservancy (U.S.), Tall Timbers Research Station. and U.S. Fish and Wildlife Service., editors. Tall Timbers Fire Ecology Conference. Proceedings (1991); Earlier Title: Tall Timbers Ecology and Management Conference. Proceedings. Tall Timbers Research Station, Tallahassee, Fla.

Plentovich S., Tucker, J.W.,Jr., Holler, N.R. and Hill, G.E. 1998. Enhancing Bachman's sparrow habitat via management of red-cockaded woodpeckers. The Journal of Wildlife Management **62**(1):pp. 347-354.

Riitters K.H., Coulston, J.W. and Wickham, J.D. 2012. Fragmentation of forest communities in the eastern United States. For Ecol Manage **263**(0):85-93.

Rudolph D.C. and Conner, R.N. 1994. Forest fragmentation and red-cockaded woodpecker population: An analysis at intermediate scale. J Field Ornithol **65**(3):365-375.

Russell K.R., Lear, D.H.V. and Guynn, D.C. 1999. Prescribed fire effects on herpetofauna: Review and management implications. Wildl Soc Bull **27**(2):374-384.

Rutledge B.T. and Conner, M.L. 2002. Potential effects of groundcover restoration on breeding bird communities in longleaf pine stands. Wildl Soc Bull **30**(2):354-360.

Saracco J.B., Siegel, R.B. and Wilkerson, R.L. 2011. Occupancy modeling of black-backed woodpeckers on burned Sierra Nevada forests. Ecosphere **2**(3):1-17.

Seaman B.D. and Krementz, D.G. 2001. Movements and survival of Bachman’s sparrows in response to prescribed summer burns in South Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies **54**:227-240.

Simberloff D. 1993. Species area and fragmentation effects on old-growth forests: prospects for longleaf pine communities in Nature Conservancy (U.S.), Tall Timbers Research Station. and U.S. Fish and Wildlife Service., editors. Tall Timbers Fire Ecology Conference. Proceedings (1991); Earlier Title: Tall Timbers Ecology and Management Conference. Proceedings. Tall Timbers Research Station, Tallahassee, Fla.

Sutherland G.D., Harestad, A.S., Price, K. and Lertzman, K. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Ecology and Society **4**(1).

Thomlinson J.R. 1995. Landscape characteristics associated with active and abandoned red-cockaded woodpecker clusters in East Texas. The Wilson Bulletin **107**(4):603-614.

Tucker J.W.,Jr., Robinson, W.D. and Grand, J.B. 2004. Influence of fire on Bachman's sparrow, an endemic North American songbird. The Journal of Wildlife Management **68**(4):1114-1123.

Van Lear D.H., Carroll, W.D., Kapeluck, P.R. and Johnson, R. 2005. History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk. For Ecol Manage **211**(1–2):150-165.

Wilson C.W., Masters, R.E. and Bukenhofer, G.A. 1995. Breeding bird response to pine-grassland community restoration for red-cockaded woodpeckers. The Journal of Wildlife Management **59**(1):pp. 56-67.

Table 1. Criteria used to define the extent of suitable Bachman's sparrow habitat in southeastern North Carolina.

		LiDAR			Land cover	
Suitability	Canopy Height	Canopy Cover	Midstory Cover[a]	Understory Cover[b]	SEGAP	LANDFIRE
Unsuitable	< 7 m	<1%	>10%	>25%	Non-pine	Non-pine
Marginal	7-13 m	>30%	5-10%	10-25%	"Other" pine	"Other" pine
Habitat	> 13 m	1-30%	<5%	<10%	Longleaf pine	Longleaf pine

[a] Vegetation 3-7 m tall

[b] Vegetation 1-3 m tall

Table 2. The number of parameters (K), AIC, ΔAIC, model weight (ω), and negative log-likelihood (-LogLike) for the 5 top-ranked models of Bachman's sparrow detection and 10 top-ranked models of occupancy in the Onslow Bight, North Carolina, USA, 2011.

Model	K	AIC	ΔAIC	ω	-LogLike
Detection (p)					
type[a] + date + date^2 + observer + BA[b] + shrub[c]	10	1351.99	0.00	1.00	666.00
type + date + date^2 + observer + shrub	9	1364.72	12.73	0.00	673.36
type + shrub + BA + observer	8	1376.38	24.38	0.00	680.19
type + shrub + observer	7	1390.68	38.69	0.00	688.34
type + date + date^2 + observer + BA	9	1401.41	49.42	0.00	691.71
Occupancy (ψ)					
shrub + PC3[d] + grass[e] + grass^2	14	1274.78	0.00	0.46	623.39
shrub + PC3 + grass + grass^2 + BA	15	1276.19	1.42	0.23	623.10
shrub + PC3 + grass	13	1277.08	2.30	0.15	625.54
shrub + PC3 + grass + BA	14	1278.60	3.82	0.07	625.30
PC3 + grass + grass^2	13	1279.33	4.55	0.04	626.67
PC3 + grass + grass^2 + BA	14	1280.40	5.62	0.03	626.20
PC3 + grass	12	1282.73	7.95	0.01	629.36
PC3 + grass + BA	13	1283.83	9.05	0.01	628.91
shrub + PC1[f] + grass + grass^2	14	1286.19	11.41	0.00	629.10
shrub + PC1 + grass + grass^2 + BA	15	1287.18	12.40	0.00	628.59

[a] survey type (i.e. active or passive)

[b] Basal Area

[c] Shrub height

[d] Percent habitat within 3 km

[e] Grass Volume

[f] Percent habitat within 1 km

Table 3. Posterior means and 95% credible intervals of parameter estimates for covariates of detection and occupancy probability for our top-ranked occupancy model of Bachman's sparrows in southeastern North Carolina, 2011.

