AN ABSTRACT OF THE DISSERTATION OF

Aaron L. Holmes for the degree of Doctor of Philosophy in Wildlife Science presented on November 12, 2010

Title: Small mammal and bird abundance in relation to post-fire habitat succession in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities

Abstract approved:

W. Douglas Robinson

Fire is an important disturbance mechanism in big sagebrush (*Artemisia tridentata*) communities, yet little is known about wildlife population dynamics during post-fire habitat succession. I estimated the abundance of small mammals and birds in relation to fire history in mountain big sagebrush (A.t. spp. *vaseyana*) communities on the Sheldon National Wildlife Refuge in the northwestern Great Basin, USA. I employed a chronosequence approach that took advantage of multiple wildfires that had occurred in similar plant communities between 7 to 20 years prior to sampling.

Belding's ground squirrel (*Spermophilus beldingii*) were approximately 10 times as abundant in burned areas relative to adjacent unburned habitat regardless of the number of years since a burn occurred. Deer mouse (*Peromyscus maniculatus*) was more abundant on more recently burned sites, but not at sites closer to full vegetation recovery. Great basin pocket mouse (*Perognathus parvus*), sagebrush vole (*Lemmiscus curtatus*),

and least chipmunk (*Tamius minimus*) abundance did not vary as a function of fire history, but some variance was explained by habitat features such as rocky areas and the canopy characteristics of sagebrush.

Bird diversity was higher in unburned habitats irrespective of the number of years of recovery out to 20 years. Nine of the 12 most widely occurring species of birds in the study have population densities influenced by fire or post-fire habitat succession to at least 13 to 20 years following a burn. Sage Sparrow (*Amphispiza belli*), Black-throated Sparrow (*Amphispiza bilineata*), and Spotted Towhee (*Pipilo maculatus*) occurred at relatively low densities and were nearly restricted to unburned habitats. Green-tailed Towhee (*Pipilo Chlorurus*), Gray Flycatcher (*Empidonax wrightii*), American Robin (*Turdus migratorius*), and Brown-headed Cowbird (*Molothus ater*) occurred at lower densities in burned areas than adjacent unburned areas although the relationship was not strong for the latter two species. The magnitude of the difference in density between burned and unburned sites within a landscape diminished with the number of years of vegetation recovery for Green-tailed Towhee. Brewer's Sparrow (*Spizella brewerii*) occurred at lower densities relative to adjacent habitat in the most recent burn, but occurred at higher densities after 20 years of habitat succession, suggesting a positive response with a multiple decade lag period. Horned Lark (*Eremophila alpestris*) and Vesper Sparrow (*Pooecetes gramineus*) respond positively to fire, but densities were similar to unburned areas after 20 years of habitat succession.

An ordination analysis captured 86% of the variation in 12 bird species with 3 orthogonal axes. My research demonstrates that strong community structure exists for birds associated with mountain big sagebrush habitats, and that fire influences community structure for multiple decades.

Small mammal and bird abundance in relation to post-fire habitat succession in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities

by
Aaron L. Holmes

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented November 12, 2010
Commencement June 2011

Doctor of Philosophy dissertation of Aaron L. Holmes presented on November 12, 2010

APPROVED:

Major Professor, representing Wildlife Science

Chair of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Aaron L. Holmes, Author

ACKNOWLEDGEMENTS

I would like to thank my Major Professor, W. Douglas Robinson for his support, encouragement, and trust, all of which made this project possible. He provided the perfect balance of freedom to pursue my ideas and offered sage counsel when it was needed most. I would also like to thank my committee members, Kate Dugger, Rick Miller, and Mike Green who provided critical review of this research from the early stages. Rick helped me to view fire and its effects on sagebrush ecosystems from a fresh perspective. Mike continues to inspire me with his dedication to bird conservation. I would also like to extend my gratitude to Matt Betts who agreed to fill in at my defense.

A lot of people assisted with data collection over 3 memory-filled summers living on the Sheldon National Wildlife Refuge. I am grateful for the company and assistance of the following people: Devon Anderson, Jonathon Berti, Kent Bloomer, Jan Boyer, James Brennan, Jennifer Bruce, Patti Brunner, Jacob Cowan, Jason Croft, Michelle Desrossiers, Elizabeth Donadio, Justin Eby-Bosler, Matt Halley, Adam Hannuksela, Sallie Herman, Tamara Hull, Alison King, Sherri Lamb, Megan Leach, Gina Pasini, Alexander Rosenthal, Frank Sicilia, Douglas Schaefer, Scott Sheldon, Monica Stevens, Keith Trainor, Aaron Viciduvich, and Ben Zyla.

The Sheldon National Wildlife Refuge provided housing for my large, and sometimes rag-tag crews of field assistants, and I would like to thank the staff, especially Brian Day and Mike Webster, for all the support provided over the years. John

Alexander, Barb Bresson, Jen Britt, Mike Green, Terry Rich, and many others made the long drive out to Badger Mountain at least once and in some cases many times. Their visits are among the brightest memories from my time on Sheldon.

This research, which reflects my longstanding interest in sagebrush communities and their feathered denizens, would never have taken place without the influence of my undergraduate mentor and good friend, Steve Herman. Steve introduced me, many years ago, to the field of ornithology and to the beauty and magic of big sagebrush. For both, I will always be grateful. I would also like to thank another mentor, Geoff Geupel, who took numerous chances on me as a budding professional and has been a constant source of support and encouragement over the past 15 years. His leadership and dedication to conservation of our public lands are unsurpassed.

I appreciate the support received through a National Science Foundation Graduate Research Fellowship from 2006-2009. Additional financial support for this research came from the United States Fish and Wildlife Service Migratory Bird Program, donations to PRBO Conservation Science, and through a grant from the United States Forest Service Joint Fire Sciences Program.

CONTRIBUTION OF AUTHORS

Dr. W. Douglas Robinson contributed to study design, interpretation of data, and writing of chapters 2-4.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

Table Page

Small mammal and bird abundance in relation to post-fire habitat succession in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities

by
Aaron L. Holmes

CHAPTER 1: INTRODUCTION

Fire is an important mechanism of disturbance in sagebrush ecosystems (Wright and Bailey 1982, Miller et al. 2011). It plays a role in nutrient cycling (Rau et al. 2007, 2008), influences hydrology (Pierson et al. 2008), and dictates shifts in vegetation community composition and structure along succession-retrogression pathways (Miller et al. 2011). It is therefore a principal driver of both the temporal dynamics and spatial distributions of wildlife habitat within the sagebrush biome. Alterations to historic fire regimes and interactions with invasive species are recognized to pose major challenges to the conservation of sagebrush ecosystems (Knick et al. 2003, Miller et al. 2011).

Numerous wildlife species are completely or largely dependent upon the woody species of sagebrush (*Artemisia*, subgenus *Tridentatae*), and a number of birds and small mammals are considered species of conservation concern across all or portions of their range (Paige and Ritter 1999, Knick et al. 2003, Dobkin and Sauder 2004). Research on the distribution and abundance of sagebrush associated songbirds has focused on physiognomic and floristic aspects of habitat (Rotenberry and Wiens 1981, Rotenberry 1985, Wiens et al. 1987, Vanderhaegen et al. 2000, Knick et al. 2003). Research on the effects of fire to sagebrush birds has mostly been on short term (<5 year) responses (reviewed in Knick et al. 2005), yet effects of fire on vegetation structure, and by extension, wildlife habitat, are much longer (Lesica et al. 2007, Baker 2011). Information on how bird assemblages and species densities fluctuate along gradients of succession-retrogression pathways (Knick et al. 2003, Reinkensmeyer et al. 2008) or among ecological states (Knick and Rotenberry 2002, Holmes and Miller 2010) is critical to informing sound policy and management decisions surrounding when to apply prescribed burning and when to suppress wildfires.

Estimates of historic fire return intervals range from 10 to >100 years for mountain big sagebrush (Miller and Rose 1999, Miller and Heyerdahl 2008). Wetter, more productive areas probably burned more frequently and were likely dominated by grasslands punctuated with scattered patches of shrubs. More xeric locations and sites with extensive rock or pumice soil components probably burned less frequently (Miller and Tausch 2001) and likely supported vegetation communities with more woody structure. Widespread reduction of fire on the landscape, corresponding to the introduction of livestock grazing has facilitated an expansion of woodlands into mountain big sagebrush (Miller and Rose 1999, Miller and Tausch 2001). Concern over impacts to ecosystem processes and decline in the availability and quality of wildlife habitat has promoted increased interest in the use of prescribed burning or fire surrogate treatments to reduce woodlands and restore mountain big sagebrush.