	Mean	2.5%	97.5%
Detection (p)			
Type	0.90	0.61	1.20
Date	-0.17	-0.31	-0.02
Date^2	0.37	0.21	0.54
Shrub	-0.72	-0.96	-0.48
BA	-0.37	-0.54	-0.19
Occupancy (ψ)			
Grass	1.73	0.72	3.02
Grass^2	-0.51	-1.21	0.19
Shrub	-1.04	-2.11	-0.17
PC3	2.28	1.13	3.93

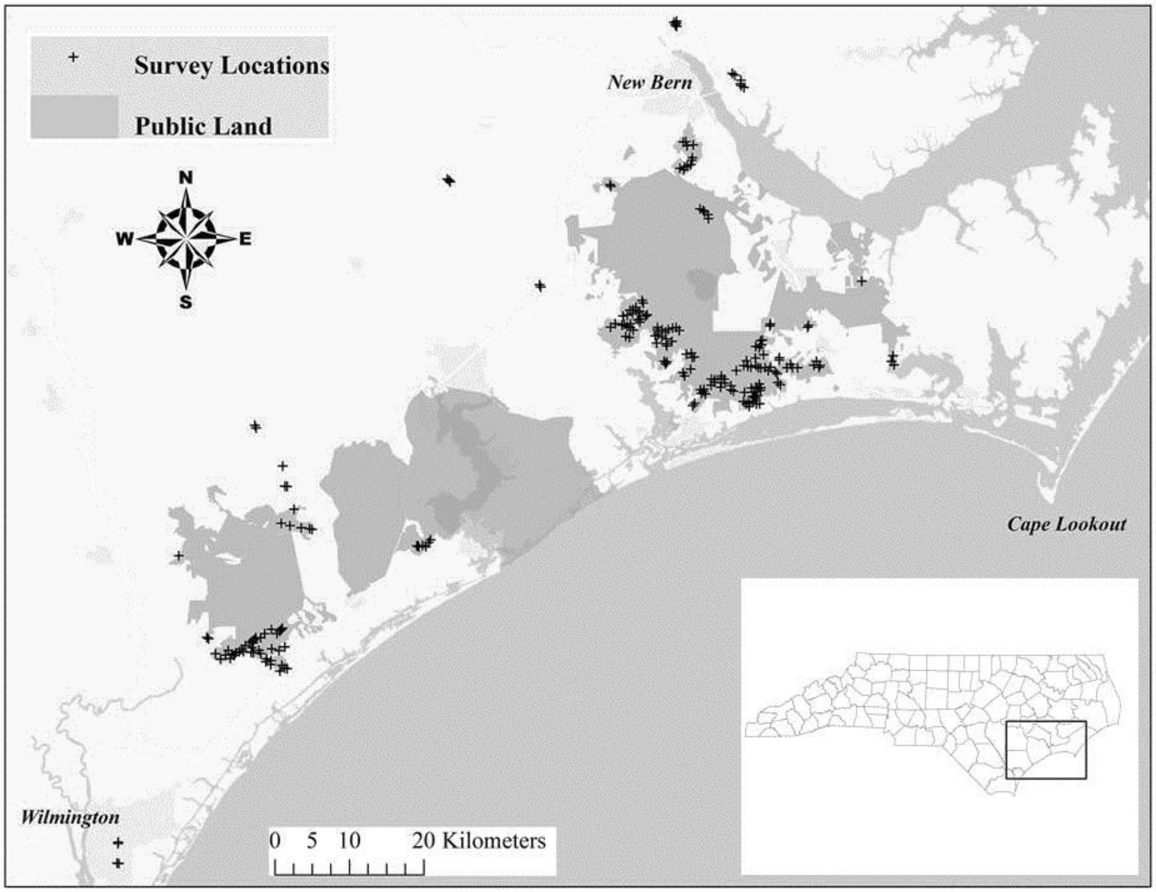

Figure 1. Map of Bachman’s sparrow survey locations in southeastern North Carolina, USA, 2011.

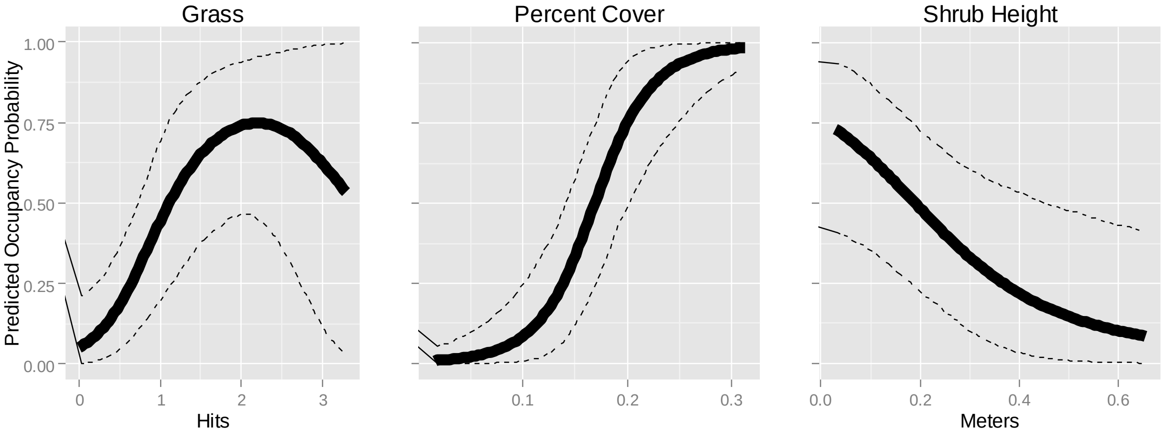

Figure 2. The predicted occupancy probability of Bachman’s Sparrows estimated across the range of grass volume, percent habitat within 3 km, and shrub height using our top-ranked model. North Carolina , 2011.