To help fill information gaps on longer term impacts of fire, and post fire wildlife dynamics, I initiated research on the Sheldon National Wildlife Refuge (SNWR), located in the northwestern portion of the Great Basin in Nevada. The SNWR is within one of few remaining large expanses of unfragmented sagebrush (Knick et al. 2003) with low densities of roads and people. Livestock was removed from this 233,000 ha refuge in the early 1990's due to conflicts with wildlife management, making SNWR one of few large landscapes in the intermountain West not used by for cattle production. Being embedded within this relatively unaltered landscape and lacking the ongoing influence of livestock grazing on fuels, fire behavior, and post-fire vegetation succession, the SNWR is an ideal place to study fire ecology and wildlife responses.

In the second chapter of this dissertation I ask whether abundances of small mammals differ between burned and unburned mountain big sagebrush habitats, and attempted to identify environmental features that correlate with observed patterns of abundance. I used multiple survey methods combined with distance sampling (Thomas et al. 2010) to estimate densities within 3 recovering burns and adjacent unburned reference areas.

In the third chapter I explore patterns of abundance for 12 species of birds in relation to a gradient of plant community succession. I used a chronosequence approach across different age fires that substituted space for time. I quantified bird densities and vegetation structure within the boundaries of four large fires that occurred from 8 to 20 years previously. Inclusion of adjacent reference sites allowed us to scale our estimates to reference sites.

In Chapter 4 I ask whether bird diversity differs between burned and unburned mountain big sagebrush habitats at different stages of vegetation succession and explore patterns of community organization as a function of disturbance history. This research was designed to address questions that would support the United States Fish and Wildlife Service to make sound decisions surrounding fire management on the SNWR. I hope they are also useful to further the discussion surrounding the appropriate use of fire as a management tool in mountain big sagebrush communities throughout the Great Basin.

LITERATURE CITED

Dobkin, D. S., and J. D. Sauder. 2004. Shrubsteppe landscapes in jeopardy. Distributions, abundances, and the uncertain future of birds and small mammals in the Intermountain West. High Desert Ecological Research Institute, Bend, OR.

Holmes, A. L., and R. F. Miller. 2010. State-and-Transition Models for Assessing Grasshopper Sparrow Habitat Use. Journal of Wildlife Management 74: *in press*

Knick, S. T., and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe landscapes and breeding passerine birds. Conservation Biology 9:1059–1071

Knick, S. T., Rotenberry, J., 2002, Effects of habitat fragmentation on passerine birds breeding in Intermountain shrubsteppe: Studies in Avian Biology, v. 25, p. 130-140.

Knick, S. T., A. L. Holmes, and R. Miller. 2005. The role of fire in structuring sagebrush habitats and bird communities. Studies in Avian Biology 30:63-75.

Lesica, P, S. V. Cooper, and G. Kudray. 2007. Recovery of Big Sagebrush Following Fire in Southwest Montana. Rangeland Ecology & Management 60:261-269.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for the avifauna of sagebrush habitats. Condor 105:611-634.

Miller, R. F., and E. K Heyerdahl. 2008. Fine scale variation of historical fire regimes in semi-arid shrubland and woodland: An example from California, USA. International Journal of Wildland Fire 17:245–254.

Miller, R. F., S. T. Knick, et al. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

Miller, R. F., and R. J. Tausch. 2001. The role of fire in pinyon and juniper woodlands: a descriptive analysis. Tall Timbers Research Station Miscellaneous Publication 11:15–30.

Pierson, F. B., P. R. Robichaud, C.A. Moffet, K.E. Spaeth, S.P. Hardegree, P.E. Clark, and C. J. Williams. 2008. Fire effects on rangeland hydrology and erosion in a steep sagebrush dominated landscape, Hydrological Processes 22: 2916-2929.

Rau B. M., R. R. Blank, J. C. Chambers, and D. W. Johnson. 2007. Prescribed fire in a Great Basin sagebrush ecosystem: dynamics of soil extractable nitrogen and phosphorus. Journal of Arid Environments 71: 362–375.

Rau, B. M., J. C. Chambers, R. R. Blank, and D. W. Johnson. 2008. Prescribed fire, soil, and plants: Burn effects and interactions in the central Great Basin. Rangeland Ecology & Management 61:169-181.

Rotenberry, J. T., and J. A. Wiens. 1980a. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67:213–217.

Paige, C., and S. A. Ritter. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, ID.

Reinkensmeyer, D. P., R. F. Miller, R. G. Anthony, V. E. Marr and C. M. Duncan. 2008. Winter and early spring bird communities in grasslands, shrubsteppe, and juniper woodlands in central Oregon. Western North American Naturalist 68: 25-35

Thomas L, S. T. Buckland, E. A. Rexstad, J. L. Laake, and S. Strindberg. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables. Conservation Biology 14:1145–1160.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21–41.

Wiens, J. A., and J. T. Rotenberry. 1985. Respons of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. Journal of Applied Ecology 22:655–668.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. Ecology 67:365–376.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology, United States and southern Canada. John Wiley and Sons, New York, NY

CHAPTER 2: CORRELATES OF SMALL MAMMAL ABUNDANCE IN POST-FIRE MOUNTAIN BIG SAGEBRUSH COMMUNITIES

ABSTRACT

Fire is an important disturbance mechanism in big sagebrush (*Artemisia tridentata*) communities, yet little is known about patterns of wildlife abundance during post-fire habitat succession. I estimated the abundance of small mammals in relation to fire history in mountain big sagebrush (A.t. spp. *vaseyana*) communities on the Sheldon National Wildlife Refuge in the northwestern Great Basin by way of a chronosequence approach that included three wildfires and adjacent unburned areas. To generate estimates of mammal density on 15 plots, I used trapping webs (2 per plot, n=30) and line transect surveys. Plots were at various stages of post fire vegetation succession and ranged from 7 to 19 years of recovery following fire. Shrub canopy cover ranged from 9 to 36 percent across all sites, and was not fully recovered on the plots at 20 years post fire. Only Belding's ground squirrel (*Spermophilus beldingii*) demonstrated a measurable response to fire that was consistent across all three burns. Their density was approximately 10 times greater in burned areas relative to adjacent unburned habitat regardless of the number of years since a burn occurred. Deer mouse (*Peromyscus maniculatus*) was more abundant on more recently burned sites, but not at sites closer to full vegetation recovery. Great basin pocket mouse (*Perognathus parvus*), sagebrush vole (*Lemmiscus curtatus*), and least chipmunk (*Tamius minimus*) abundance did not vary as a function of fire history, but some variance was explained by habitat features such as rock cover and sagebrush height. Overall, effects of fire on small mammals in this landscape were relatively small and vegetation recovery progressed as a function of time since fire.

INTRODUCTION

Small mammal abundance and diversity has been correlated with vegetation structure and complexity in arid ecosystems (Rosenzweig and Winakur 1969, Kerley 1992). The relative dominance of shrub versus herbaceous vegetation and related vegetation heterogeneity has been suggested as a determining factor for small mammal abundance and diversity in western shrublands (Germano and Lawhead 1986). Shrub cover may be important as a source of refuge from predators (Zou et al. 1989) and could influence population density for some species by reducing home range size through the addition of vertical structure provided by shrubs.

Despite lasting influences of fire on vegetation structure in big sagebrush (*Artemisia tridentata*) communities, few empirical data exist to describe long-term dynamics of small mammal abundances as they relate to habitat succession after fire. The conversion of lower elevation sagebrush communities to exotic annual grasslands has reduced small mammal abundance and species richness (Ostoja 2009), yet this type of conversion is not just a loss of shrub cover and corresponding structural heterogeneity, but a fundamental shift in ecological state that likely affects arthropods, seedbanks, and other food resources used by small mammals. In less altered systems where understory vegetation recovers quickly the effects of fire on food resources may be more ephemeral than those on shrub canopy structure. Experimental work involving manipulation of shrub cover in sagebrush communities has generally failed to demonstrate a clear relationship between shrub structure and small mammal abundance (Parmenter and MacMahon 1983, Zou et al. 1989, Borchgrevink et al. 2009).