THE IMPORTANCE OF BURN SEVERITY AND TIME SINCE BURN FOR EARLY SUCCESSIONAL BIRDS

ABSTRACT

In the conifer-dominated forests of western North America, wildfire plays a fundamental role in creation and maintenance of early successional vegetation. The unique structure and composition of these communities provide habitat for a suite of bird species that are often rare or absent from the surrounding forest. However, decades of fire suppression and intensive silvicultural practices have drastically altered the disturbance regime of these areas. A better understanding of avian community response to wildfire is needed to make more informed management decisions. To address this need we surveyed the avian community after 3 wildfires in the northern Sierra Nevada, CA during the breeding season from 2009 to 2012. We used a distance sampling framework to model abundance of 6 bird species associated with early successional vegetation as a function of burn severity and time since burn. Analysis of the best model for each species suggested high severity burns are especially important to establishing and maintaining habitat for early successional birds, though more moderate severity fire is more beneficial for oak-dependent species such as Nashville warbler. In addition, some species we studied, such as lazuli bunting and chipping sparrow, increased in abundance in the first few years following a fire, whereas shrub-associated birds like fox sparrow did not reach peak abundance for at least 10 years. The reincorporation of high severity fire, particularly in community types such as montane chaparral that were historically characterized by a disturbance regime of primarily high

severity fire, at return intervals of 20-30 years will most effectively maintain habitat for early successional species in the montane, fire-maintained forests of western North America.

INTRODUCTION

In western North America, several anthropogenic factors, including climate change, fire suppression, and post-fire forest management, have changed the ecological processes shaping forests. For the past century, widespread fire suppression has favored less fire-tolerant species at the expense of fire-dependent successional communities, namely montane chaparral, which have steadily declined in the Sierra Nevada (Taylor & Skinner 2003; Nagel & Taylor 2005). In recent decades fires have become larger, more frequent, and more severe, possibly as a result of accumulating fuel loads associated with fire suppression (Taylor & Skinner 1998; Taylor & Skinner 2003; Miller et al. 2009a). Concurrently, this pattern is likely exacerbated by anthropogenic climate change, which is predicted to produce conditions favoring larger and more severe fires (Flannigan et al. 2000). Such changes have potentially important implications for the successional communities that develop following fire.

Post-fire environments provide critical habitat for a unique avian community (Hutto 1995), and the high conservation value of these areas has prompted an increase in research to determine how fire suppression, climate change, and post-fire management practices affect post-fire communities (Driscoll et al. 2010). The majority of research on birds has focused on species that respond strongly to fire, such as cavity nesters, and their susceptibility to salvage logging (Saab 1998; Hutto 2008). However, the response of other species found in post-fire environments is less well understood and likely depends on several factors including burn severity, time since burn, and pre-fire forest condition.

As wildfire extent, frequency, and severity change, there is growing need to understand the factors determining how birds respond to these fires. In their review of previous studies of the responses of birds to fire, Smucker et al. (2005) described conflicting results for several species, referred to as "mixed responders". However, they concluded that the incorporation of burn severity and time since burn helped to reconcile these disparities for species that did not respond uniformly across fire severity and fire age in the Northern Rocky Mountains in Montana (Smucker et al. 2005). We were interested if burn severity and time since burn also affect patterns in bird abundance following wildfire in the Sierra Nevada. Furthermore, we surveyed fires of different ages to investigate a larger spectrum of time since burn, because fire can shape future forests on time scales longer than 4 years (Brawn et al. 2001).

We focused our attention on birds associated with early successional vegetation because fire is the primary mechanism for the establishment and maintenance of successional communities in the montane conifer forest regions of western North America (Barro & Conard 1991; Nagel & Taylor 2005). Although other types of disturbance, both natural and anthropogenic, result in conditions selected by early succession bird species in other regions, fire is particularly important to establishing and maintaining these habitats in the montane West where early successional bird species often are rare or absent in later successional, conifer forest communities (Raphael et al. 1987; Burnett & Humple 2010). A better understanding of how the abundance of early successional bird species change over time following wildfires of different severities is required to effectively manage for these species.

To quantify these relationships, we modeled the abundance of 6 early successional bird species (Table 1) as a function of burn severity and time since burn following 3 different fires in the northern Sierra Nevada, CA. Patterns in abundance over time and the factors affecting them can be used not only to guide management of post-fire areas, but also to help predict how the avian community will respond to long term changes in ecological processes and forest structure resulting from fire suppression and climate change.

METHODS

Study Location

We conducted our study on the Plumas and Lassen National Forests in the Northern Sierra Nevada. We surveyed three wildfires − the Cub, Moonlight and Storrie fires − which burned in 2008, 2007, and 2000, respectively (Fig. 1). Pre-fire habitat type was primarily Sierran Mixed Conifer forest, but there were also small areas of Montane Chaparral, Eastside Pine, and True Fir. The elevations of sites surveyed ranged from 1126 – 1998 m with a mean of 1658 m in the Cub fire, 1199 – 2190 m with a mean of 1779 m in the Moonlight Fire, and 1107 – 2011 m with a mean of 1528 m in the Storrie fire.

Site Selection

We selected 63 random starting points within the boundaries of the fires in ArcGIS 9.2 and added 4 points along a random compass bearing at 250-m intervals to each starting point, resulting in 315 points grouped into 1-km transects of 5 points each (ESRI 2004). We maintained a minimum distance between transect starting points of 1500 m to ensure transects would not overlap. The original sampling area was limited to US Forest Service land with a slope of less than 40 degrees to allow access and safe navigation on foot in a timely manner. However, due to steep topography and large road-less areas in the Cub and Storrie fires, our sampling was not as evenly distributed across these fires as it was in the Moonlight (Fig. 1).

Bird community surveys

During the breeding seasons (May 1-June 30) from 2009 through 2012, we surveyed the avian community using a 5-min point-count survey (Reynolds et al. 1980; Ralph et al. 1995). Prior to the start of the season, all technicians underwent two weeks of extensive training in bird identification and distance estimation. Distances were measured using a laser range-finder when possible, and estimated otherwise. All birds detected at each point during the 5-min survey were recorded according to their initial distance from the observer. The method of initial detection (song, visual, or call) for each individual also was recorded. Counts began within 15 min after local sunrise, were completed within 4 hr, and did not occur in inclement weather. We conducted 2 visits each season and alternated the observer and transect direction each visit. Because of weather and access issues, only 216 sites were surveyed all eight visits, and thus included in this analysis.

Analysis

We selected 6 species (chipping sparrow, dusky flycatcher, fox sparrow, lazuli bunting, MacGillivray’s warbler, and Nashville warbler; scientific names in Table 1) that commonly occurred in the fires we surveyed and that were associated with shrubs and/or early successional vegetation (Betts et al. 2010). Change in percent canopy cover was measured as a surrogate for burn severity using the satellite-derived, Relative difference Normalized Burn Ratio (RdNBR; Miller et al. 2009b) averaged within 100 m of the survey location. For each fire, these data were collected within 1 week of fire containment. Values of burn severity for our survey sites ranged from 17.29 to 1285.89 ($\bar{x}$=617.65, *sd*=343.24). We used a hierarchical framework to model detection probability (p) and abundance (λ), using the function “distsamp” in the R package “Unmarked” (Fiske & Chandler 2011). We grouped observations by detection distance into the following bins: 0-20m, 21-40m, 41-60m, 61-100m, 101-200m, 201-301m. We modeled detection probability by combining the observations across visits and fitting a function to the observations of each species. A preliminary analysis of the null model for each species showed that a half-normal function best fit the observations for chipping sparrow, MacGillivray’s warbler, and Nashville warbler, while a hazard function fit best for dusky flycatcher, fox sparrow, and lazuli bunting. As such, we used the respective functions in all subsequent models. We did not include any covariates on detection.

We fit the same suite of 5 models for each species (Table 2). The structure of our data required we incorporate time since burn in all models to differentiate the different years. In addition, we fit models with a linear and quadratic effect of burn severity, as well as an interaction term between time since burn and burn severity. In all models with an interaction or quadratic effect, the main effects were included in the model. We selected the best model for each species according to lowest Akaike information criterion (AIC; Burnham & Anderson 2002). We investigated parameter estimates and p-values of all terms in the best model for each species and interpreted effects with p-values <0.05 as significant. Also, we used the best model to predict abundance across the ranges of burn severity and time since burn that we sampled.

RESULTS

Mean abundance per point ranged from 3.8 individuals for MacGillivray's warbler to 13.1 individuals for lazuli bunting. The best models of abundance for each species included similar terms (Table 2), though the magnitude and the direction of individual effects varied (Table 3). The global model was ranked highest for all species except dusky flycatcher and MacGillivray's warbler. The best model for these two species included time since burn, burn severity, and an interaction between these covariates, but did not include a quadratic effect of burn severity (Table 2).

Because all models contained the effect of time since burn, our model selection procedure did not evaluate the role of this effect; however, analysis of parameter estimates from the best model for every species suggested it was important to predicting abundance. The relationship between abundance and time since burn was significant ($p<0.05$) for all species except lazuli bunting (Table 3). Most species became more abundant with time since burn, but dusky flycatcher decreased in abundance with time, though only in high severity burns (Fig. 1).

The response to burn severity was similar across most species (Table 3). Generally, early successional species were more abundant in high severity burns, particularly lazuli bunting. However, Nashville warbler reached a maximum abundance at moderate severity

(Fig. 2). In the best model for this species, the magnitude of the quadratic effect of burn severity was large relative to the linear effect, resulting in low estimated abundance following fires of high and low severities. We observed some evidence of a similar response of lazuli bunting and chipping sparrow to moderate severity burns as time since burn increased, though parameter estimates for the quadratic effect of burn severity were small relative to the positive linear effects of burn severity (Table 3).

Though the interaction between the two covariates was significant for most species, the direction of the effect was variable (Table 3). Parameter estimates for this term were positive for fox sparrow and Nashville warbler, and the positive effect of burn severity increased as time since burn increased. On the other hand, differences in abundance across burn severity for dusky flycatcher and MacGillivray's warbler became less apparent over time (Fig 1). Chipping sparrows were most abundant in high severity burns immediately following fire, but as time since burn increased, they were most abundant in more moderate severity areas. Lazuli bunting was the only species for which the effect of an interaction between burn severity and time since burn was not significant (Table 3).