Fire regimes in most sagebrush ecosystems are believed to have changed during the past century because of invasion of exotic plant species, shifts in land use practices that have altered composition and configuration of habitats, and fire suppression (D'Antonio and Vitousek 1992, Miller et al. 2011). Prior to the introduction of livestock in the late 1800's, spatial and temporal variation in recurrent fires likely resulted in a mosaic of sagebrush communities in different stages of community succession (Young et al. 1979). Even during protracted periods without fire, mature stands of sagebrush likely fluctuated in vegetation structure as a result of climatic patterns and insect outbreaks (Baker 2011). Historical fire regimes in big sagebrush communities have been altered with either an increased frequency related to invasions of exotic grasses (Whisenant 1990, Peters and Bunting 1994) or lengthened fire return intervals resulting from a number of factors, notably livestock grazing and active fire suppression (Miller and Wigand 1994, Miller and Rose 1999). This reduction of fire, which has occurred primarily in mid- and high-elevation mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities, has led to increases in the density of pinyon and juniper woodlands in portions of the North American Great Basin (Miller and Tausch 2001). Growing concern about woodland expansion has catalyzed efforts to reintroduce fire, or to use fire surrogate management activities in mountain big sagebrush ecosystems, elevating the importance of understanding wildlife responses to fire and habitat dynamics after fire.

Mountain big sagebrush is fire intolerant (West and Young 2000), so regeneration must take place from seed present in the seedbank, or from seed produced by mature individuals outside the fire perimeter. Some portion of mountain big sagebrush seeds buried in the soil remain viable for at least 3 years (Ziegenhagen and Miller 2009, Wijayratne and Pyke 2009), and recruitment has been observed following a fire in seed produced at least three years previously (Ziegenhagen 2003). Recovery of the shrub canopy can occur within 25 to 36 years (Lesica 2007, Ziegenhagen and Miller 2009, Baker 2011). In some cases, however, recovery may take 75-100 years following larger and more severe fires, where presumably, recruitment from existing local seed failed (Welch and Criddle 2003).

Small mammal populations in arid environments are highly variable, with variation driven at least in part by seasonal rainfall and seed production (Shenbrot et al. 2010, Thibaut et al. 2010). A chronosequence approach that substitutes space for time may thus be a useful approach to gaining insight into how post-fire habitat succession shapes small mammal communities: it should minimize variation due to climatic patterns that might otherwise overshadow more subtle effects related to habitat structure. Here I take advantage of multiple fires at various stages of recovery to investigate the longevity of fire effects (if any) on small mammals, while furthering our understanding of how vegetation structure correlate with abundance.

The primary goals of this study were thus to 1) estimate abundance of multiple small mammal species in mountain big sagebrush communities, 2) assess whether there are effects of fire on small mammal abundance that persist through the canopy recovery period, and 3) explore the relationship between habitat structure and small mammal abundance in the sagebrush biome.

METHODS

Study area

I quantified vegetation structure and small mammal abundances within mountain big sagebrush communities on Bald and Badger Mountains within the Sheldon National Wildlife Refuge (SNWR) in northwestern Great Basin, USA. The SNWR includes 232,694 ha, most of which occurs as a mosaic of low sagebrush (*Artemisia arbuscula*) and big sagebrush, with the higher elevations supporting mountain big sagebrush.

Refuge records indicate aggressive control of natural fires between 1935 and the early 1980's. Lightning strikes in this part of the Great Basin occur mostly between June and September in conjunction with wet thunderstorms. A lack of fine fuels due to livestock grazing, coupled with effective suppression, restricted most lightning-induced fires to small extents during this period. Between 1984 and 2001 the acreage burned annually by wildland fires was variable, with little to none in most years and large fires (>500ha) in only several years. Excluding prescribed fires the median size of the 27 fires that occurred during those years was 45 ha. To evaluate correlates of small mammal abundance in mountain big sagebrush habitats as a function of time since fire, I selected landscapes with similar elevation, slopes, and plant community composition that had experienced sufficiently large fires to include sites for estimating small mammal abundances. Landscapes that met my criteria included Bald Mountain where an ~915 ha fire burned in 1988 with adjacent, similar vegetation communities that had not burned since at least the 1930's, and Badger Mountain, approximately 32 km to the southeast. At Badger Mountain there were two larger burns suitable for study; a ~15,380 ha wildfire that occurred in 1999, and a 2,792 ha area that burned in 1994.

Within those two landscape areas, I selected study sites using a Geographic Information System (GIS) that detailed habitat type and fire boundaries (1984-2001). First I generated 2 random numbers between 1 and 1000 corresponding to the last 4 digits of a UTM coordinate. From this seed location I extended a 1000-m grid across the study areas. The centers of these 1-km^2 grid cells corresponded to centers of potential 600 x 600 m study plots. This approach ensured that no two plot boundaries would be closer than 400 m to each other in the event that two adjacent plots were selected. All potential plots were then evaluated to ensure that >70% of the area was either mountain big sagebrush or mountain big sagebrush-bitterbrush, with the remainder being inclusions of low sagebrush, small meadows, or mountain shrub communities with a sagebrush component. This resulted in seven, eight, and nine potential plots in the three Badger Mountain fire histories, of which three were selected at random in each. There were three burned plots available on Bald Mountain (all were selected), and 10 unburned plots, of which three were selected for a total of 15 plots where small mammals were studied. Average elevation ranged from 1875 to 1960 m for plots at Bald Mountain, and from 1910 to 2075 m at Badger Mountain.

Mammal abundance

To estimate abundances of nocturnal small mammals I established 200-m diameter trapping webs following protocols outlined in Parmenter et al. (2003). Trapping webs consisted of 12 radial lines of 100 m each. Each line had 12 trap stations corresponding to 5, 10, 15, 20, 30, 40, 50, 60, 70, 80, 90, and 100 m from the center. Four additional traps were placed approximately 1 m from the center of the web for a total of

148 traps within a circular area of 3.14 ha. In 2006 I placed webs in the center of each plot, and in 2007 I relocated webs at least 200 m away by randomly selecting one of the other eight 200 m X 200 m sections within the 36 ha plot (Figure 1). Thus, a total of 30 webs were run within the 15 plots over the 2 years of trapping.

I used small Sherman live traps (7.5 X 9.5 X 25.5 cm; H.B. Sherman, Tallahassee, Florida, USA) baited every evening with peanut butter and rolled oats and checked each morning between 0530 and 0800. Cotton batting was provided as nesting material, and replaced following captures. Captured mammals were identified to species, and weighed to the closest 0.5 g using a pesola scale, or 0.1 g with a digital scale. Deer mice (*Peromyscus maniculatus*) were ear-tagged with a unique number (Monel #1, National Band and Tag Co., Lexington, Kentucky, USA) and marked with a non-toxic permanent ink on their other ear and with a stripe down their backs. All other species were marked only with ink. Animals were aged as juvenile or adult based on weight and reproductive condition. I left traps closed during the day and ran each web for 5 consecutive nights. To minimize variation in trapping rates due to weather and moon phase (Price et al. 1984) among webs in different burn histories and/or mountains I ran webs simultaneously on each of the 5 treatments (one plot per treatment per week for 3 consecutive weeks in each year). I ran trapping webs between 10 June and 2 July in 2006, and again between 9 June and 27 June in 2007.

To estimate abundances of diurnal small mammals I surveyed four parallel 600 m transects on each plot. Transects ran north to south and were spaced 150 m apart from each other with 75 m between the outer transects and the sides of the plots (Figure 1). I completed surveys between the hours of 0700 and 1000, during 29 May through 17 June in 2006, 2007, and 2008. I used a handheld GPS unit to follow the transect line and walked slowly while scanning continuously from side to side. To minimize any bias from seasonal trends in detection probability I rotated through the plots such that each mountain by burn history combination had one plot surveyed during the first 5 days, a second plot surveyed during the next 5 days, and the third plot surveyed in the final 5 days. I estimated the distance and compass bearing to each animal detected. This was facilitated with the use of a laser rangefinder with a 7 power monocular (Leica LRF900). In addition to species, I recorded how the detection was made (visual or aural) and group size where multiple animals were observed with one detection cue. All surveys were conducted by a single observer (ALH).

Vegetation sampling

At each trapping web I measured vegetation along three 100 m transects (Figure 2.1). I recorded the species, height, and intercept of each shrub canopy along the transect (Canfield 1941). I excluded discrete gaps in shrub canopy greater than 20-cm from cover estimates. Herbaceous vegetation and ground cover was measured every 5 m along these transects using a 0.2 m^2 frame (40 cm x 50 cm). This approach is a modification of Daubenmire (1959) in several ways. First, cover is estimated on a continuous scale to the nearest percent rather than in cover classes, and second, estimates are made of total horizontal coverage when viewed from above as opposed to several discrete strata. Within each frame I estimated cover of bare ground, litter, cryptobiotic soil crust, annual grasses, perennial grasses, and forbs. I conducted all vegetation sampling associated with the trapping webs during July of the same year in which trapping occurred.

As potential correlates of diurnal mammal abundance I also measured vegetation within each of the additional seven 4-ha sub-sampling areas and averaged for plot-level estimates that correspond spatially to the extent of the survey transects. I completed two 50-m vegetation transects within each of the other seven sub-sampling areas. For these, the compass bearing of the 1st transect was selected randomly and began 20 m from the middle point of the 4-ha cell. The 2nd transect was oriented perpendicular to the first and was centered 65 m away from the beginning of the 1st transect (Figure 2.1). In total I completed 1300 m of line intercept sampling to measure shrub cover, and sampled ground cover using 260 cover frames within each of the 15 plots. I conducted vegetation sampling at the seven sub-sampling points not associated with trapping webs during 2008. All vegetation sampling was conducted by four personnel.

Statistical analysis

I used program DISTANCE to estimate density at trapping webs (excluding juveniles) for species with sufficient data (Thomas et al. 2010). I established distance intervals primarily by the midpoints between traps along the radial lines of the webs, although I grouped some traps into distance intervals to improve fit. I did not truncate data and only included new captures in analyses. Trapping webs, unlike traditional trapping grids, carry no assumption of population closure. Where sufficient data allowed, I also used program DISTANCE to estimate densities of diurnal small mammals at the scale of the 36-ha plots. Data, however, was fairly sparse even for the most abundant diurnal species. Since the same transects were surveyed in all three years, with approximately the same number of detections annually (suggesting no year effect), I combined all surveys for analyses. Resulting models thus ignored year and included a divisor in the density estimator to account for the repeat surveys. Truncation distances (*w*) for the transect data were selected based approximately at the point where detection probability dropped below 20% (Buckland et al. 2001).

I used Half-normal, hazard rate, and negative exponential key functions to model both global and strata-specific detection functions. One or more adjustment terms were also evaluated and included in models where they reduced AIC relative to models without adjustment terms. Half normal key functions were paired with cosine adjustment terms while the other key functions used simple polynomial adjustment terms. The key function with the lowest AIC was selected for a given model structure. To reduce potential bias in density estimates due to variation in detection probability associated with vegetation structure, or driven by year to year variation in demographic parameters, I also evaluated models with a global detection function that included one or more covariates (burn history, year, shrub cover), including detection cue type (visual or aural) for the diurnal surveys. Models with covariates were developed following guidelines put forth in Marquez et al. (2004, 2007), and were only estimated with the hazard rate and half normal key functions. Model sets were ranked based on the lowest AIC scores, and density estimates were generated from the highest ranked model for each species.

Patterns of abundance were related to fire histories and vegetation structure using ANOVA and linear regression. Where an ANOVA showed an effect of fire, I further explored the relationship with linear comparisons between burned and unburned portions of each mountain. To relate density estimates to habitat variables measured on the trapping webs and survey plots I first looked for univariate correlations with habitat variables and then estimated one or more candidate models including correlates that were significant at $P \leq 0.1$. Final models accounted for design effects (multiple webs per plot and stratified random design), and included only terms that were significant within the model at $P \leq 0.05$. I examined residual plots and formally tested their distribution (sktest and hettest: STATAcorp, College Station, Texas, USA) to ensure that assumptions of heteroscedasticity and normality were not violated.

Differences in environmental variables that may be related to fire and post-fire succession (shrub cover and height) were estimated using linear regression followed by pair-wise linear comparisons between each burn and the adjacent unburned areas. I used data from the 9 sub-sampling plots within each of the 15 larger study plots ($n = 135$, $N=15$) so variance was calculated using a 2-stage, stratified random design.

RESULTS

Abundance of small mammals

A total of 1398 individuals representing eight species of nocturnal mammals were captured over a total 150 web nights (22,200 trap nights). Of these individuals, 1031 were classified as adults, or sub-adults of breeding age based on mass and/or breeding condition. Deer mice (*Peromyscus maniculatus*) were the most abundant with 598 adults captured, followed by great basin pocket mouse (*Perognathus parvus*; n=281), sagebrush vole (*Lemmiscus curtatus*; n=103), montane vole (*Microtus montanus*; n=17), northern grasshopper mouse (*Onychomys leucogaster*; n=16), vagrant shrew (*Sorex vagrans*; n = 7), and one each of Ord’s Kangaroo rat (*Dipodomys ordii*), and bushy-tailed woodrat

(*Neotoma cinera*). I present summaries of captures by trapping web (Appendix A, tables A1 and A2).

I estimated density using program DISTANCE for only the 3 most abundant of these species at the resolution of strata by year (Table 2.1). The coefficients of variation for most estimates were too large to allow for meaningful investigation of differences. In no case was there support, based on AIC, for modeling separate detection functions by strata (Appendix A, Table A3). For all 3 species the best model estimated detection probability using a negative exponential key function with 2 simple polynomial adjustment terms of the 2nd and 4th order. This key function is seldom recommended for use in program DISTANCE (Thomas et al. 2009), primarily because it lacks a shoulder but also because of known biases if the true detection function is something other than negative exponential. In this study, with multiple traps placed near the center and closer trap spacing for the first 20 m of the web, capture probability declined precipitously in the first 20 m, resulting in no shoulder in the detection function, which is represented best by the negative exponential. The selected function was qualitatively similar for all 3 species and was characterized by a rapid decline from the center of the web until about 25 m before it stabilized and appeared constant at further distances.

Deer mouse was ubiquitous, occurring on all 30 trapping webs. Estimated deer mouse densities ranged among burn histories and mountains from a low of about 17 individuals/ha to a high of 63 individuals/ha (Table 2.1). Densities were greater in 2006 than in 2007 and there was a significant burn by mountain interaction (Tables 2.1 and 2.2). Further exploration of that interaction revealed higher densities in the burned areas than unburned for the more recent fires on Badger Mountain, but not for Bald Mountain.

Great basin pocket mouse was nearly ubiquitous, occurring on 28 of 30 trapping webs with densities ranging from 5.7 to 46.9 individuals/ha (Table 2.1). Their density did not differ between burned and unburned portions of the mountains, or by year, but they tended to be more abundant on Badger Mountain than on Bald Mountain. Sagebrush voles were more abundant on Bald Mountain where they occurred on 11 of the 12 trapping webs than on Badger Mountain where they occurred on only 5 of the 18 webs. Estimated densities for burn history and mountain strata ranged from 0 to 51.3 individuals/ha; there was no significant effect of fire or year. Northern grasshopper mouse was captured only rarely, and only on Badger Mountain (6 of 18 webs), while montane vole was captured on 4 of 12 webs at Bald Mountain and only on 1 of 18 webs at Badger Mountain.

Diurnal surveys totaling 108 km of walking transects resulted in 380 detections of 6 species. The most numerous was Belding's ground squirrel (*Spermophilus beldingii*) with 203 detections, followed by least chipmunk (*Tamias minimus*; n=89), Townsend's ground squirrel (*Spermophilus townsendii*; n=35), yellow-bellied marmot (*Marmota flaviventris*; n=25), golden-mantled ground squirrel (*Spermophilus lateralis*; n=25), and cottontail rabbits (*Sylvilagus nuttallii*; n = 10). Additional species of small- and medium-sized mammals observed on the plots but not during surveys included short-tailed weasel (*Mustela erminea*), long-tailed weasel (*M. frenata*), American badger (*Taxidea taxus*), and black-tailed jackrabbit (*Lepus californicus*). I developed density models in program DISTANCE for the 2 most abundant species only due to insufficient observations for the others. For both, the best model used a hazard-rate key function and included a covariate for detection type (call or visual; Appendix A, Table A1). Detection probabilities remained very high for aural detections out the to the truncation points (80 m for Belding's ground squirrel and 35 m for least chipmunk), but declined rapidly with distance from the observer for visual detections.