DISCUSSION

Our results highlight the role of severe fire in maintaining early successional conditions. The mortality of canopy trees in high severity fires reduces competition for space, light, and soil resources and allows the establishment of the understory layer of young shrubs and herbaceous plants used by early successional birds (Raphael et al. 1987; Fontaine et al. 2009). In fact, we found lazuli bunting was one of the most abundant bird species in areas that burned at high severity, while being exceedingly rare in most other habitat types in the Sierra Nevada (Burnett et al. unpubl. data), including low severity burns. The limited mortality of canopy trees in lower severity fires permits only limited understory vegetation development. Because logistical and safety concerns limit prescribed fires to burning primarily at low intensity, the use of prescribed fire may not sufficiently promote habitat conditions required by many early successional bird species (Smucker et al. 2005). However, prescribed burning of montane chaparral at high severity may be more feasible and would most effectively create and maintain early successional vegetation conditions (Fontaine et al. 2009). Nonetheless, low severity prescribed fire remains essential to management of other vegetation types, particularly late-successional forests (Taylor & Skinner 1998) and pine-oak forests (Bagne & Purcell 2009), and is thought to more closely resemble natural disturbance processes in the surrounding conifer forest (Bagne & Purcell 2011).

The use of deciduous trees, particularly oaks (*Quercus* spp.), rather than other shrubs and herbaceous plants, likely explains the abundance of Nashville Warblers a decade following moderate severity fire. Nashville Warblers commonly decrease in abundance in the first few years following fire as the oaks die (Bagne & Purcell 2011). However, despite short-term declines following fire, fire suppression is thought to be detrimental to oak dependent birds in these systems in the long-term (Garrison et al. 2002), because fires promote oak re-sprouting and limit the encroachment of faster-growing pines (*Pinus* spp.) And, moderate severity fire appears to best create and maintain habitat conditions unique to oak-dependent species (Purcell & Drynan 2008). The combination of a continuous scale of burn severity and the incorporation of an interaction between burn severity and time since burn made it possible for us to quantitatively describe these dynamics of oak-dependent birds. Otherwise, the effect of burn severity likely would be much less significant for Nashville warbler in our study.

The successional changes in post-fire environments result in parallel shifts in composition of the bird community. For example, immediately following the fire, chipping sparrow and lazuli bunting were relatively abundant as grasses and young shrubs first reestablished. Shrub-associated species like fox sparrow and Nashville warbler became more abundant only after shrubs and oaks begin to mature after roughly 5 years and may reach their peak abundance after as many as 20 years (Raphael et al. 1987). Studies of post-fire bird dynamics lasting less than 5 breeding seasons might fail to describe patterns of these late responders. Long-term studies often are expensive and logistically difficult, but studies that simultaneously investigate several fires of various ages may help to minimize these challenges while still examining longer-term spectrum of fire age.

We observed changes in abundance of some species that contradict findings from previous studies. Smucker et al. (2005) observed dusky flycatcher decreasing the most from pre-fire levels in high severity burns, whereas in our study they were most abundant in higher severity burns compared to lower severity burns. However, of the species we studied, dusky flycatcher was the most common in the surrounding forest matrix (Burnett et al. unpubl. data), and as a result the response to fire may be less clear and more variable (Smucker et al.

2005). Similarly, Smucker et al. (2005) observed lazuli bunting increasing in abundance from pre-fire levels in all severities, rather than just high severity, and increases were dependent on time since burn. Instead, we observed consistent abundance over time for lazuli bunting. These unexplained discrepancies among studies are potentially the result of geographic variability in forest type, climate, pre-fire condition, and fire history. Large scale studies comparing fires in different geographic regions may reveal geographic variability in the response of the avian community following wildfire and imply that more location-specific approaches for post-fire management are needed.

Our results suggest that recent increases in fire frequency and intensity in the Sierra Nevada should benefit early successional birds, yet many of these species continue to decline and are of conservation concern (Brawn et al. 2001). Though the area of forest experiencing high severity fires appears to be returning to historical levels (Miller et al. 2009a), fire suppression has drastically altered pre-fire forest composition and structure (Nagel & Taylor 2005). As such, a high severity fire today might produce a much different response by wildlife communities than a similar, pre-suppression era fire. Historically, high severity fires were smaller and to some extent limited to montane chaparral rather than dense, fire-suppressed forests (Barro & Conard 1991; Keeley et al. 2005). Restoration of montane chaparral communities by re-establishing a fire regime of high severity fire would benefit early successional species, especially as the increases in abundance of these birds are amplified when these areas are subjected to repeat burns (Fontaine et al. 2009). Meanwhile, continued use of thinning and low severity prescribed fire should be used to promote development of late successional communities and also control fuel loads to reduce the risk of unnaturally large and devastating fires (Taylor & Skinner 1998; Bagne & Purcell 2009; Bagne & Purcell 2011).

LITERATURE CITED

Bagne K.E. and K.L. Purcell 2009. Lessons learned from prescribed fire in ponderosa pine forests of the southern Sierra Nevada. Proceedings of the sixth symposium on oak woodlands, 13-16 February 2008. Partners in Flight.

Bagne K.E. and Purcell, K.L. 2011. Short-term responses of birds to prescribed fire in fire-suppressed forests of California. Journal of Wildlife Management **75**(5):1051-1060.

Barro S.C. and Conard, S.G. 1991. Fire effects on California chaparral systems: an overview. Environment International **17**(2–3):135-149.

Betts M.G., Hagar, J.C., Rivers, J.W., Alexander, J.D., McGarigal, K. and McComb, B.C. 2010. Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. Ecological Applications **20**(8):2116-2130.