Estimated densities of least chipmunk varied from 0.13 to 0.42 individuals/ha among strata and there were no significant differences associated with burn history or mountain (Tables 2.1, 2.2). Belding's ground squirrel was patchily distributed and densities were extremely low in unburned portions of both mountains (0.02 to 0.04 per ha), and greater in all 3 burned strata (0.27 to 0.30 per ha; Table 1). There was a strong effect of burn history with no significant interaction with mountain (Table 2.2).

Townsend's ground squirrel was detected on all 3 of the plots that had burned in 1994, 2 of the 3 plots burned in 1999 and one of the plots burned in 1988, but were not detected on the unburned plots of either mountain. Golden-mantled ground squirrels (detected on 9 of 15 plots) and yellow-bellied marmots (detected on 7 of 15 plots) showed no pattern in relation to burn history, with detections of both generally occurring on rocky outcrops. Rock cover was a significant predictor of marmot abundance (number of detections = -0.29 + 0.22*rock cover, P=0.027, $R^2 = 0.32$), but not for the golden-mantled ground squirrel. Cottontail were detected on two of three unburned plots on each mountain, but only a single plot in the 1994 burn and a single plot in the 1988 burn.

For the 2 species that showed significant effects of fire (deer mouse and Belding's ground squirrel) I conducted additional regression analyses and linear comparisons. The deer mouse was more abundant in the unburned habitat than in the 1994 burn at Badger Mountain by 14.2 animals/ha (CI = -1.7, 30, P = 0.075), and the 1999 burn by 20.3/ha (4.9 – 35.7, P = 0.015). Their estimated abundance was also greater in the 1994 burn than in the 1999 burn by 6.1 animals/ha, although this was not statistically significant (CI: -14.08, 26.39, P = 0.51). There was no relationship with fire for deer mouse at Bald Mountain.

Belding's ground squirrel was more consistent in patterns of abundance in relation to fire history. They were significantly more abundant at plots within the 1988 burn than on adjacent unburned plots of Bald Mountain (by 0.22 per ha, CI: 0.05, 0.40; P = 0.018). At Badger Mountain they occurred at greater densities in both the 1994 burn (by 0.28 per ha, CI: 0.06, 0.50; P = 0.017) and 1999 burns (by 0.26 per ha, CI: 0.07, 0.59; P = 0.108). The two burns on Badger Mountain did not differ in estimated ground squirrel abundance (estimated difference of 0.02 per ha, CI: -.37, 0.42; P=0.902).

Habitat variables

Shrub cover, big sagebrush cover, and average shrub height differed among mountains and burn histories, but other variables did not show clear-cut patterns related to fire (Table 2.3). Even after approximately 20 years of recovery at Bald Mountain, percent cover of shrubs was greater on the unburned study sites (mean difference in cover = 9%, CI: 0.04,17.9; P = 0.049). Cover of big sagebrush was not significantly greater (mean difference in cover = 1.2%, CI = -9.03 - 11.56; P = 0.79), but the average height of big sagebrush shrubs was 11.5 cm taller outside of the fire perimeter (CI = 5.32, 17.64; P = 0.002). At Badger Mountain, the unburned study areas had greater percent shrub cover than the 1994 burn (mean = 15.3, CI: 9.3, 21.3; P <0.001) as well as the 1999 burn (mean = 24.2, CI: 12.4, 36.0; P = 0.001). The same pattern held true for big sagebrush cover where the unburned study sites had greater cover than the 1994 burn (mean difference =

5.4, CI: 0.9; 9.9; P = 0.024) and 1999 burn (mean difference = 12.4, CI: 7.9, 16.9; P <0.001). In addition, the 1994 burn had higher percent sagebrush cover than the 1999 burn (mean = 7.0, CI: 6.3, 7.6; P<0.001). Average sagebrush height was not significantly greater in the unburned than the 1994 burn (7.3 cm, CI: -5.3, 19.9 cm; P=0.228), but was greater relative to the 1999 burn (24.2 cm, CI: 12.4, 36.0 cm; P=0.001). Sagebrush height was on average 17.0 cm (CI: 5.6, 28.3; P = 0.007) greater in the 1994 fire area than in the 1999 burn.

Litter cover followed a similar pattern to shrub cover, but was not analyzed further because it was highly correlated with shrub cover across all study areas (r = 0.96) since most litter was located under shrubs. Percent cover of grasses and forbs on study plots were not related to burn history, although bunchgrass cover tended to be higher at Bald Mountain than Badger, and Badger Mountain was rockier than Bald Mountain reflecting differences in soils and overall productivity.

Habitat correlates and predictive models

Univariate correlations between density estimates and habitat variables for Belding's ground squirrel included a positive relationship with bare ground and bunchgrass cover and a negative correlation with shrub cover. The final linear regression model was D = 0.152 – 0.012*shrub cover + 0.185*bunchgrass cover ($R^2 = 0.46$, $F_{(2,9)} = 12.49$, P = 0.0025). Univariate correlations between least chipmunk density and habitat variables included a positive correlation with rock cover and negative correlations with bunchgrass and forb cover. The final model, which did not include bunchgrass cover due to covariation with rock cover, was D = 0.283 + 0.0190*rock cover -0.022*forb cover (R^2 = 0.53, $F_{(2,9)}$ = 15.84, P = 0.0011).

There were no significant habitat correlates with deer mouse density, even after controlling statistically for the strong year effect revealed through ANOVA. Great basin pocket mouse density was weakly and negatively correlated with bunchgrass cover and positively with rock cover. The linear regression model estimated for pocket mouse density at trapping webs was D = 21.0 + 1.29*rock cover (R^2 = 0.23, $F_{(1,10)}$ = 9.42, P = 0.0119). Sagebrush vole density was weakly and positively correlated with total shrub and bunchgrass cover as well as the average height of big sage sagebrush, but only sagebrush height was included in the final model (D = -24.71 + 0.76*mean sagebrush height, R^2 = 0.17, $F_{(1,10)}$ = 5.17, P = 0.0463).

DISCUSSION

Shrub cover and average shrub height was lowest on sites burned most recently and highest in the unburned study sites. All three burns investigated appeared to be on a similar trajectory of canopy recovery with ratios of shrub cover between burned and unburned areas progressing in a linear fashion with time since fire from 0.3 (~7 years post fire), to 0.48 (~13 years post fire), to 0.75 (~19 years post fire). If this linear relationship is carried out further it suggests that shrub canopy cover will be comparable to adjacent unburned areas after approximately 25 years of recovery, which is within the range of recovery periods documented elsewhere for mountain big sagebrush (Harniss and Murray 1973, Lesica 2007, Ziegenhagen and Miller 2009, Nelle et al. 2000). Other habitat variables such as bunchgrass and forb cover did not vary as a function of burn history. Only Belding's ground squirrel demonstrated consistent long-term differences in abundance in relation to wildfire. They were approximately 10 times more abundant on burned plots than unburned plots regardless of the number of years since burning. Deer mice showed a variable response with increased densities occurring on the more recent burns on Badger Mountain relative to adjacent unburned areas, but not at the older burn on Bald Mountain. Densities of sagebrush vole, great basin pocket mouse, and least chipmunk varied independently of fire history, but were weakly correlated with habitat variables measured at the scale of the study plots. These findings suggest that, at least in relatively intact high-elevation sagebrush steppe communities where shrub recruitment facilitates rapid canopy development, the effects of fire on most species of small mammals are not long-lived. Variation in shrub recovery rates related to shrub recruitment in the years immediately following a fire, or in cases where initial recruitment fails, related to fire size and distance from edge may influence the longevity of effects on Belding's ground squirrel and sagebrush vole – the two species that were correlated with shrub canopy variables.

The estimated density of deer mouse in mountain big sagebrush communities on SNWR were higher than densities reported from forested habitats in Oregon (Verts and Carraway 1998). In the nearby Harney Basin in Oregon, deer mice were reported to be more abundant in big sagebrush habitats than grasslands (Feldhammer 1979). Further north in the Columbia Basin they were trapped at greater numbers in a sagebrush-juniper community than in grasslands (Rogers and Hedlund 1980), suggesting that woody vegetation provides some resource value. In this study, deer mouse densities were not correlated with shrub cover, but all of the trapping webs were located in mountain big sagebrush / bitterbrush communities and all had some degree of shrub structure. Most other research in sagebrush communities also failed to find effects of shrub removal on deer mouse abundance, or correlations with shrub cover (Parmenter and MacMahon 1983, Zou et al. 1989, Borchgrevink et al. 2009).

Olson et al. (2003) used a chronosequence approach similar to ours by examining paired burned and unburned plots in Wyoming big sagebrush shrublands that had burned at various times and as much as 12 years prior to study. They found that deer mice occurred in greater numbers at burned sites than unburned, especially in the early years after a fire. McGee (1982) found no effects of either spring or fall burns on deer mice in mountain big sagebrush. In this study I found deer mice were more abundant on plots that had burned between 6 and 14 years prior than in nearby communities outside those burns boundaries, but were not more abundant within a burn that had 18 years of recovery time. In contrast, a study conducted in the 1st and 2nd years following a fire in a southeastern Idaho sagebrush community found that trap-night indices for deer mice were not higher at the burned site (Halford 1981).

Research in other habitats has established that deer mice can rapidly colonize and take advantage of increased grass and forb seed production provided in some post-fire vegetation communities (Tevis 1956, Stout et al. 1971, McGee 1982). A short-term increase in forb production does occur after some fires in mountain big sagebrush communities (Martin 1990, Pyle and Crawford 1996, Holmes 2006) but not others (Nelle et al. 2000). Data from Olsen (2000), and in this study suggest that any increased densities of deer mice following fire in sagebrush habitats are likewise relatively short-lived.

Estimated densities of great basin pocket mouse at trapping webs in this study never exceeded 45 ind/ha. This is lower than the estimated maximum density of great basin pocket mice in eastern Washington (80 ind./ha; Schreiber 1978), and lower than reported densities for a trapping grid study in Oregon (Small and Verts 1983). During a study in eastern Washington pocket mice were only one-third as abundant on recently burned plots as compared to nearby plots outside the burn perimeter (Gano and Rickard 1982). I observed no differences in densities between unburned habitat and nearby sites that had burned 7 to 19 years prior. It is possible that food resources are limited in the first year or two after a fire where seed banks may be depleted, and that the effects do not persist after several years.

Estimates of least chipmunk density in lower elevation sagebrush habitats of eastern Oregon ranged from 2.0 to 13.9 ind./ha (Small and Verts 1983). These are considerably higher than the plot-level estimates I generated with survey data, which never exceeded 1 ind./ha. Least chipmunk at SNWR was associated with rocky outcrops, and density was positively correlated with cover of rocks. Hansen (1956) also observed that they occurred most frequently in rocky areas during surveys conducted on the nearby Steens Mountain in Oregon.

The relatively weak correlations between habitat variables and density estimates found in this study may reflect weak responses of mammals to habitat changes after fire or could also be related to measurement at an inappropriate scale. Most of the small mammals I studied experience population fluctuations across time and space that could mask all but the strongest and most extensive effects of habitat change. Although the 36-ha study plots were large as compared with typical home ranges of the small mammals I studied, they may have been too small to detect moderate to weak effects of changes in habitat structure. In addition, by averaging habitat measurements across 9 sub-sampling areas heterogeneity in both habitat features and mammal use within the plots was ignored. Nonetheless, the scale of study is appropriate from a management perspective.

The chronosequence approach carries with it several key assumptions that are seldom evaluated and as such has been criticized as a means of understanding long-term patterns of succession (Johnson and Miyanishi 2008). Most importantly, the approach requires that biotic and abiotic conditions have been similar over the time span of the successional stage being investigated, and in this case, that burned and unburned areas were not determined by inherent site differences. Rocky areas, for example, with low fuel loadings and poor horizontal connectivity of fuels can inhibit the spread of fire. In this case bare ground and rock cover were similar between burned and unburned portions of both mountains, suggesting that boundaries were not determined by environmental differences. Each of the fires that I studied was actively suppressed, and boundaries between burned and unburned areas included lines of suppression. In addition, each of the fires were large fires that occurred under extreme conditions: high fuel loads and hot and dry conditions that facilitated rapid spread into portions of the landscapes that may not have burned under average conditions. Recovery rates of shrub canopy cover are related to recruitment in the initial years following a fire (Baker 2011), which suggests that these results may not appropriately extend to fires that are on different recovery trajectories due to poor initial recruitment.

I found few effects of fire on small mammal population densities. Vegetation communities recovered over time and I expect that, as long as fires are not excessive in severity or extent, that the small mammal communities in mountain big sagebrush communities are resilient to the effects of fire. Additional research on demographic parameters such as reproductive success and survival would promote better understanding of the influence of disturbance and succession on small mammal communities.

ACKNOWLEDGEMENTS

I am grateful to the numerous people that assisted with running the trapping webs: J. Berti, K. Bloomer, J. Brennan, P. Brunner, J. Cowan, E. Donadio, M. Halley, T. Hull, A. King, S. Lamb, M. Leach, G. Pasini, A. Rosenthal, F. Sicilia, D. Shaefer, S. Sheldon, M. Stevens, and A. Viciduvich, and for those that assisted with vegetation sampling: A. Hannuksela, S. Herman, and S. Sheldon. Logistical support was provided by Brian Day and the staff of the SNWR. Funding for this work was provided through a grant from the Joint Fire Sciences Program, and through a National Science Foundation graduate research fellowship. Additional financial support came from donations to PRBO Conservation Science. Field data were collected under IAUC permit number 3349.

LITERATURE CITED

Baker, W. L. 2011. Pre-Euroamerican and recent fire in sagebrush ecosystems. In S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L Laake, D. L. Borchers and L. Thomas. 2001. Introduction to Distance Sampling: Estimating abundance of biological populations. Oxford University Press. 448 pages.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388-394.

d'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63-87.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43-63.

DeBano, L. F., Neary, D. G., and P. F. Ffolliott. 1998. Fire's Effects on Ecosystems. John Wiley & Sons, Inc. New York, N.Y.

Feldhamer, G. A. 1979. Vegetative and edaphic factors affecting abundance and distribution of small mammals in Southeast Oregon. The Great Basin Naturalist, 39:207-218.

Gano, K., and W. H. Rickard. 1982. Small mammals of a bitterbrush-cheatgrass community. Northwest Science, 56:1-7.

Germano, D. J., and D. N. Lawhead. 1986. Species diversity and habitat complexity: Does vegetation organize vertebrate communities in the Great Basin? Great Basin Naturalist 46:711-720.

Harniss, R. O., and R. B. Murray. 1973. Thirty years of vegetal change following burning of sagebrush-grass range. Journal of Range Management 26:322 - 325.

Hansen, C. G., 1956. An ecological survey of the vertebrate animals on Steen's Mountain, Harney County, Oregon. Ph.D. dissertation, Oregon State College, Corvallis, 199pp.

Hedlund, J. D. and W. H. Rickard. 1981. Wildfire and the short-term response of small mammals inhabiting a sagebrush-bunchgrass community. Murrelet, 62: 10-14.

Johnson, E. A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11: 419-431.

Johnson, K. H., R. A. Olson, and T. D. Whitson. 1996. Composition and diversity of plant and small mammal communities in tebuthiuron-treated sagebrush (Artemisia tridentata). Weed Technology 10:404–416.

Kerley, G. I. H. 1992. Ecological correlates of small mammal community structure in the semi-arid Karoo, South Africa. Journal of Zoology 227:17–27.

Koehler, D. K., and S. H. Anderson. 1991. Habitat use and food selection of small mammals near a sagebrush/crested wheatgrass interface in southeastern Idaho. Great Basin Naturalist 51:249–255.

Lesica, P, S. V. Cooper, and G. Kudray. 2007. Recovery of Big Sagebrush Following Fire in Southwest Montana. Rangeland Ecology & Management 60:261-269.

Maier, A. M., B. L. Perryman, R. A. Olson, and A. L. Hild. 2001. Climatic influences on recruitment of 3 subspecies of Artemisia tridentata. Journal of Range Management 54:699–703.

Marques, F.F.C. and S. T. Buckland. 2004. Covariate models for the detection function. Advanced Distance Sampling (eds S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas), pp. 31–47. Oxford University Press,Oxford.