Brawn J.E., Robinson S.K., Thompson III F.R. 2001. The role of disturbance in the ecology and conservation of birds. Annual Review of Ecology and Systematics. **32**:251-76.

Burnett R.D. and Humple, D.L. 2010. Nesting ecology of yellow warblers (*Dendoica petechia*) in montane chaparral habitat in the Northern Sierra Nevada. Western North American Naturalist **70**(3):355.

Burnham K.P. and D.R. Anderson. 2002. Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York.

Driscoll D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith, D.A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J.E.M., Williams, R.J. and York, A. 2010. Fire management for biodiversity conservation: Key research questions and our capacity to answer them. Biol Conserv **143**(9):1928-1939.

Fiske I. and Chandler, R. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software **43**(10):1548.

Flannigan M.D., Stocks, B.J. and Wotton, B.M. 2000. Climate change and forest fires. Sci Total Environ **262**(3):221-229.

Fontaine J.B., Donato, D.C., Robinson, W.D., Law, B.E. and Kauffman, J.B. 2009. Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. For Ecol Manage **257**(6):1496-1504.

Garrison B.A., Wachs, R.L., Jones, J.S. and Triggs, M.L. 2002. Some factors influencing seedling density of California black oak (*Quercus kelloggii*) in the central Sierra Nevada, California. Madrono **49**:115-121.

Hutto R.L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. Conserv Biol **9**(5):1041-1058.

Hutto R.L. 2008. The ecological importance of severe wildfires: some like it hot. Ecol Appl **18**(8):1827-1834.

Keeley J.E., Pfaff, A.H. and Safford, H.D. 2005. Fire suppression impacts on postfire recovery of Sierra Nevada chaparral shrublands. International Journal of Wildland Fire **14**(3):255-265.

Kennedy R.S.H. and Spies, T.A. 2005. Dynamics of hardwood patches in a conifer matrix: 54 years of change in a forested landscape in Coastal Oregon, USA. Biological Conservation **122**(3):363-374.

Lindenmayer D. 2008. Salvage logging and its ecological consequences. Island Press, Washington.

Miller J.D., Safford, H.D., Crimmins, M. and Thode, A.E. 2009a. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. Ecosystems **12**(1):16-32.

Miller J.D., Knapp, E.E., Key, C.H., Skinner, C.N., Isbell, C.J., Creasy, R.M. and Sherlock, J.W. 2009b. Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. Remote Sensing and the Environment **113**(3):645-656.

Nagel T.A. and Taylor, A.H. 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada. Journal of the Torrey Botanical Society **132**(3):442.

Prestemon J.P., Wear, D.N., Stewart, F.J. and Holmes, T.P. 2006. Wildfire, timber salvage, and the economics of expediency. Forest Policy and Economics **8**(3):312-322.

Purcell K.L. and D.A. Drynan 2008. Use of hardwood tree species by birds nesting in Ponderosa pine forests. Proceedings of the sixth symposium on oak woodlands: today's challenges, tomorrow's opportunities. U.S. Forest Service General Technical Report, PSW-217.

Ralph C.J., Sauer, J.R. and Droege, S. 1995. Monitoring bird populations by point counts. USDA Forest Service Publication, Gen. Tech. Rep. PSW-GTR-149, Albany, CA.

Raphael M.G., Morrison, M.L. and Yoder-Williams, M.P. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. The Condor **89**(3):614-626.

Reynolds R.T., Scott, J.M. and Nussbaum, R.A. 1980. A variable circular-plot method for estimating bird numbers. The Condor **82**(3):309-313.

Saab V.A. 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in Ponderosa pine/Douglas-fir forests of southwestern Idaho. U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT (324 25th St., Ogden 84401).

Smucker K.M., Hutto, R.L. and Steele, B.M. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications **15**(5):pp. 1535-1549.

Swanson M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B. and Swanson, F.J. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment **9**(2):117-125.

Taylor A.H. and Skinner, C.N. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management **111**(2–3):285-301.

Taylor A.H. and Skinner, C.N. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications **13**(3):704-719.

Table 1. List of focal bird species surveyed in 2009-2012, with 4-letter codes and scientific names.

Species Code	**Common Name**	**Scientific Name**
CHSP	Chipping Sparrow	*Spizella passerina*
DUFL	Dusky Flycatcher	*Empidonax oberholseri*
FOSP	Fox Sparrow	*Passerella iliaca*
LAZB	Lazuli Bunting	*Passerina amoena*
MGWA	MacGillivray’s Warbler	*Geothlypis tolmiei*
NAWA	Nashville Warbler	*Oreothlypis ruficapilla*

Table 2. The number of parameters (K), AIC, ΔAIC, and model weight (ω) for models with combinations of time since burn (tsb) and burn severity (burnsev) as covariates of abundance for 6 bird species in the Northern Sierra Nevada, CA (2009-2012).