Marques, T.A., L. Thomas, S.G. Fancy and S.T. Buckland. 2007. Improving estimates of bird density using multiple covariate distance sampling. The Auk 127: 1229-1243.

McGee, J. M. 1982. Small mammal populations in an unburned and early fire successional sagebrush community. J. of Range Management 35:177-180.

Miller, R. F., and E. K Heyerdahl. 2008. Fine scale variation of historical fire regimes in semi-arid shrubland and woodland: An example from California, USA. International Journal of Wildland Fire 17:245–254.

Miller, R. F., S. T. Knick, et al. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Miller, R. F., and P. F. Wigand. 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44:465-474.

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

Nelle, P. J., K. P. Reese, and J. W. Connelly. 2000. Long-term effects of fire on sage grouse habitat. Journal of Range Management 53:586-591.

Olson, R. A., B. L. Perryman, S. Petersburg, and T. Naumann. 2003. Fire effects on small mammal communities in Dinosaur National Monument. Western North American Naturalist 63(1): 50-55.

Ostoja, S. M. 2009. Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. Diversity and Distributions 15: 863-870.

Parmenter, R. R., and J. A. MacMahon. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: The role of shrubs. Oecologia 59:145–156.

Parmenter, R. R., T. L. Yates, D. R. Anderson, K. P. Burnham, J. L. Dunnum, A. B. Franklin, M. T. Friggens, B. C. Lubow, M. Miller, G. S. Olson, C. A. Parmenter, J. Pollard, E. Rexstad, T. M. Shenk, T. R. Stanley, and G. C. White. 2003. Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. Ecological Monographs 73:1–26.

Peters, E. F., and S. C. Bunting. 1994. Fire conditions pre- and post-occurrence of annual grasses on the Snake River Plain. Pages 31-36 in S. B. Monsen and S. G. Kitchen, compilers. Proceedings—ecology and management of annual grasslands. USDA Forest Service, Intermountain Research Station, General Technical Report INT-GTR-313. Ogden, Utah.

Price, M. V., N. M. Waser. and T.A. Bass. 1984. Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65(2): 353–356.

Rogers, L. E., and J. D. Hedlund. 1980. A comparison of small mammal populations occupying three distinct shrub-steppe communities in eastern Oregon. Northwest Science, 54:183-186.

Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: Habitats and environmental complexity. Ecology 50:558–572.

Schreiber, R. K. 1978. Bioenergetics of the Great Basin pocket mouse, Perognathus parvus. Acta Theriologica, 23: 469-487.

Shenbrot, G., B. Krasnov, and S. Burdelov. 2010. Long-term study of population dynamics and habitat selection of rodents in the Negev Desert. Journal of Mammalogy 91:776-786.

Small, R. J., and B. J. Verts. 1983. Responses of a population of Perognathus parvus to removal trapping. Journal of Mammalogy, 64:139-143.

Stout, J., A. L. Farris, and V. L. Wright. 1971. Small mammal populations of an area in Northern Idaho severely burned in 1967. Northwest Science. 45:219-226.

Tevis, L. Jr. 1956. Effect of a slash burn on forest mice. Journal of Wildlife Management 20:405-409.

Thibault, K. M., S. K. Ernest, E. P. White, J. H. Brown, J. R. Goheen. 2010. Long-term insights into the influence of precipitation on community dynamics in desert rodents. Journal of Mammalogy: 91:787-797.

Thomas L, S. T. Buckland, E. A. Rexstad, J. L. Laake, and S. Strindberg. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. Pp. 4-10 in E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller (editors). Proceedings Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. GTR INT-276, USDA, Forest Service, Intermountain Research Station, Ogden, UT.

Wijayratne, U., and D. A. Pyke. 2009. Investigating Seed Longevity of Big Sagebrush (Artemisia tridentata): U.S. Geological Survey Open-File Report 2009-1146, (http://pubs.usgs.gov/of/2009/1146/pdf/ofr20091146.pdf, accessed 28 September, 2010.).

Wright, H. A., and A. W. Bailey. 1982. Fire ecology, United States and southern Canada. John Wiley and Sons, New York, NY.

Young, J. A., R. E. Eckert, and R. A. Evans. 1979. Historical perspectives regarding the sagebrush ecosystem. Pp. 1-13 in The sagebrush ecosystem: a symposium. Utah State University, College of Natural Resources, Logan, UT.

Ziegenhagen, L.L., 2003. Shrub Reestablishment Following Fire in the Mountain Big Sagebrush (Artemisia tridentata Nutt. ssp. vaseyana (Rydb.) Beetle) Alliance: M.S. Thesis, Oregon State University, Corvallis, OR.

Zeigenhagen, L. L. and R. F. Miller. 2009. Postfire Recovery of Two Shrubs in the Interiors of Large Burns in the Intermountain West, USA. Western North American Naturalist 69:195-205.

Zou, J., J. T. Flinders, H. L. Black, and S. G. Whisenant. 1989. Influence of experimental habitat manipulations on a desert rodent population in southern Utah. Great Basin Naturalist 48:435–448.

Table 2.1. Density estimates (D, number/ha) for small mammals by burn history and mountain for two years on Badger and Bald Mountains, Sheldon National Wildlife Refuge, Nevada.

						95% CI	
Species	Mountain	Fire year	year	D	%CV	low	high
Peromyscus maniculatus	Badger	1999	2006	58.7	19	39.1	88.1
			2007	31.1	33	11.6	83.5
	Badger	1994	2006	44.9	24	24.8	81.2
			2007	32.6	21	19.9	53.4
	Bald	1988	2006	63.0	16	45.5	87.3
			2007	27.5	33	10.1	75.3
	Badger	-	2006	32.6	28	15.2	69.8
			2007	16.7	32	6.4	43.5
	Bald	-	2006	71.0	16	51.2	98.3
			2007	55.0	50	9.4	320.7
Perognathus parvus	Badger	1999	2006	42.4	47	9.9	182.7
			2007	36.9	31	17.2	78.7
	Badger	1994	2006	44.7	36	16.6	119.9
			2007	19.0	55	3.2	112.3
	Bald	1988	2006	22.3	60	3.1	160.0
			2007	5.6	75	0.4	70.5
	Badger	-	2006	46.9	57	7.1	307.0
			2007	38.0	39	12.6	114.7
	Bald	-	2006	32.4	39	10.7	98.0
			2007	25.7	31	12.0	55.1
Lemmiscus curtatus	Badger	1999	2006	9.5	58	1.6	55.9
			2007	7.6	103	0.3	212.8
	Badger	1994	2006	22.8	103	0.8	638.4
			2007	1.9	103	0.1	53.2
	Bald	1988	2006	51.3	30	27.0	97.5
			2007	30.4	56	5.5	167.5
	Badger	-	2006	0	-	0	0
			2007	0	-	0	0
	Bald	-	2006	45.6	44	13.4	155.0
			2007	32.1	52	7.7	168.7
Tamius minimus	Badger	1999	’06-‘08	0.21	56	0.04	1.12
	Badger	1994		0.31	32.8	0.13	0.72
	Bald	1988		0.18	56	0.03	0.92
	Badger	-		0.42	42	0.12	1.60
	Bald	-		0.13	45	0.04	0.37

Table 2.1 (continued)

Spermophilus beldingii	Badger	1999	’06-‘08	0.28	52	0.04	2.06
	Badger	1994		0.30	34	0.09	1.00
	Bald	1988		0.27	28	0.10	0.71
	Badger	-		0.02	54	0.01	0.09
	Bald	-		0.04	61	0.01	0.21