Species	Model	K	AIC	ΔAIC	ω
CHSP	burnsev + burnsev^2 + tsb + tsb*burnsev	6	2925.55	0.00	0.51
	tsb + burnsev + tsb*burnsev	5	2927.04	1.49	0.24
	tsb + burnsev	4	2928.19	2.64	0.14
	tsb + burnsev + burnsev^2	5	2976.1	3.09	0.11
	tsb	3	2976.10	50.56	0.00
DUFL	tsb + burnsev + tsb*burnsev	6	5135.38	0.00	0.69
	burnsev + burnsev^2 + tsb + tsb*burnsev	7	5136.96	1.58	0.31
	tsb + burnsev	5	5153.63	18.25	0.00
	tsb	4	5195.76	60.38	0.00
	tsb + burnsev + burnsev^2	5	5208.76	73.38	0.00
FOSP	burnsev + burnsev^2 + tsb + tsb*burnsev	7	7617.94	0.00	0.78
	tsb + burnsev + tsb*burnsev	6	7620.50	2.56	0.22
	tsb + burnsev	5	7636.77	18.83	0.00
	tsb + burnsev + burnsev^2	5	7647.86	28.92	0.00
	tsb	4	7874.85	256.92	0.00
LAZB	burnsev + burnsev^2 + tsb + tsb*burnsev	7	4533.23	0.00	0.98
	tsb + burnsev + burnsev^2	5	4541.22	8.00	0.02
	tsb + burnsev + tsb*burnsev	6	4591.91	58.69	0.00
	tsb + burnsev	5	4594.56	61.34	0.00
	tsb	4	5309.65	776.42	0.00
MGWA	tsb + burnsev + tsb*burnsev	5	3593.02	0.00	0.51
	burnsev + burnsev^2 + tsb + tsb*burnsev	6	3593.09	0.08	0.49
	tsb + burnsev	4	3602.12	9.10	0.01
	tsb + burnsev + burnsev^2	5	3604.11	11.095	0.00
	tsb	3	3623.55	30.54	0.00
NAWA	burnsev + burnsev^2 + tsb + tsb*burnsev	6	2777.41	0.00	0.78
	tsb + burnsev + burnsev^2	5	2779.89	2.48	0.22
	tsb + burnsev + tsb*burnsev	5	2793.46	16.05	0.00
	tsb + burnsev	4	2803.63	26.22	0.00
	tsb	3	2804.80	27.39	0.00

Table 3. Parameter estimates (on log scale) with standard errors (SE), for the top-ranked model of abundance for 6 species of birds in the northern Sierra Nevada (2009-2012). Shaded cells indicate the effect was not significant ($p>0.05$).

Species Code[a]	Burnsev[b]	SE	Burnsev^2	SE	TSB[c]	SE	Burnsev^{x}TSB	SE
CHSP	0.38	0.05	-0.11	0.06	0.13	0.05	-0.12	0.05
DUFL	0.18	0.03	--	--	-0.07	0.03	-0.15	0.03
FOSP	0.37	0.02	-0.06	0.03	0.26	0.02	0.08	0.02
LAZB	1.24	0.07	-0.37	0.05	-0.06	0.05	-0.06	0.05
MGWA	0.22	0.04	--	--	0.28	0.04	-0.13	0.04
NAWA	-0.18	0.06	-0.27	0.06	0.59	0.04	0.10	0.05

[a] Species names found in Table 1

[b] Burn severity

[c] Time since burn

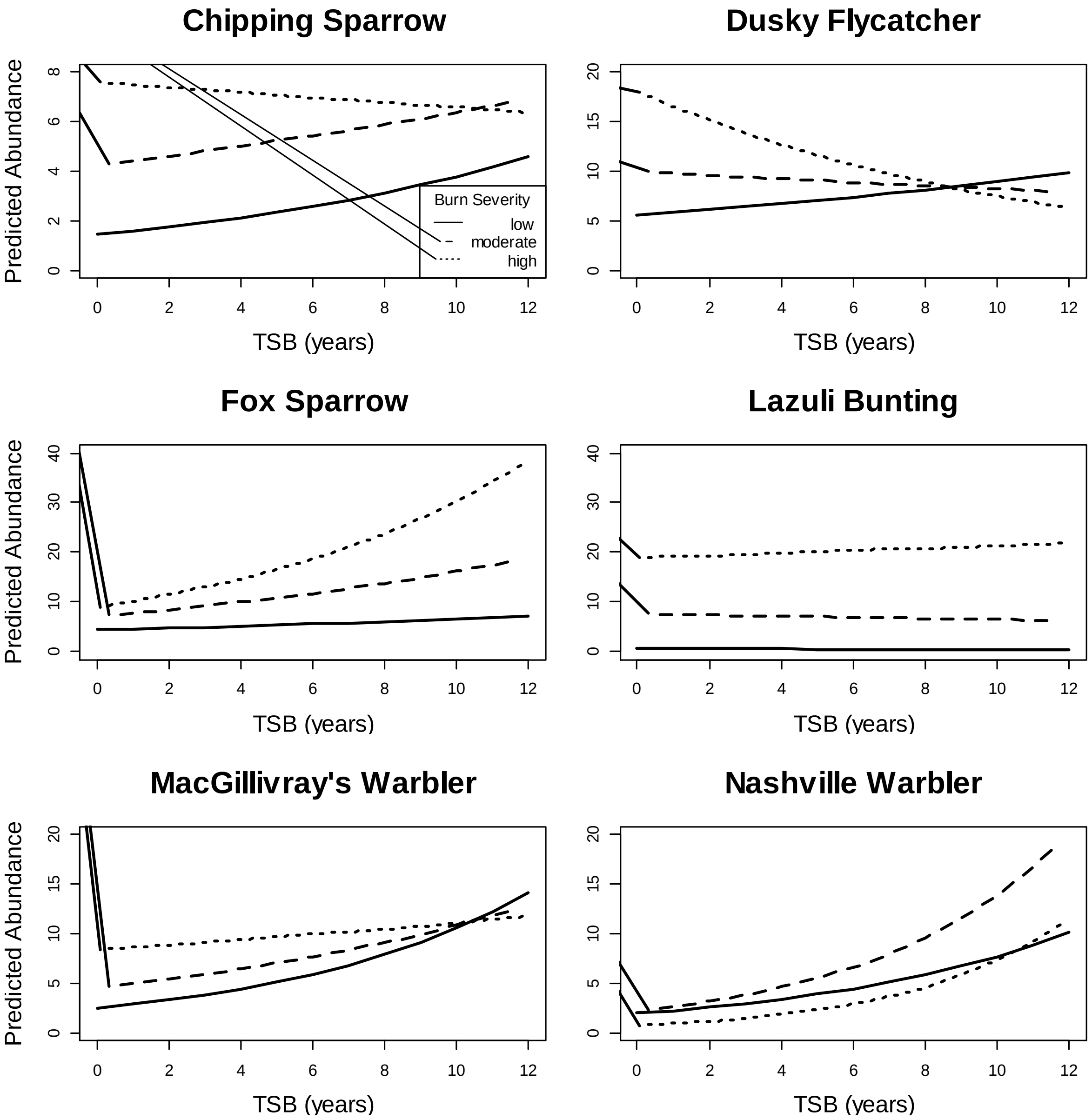

Figure 1.The predicted abundance as a function of time since burn in high severity (red), moderate severity (orange), and low severity (green) fire for 6 early successional bird species in the northern Sierra Nevada, CA (2009-2012).

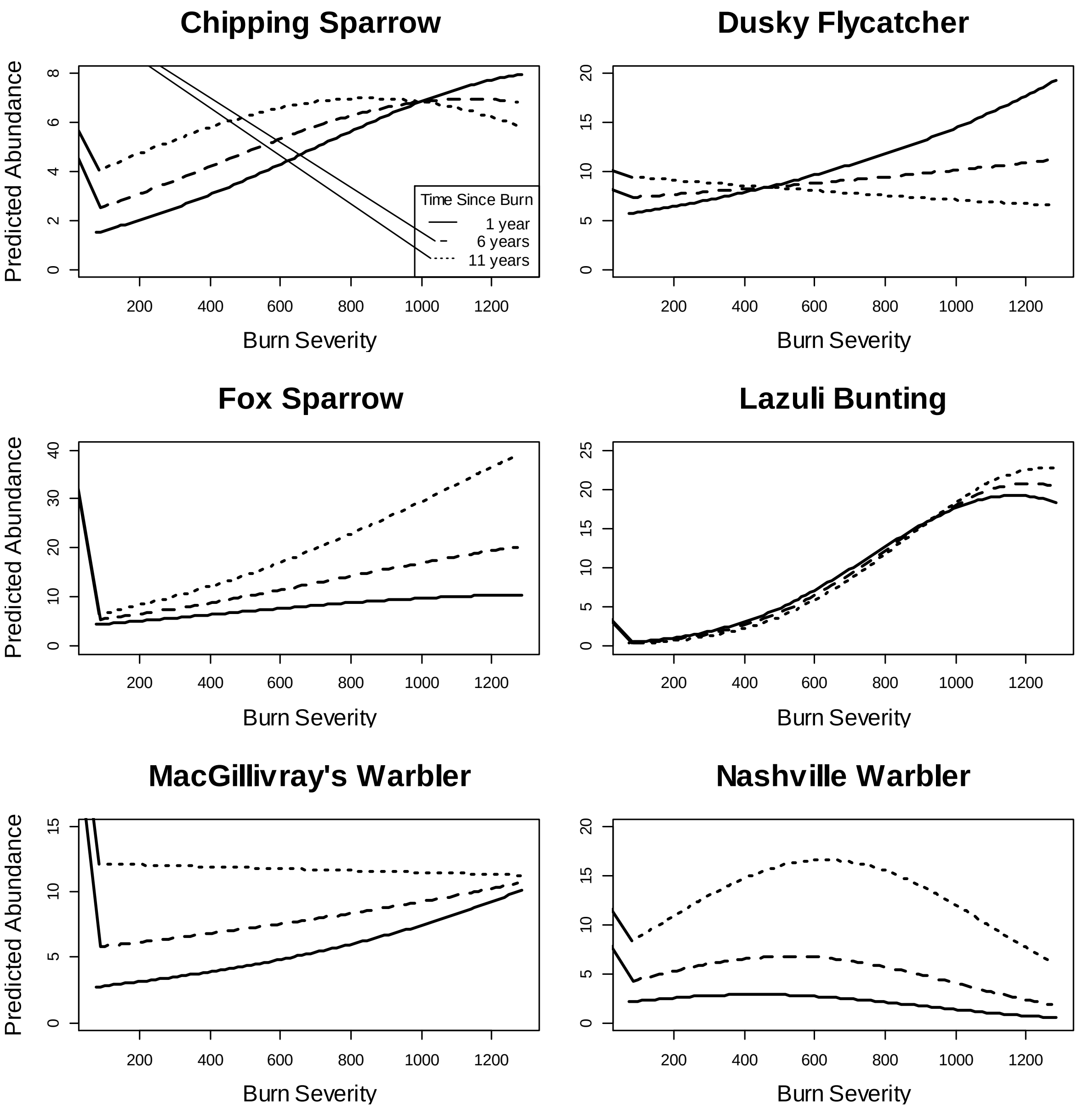

Figure 2. Predicted abundance using the top-ranked model for each of 6 early successional bird species, across the range of burn severity that we sampled at 1 yr post burn (solid line), 6 yr post burn (dashed line), and 11 yr post burn (dotted line) in 3 fires in the northern Sierra Nevada, CA (2009-2012).