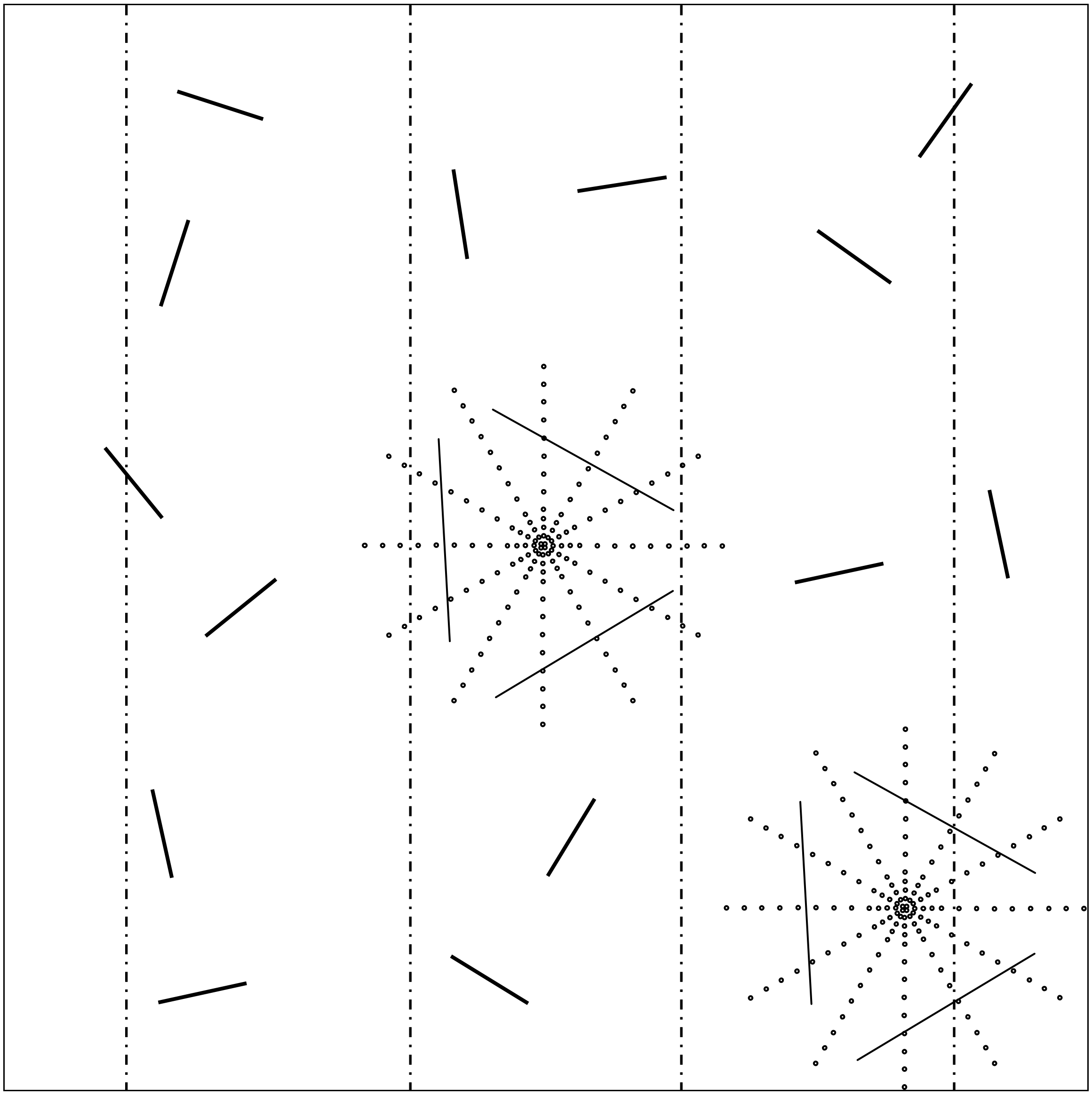
Table 2.2. Factors effecting small mammal densities in mountain big sagebrush habitats on Bald and Badger Mountains, Sheldon National Wildlife Refuge, Nevada. Analyses (ANOVA) were only conducted for species captured on greater than half of the trapping webs in 2006 and 2007 (nocturnal, n = 30 webs), or detected on greater than half of the survey plots 2006-2008 (diurnal, n = 15).

Species		R^2_{adj}	F	P
Peromyscus maniculatus	Model	0.41	4.39	0.0043
	Mountain		9.58	0.0051
	Burn		0.00	0.9753
	Year		10.23	0.0040
	Mountain * burn		6.68	0.0166
	Year * burn		0.63	0.4369
	Mountain * year		0.46	0.5064
Perognathus parvus	Model	0.07	1.38	0.2633
	Mountain		4.24	0.0510
	Burn		1.63	0.2151
	Year		1.98	0.1731
	Mountain * burn		0.24	0.6286
	Year * burn		0.23	0.6349
	Mountain * year		0.00	0.9851
Lemmiscus curtatus	Model	0.38	3.98	0.0071
	Mountain		21.03	0.0001
	Burn		0.45	0.5079
	Year		1.85	0.1873
	Mountain * burn		0.45	0.5080
	Year * burn		0.55	0.4660
	Mountain * year		0.38	0.5428
Tamius minimus	Model	0.14	1.73	0.2185
	Mountain		4.11	0.0675
	Burn		0.41	0.5370
	Mountain * burn		1.41	0.2607
Spermophilus beldingii	Model	0.37	3.72	0.0455
	Mountain		0.00	0.9750
	Burn		10.20	0.0086
	Mountain * burn		0.09	0.7732

Table 2.3. Mean vegetation and ground cover measurements (SE) for each mountain and burn history. Estimates are derived from a stratified sampling design with 9 sub-sampling locations within each of 3 36ha plots for each of the 5 strata.

	Badger			Bald	
	1999	1994	unburned	1988	unburned
shrub cover (%)	9.0 (1.0)	13.9 (0.8)	29.2 (2.5)	27.0 (0.9)	36.0 (3.9)
A. tridentata (%)	1.1 (0.2)	8.1 (0.2)	13.5 (2.0)	13.0 (4.0)	14.2 (2.3)
A. tridentata ht (cm)	32.2 (3.3)	49.2 (3.9)	56.5 (4.1)	59.7 (1.6)	71.1 (2.2)
bunchgrass cover (%)	13.4 (1.4)	15.1 (1.7)	12.4 (1.0)	23.5 (2.8)	20.6 (1.2)
Poa sandbergii (%)	3.0 (0.6)	2.1 (0.1)	5.5 (5.5)	3.7 (1.2)	2.9 (0.9)
Bromus tectorum (%)	8.1 (3.5)	1.5 (0.5)	3.2 (1.0)	2.2 (1.2)	3.4 (1.4)
forb (%)	10.9 (0.9)	3.4 (0.5)	5.6 (1.9)	9.8 (1.1)	9.4 (2.3)
bare ground (%)	41.1 (5.6)	53.0 (3.3)	35.8 (3.8)	35.6 (0.4)	29.0 (2.6)
rock (%)	12.1 (4.7)	9.0 (4.2)	8.9 (0.5))	3.4 (0.9)	4.0 (0.5)
litter (%)	11.3 (1.0)	15.5 (1.3)	26.9 (1.9)	21.6 (0.9)	29.2 (1.9)

Figure 2.1. Small mammal sampling plot layout for a 36 ha plot. Dots represent live traps in trapping webs, dot-dash lines indicate walking transects for diurnal mammals, and solid lines represent 50 m vegetation transects (outside of trapping webs) and 100 m vegetation transects (inside of trapping webs). Each set of 2 vegetation transects is placed in one of the 9 sub-sampling areas, 2 of which also contain trapping webs.



CHAPTER 3: POPULATION DENSITIES OF SONGBIRDS IN RELATION TO FIRE HISTORY IN MOUNTAIN BIG SAGEBRUSH

ABSTRACT

I employed a chronosequence approach to evaluate patterns of bird abundance in relation to post-fire vegetation recovery in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*). I estimated density for 12 species of birds within the perimeters of 4 fires that had undergone 8 to 20 years of vegetation recovery and on adjacent unburned areas in the northwestern Great Basin, USA. Six species showed negative responses of fire persisting up to 20 years. Two species showed positive responses with effects persisting for <20 years. Understory vegetation was generally similar between burned and unburned areas irrespective of recovery time, and shrub canopy cover was similar between burned and unburned sites after 20 years of recovery. Persistent reductions in bird densities lead us to conclude that shrub canopy cover alone is not a sufficient metric for measuring recovery of songbird abundances in mountain big sagebrush.

INTRODUCTION

Fire is an important mechanism of disturbance in big sagebrush (*Artemisia tridentata*) communities throughout the Intermountain West of North America (Blaisdell et al. 1982, Wright and Bailey 1982). Transitions between vegetation community phases characterized by a dominance of grasses, shrubs, or trees are typically triggered by fire, or by extended periods of time without fire (Miller and Tausch 2001, Holmes and Miller 2010, Miller et al. 2011). Thus, spatial and temporal variation in the occurrence of fire, the characteristics of unburned patches within the boundaries of a fire, and, dynamics of post-fire vegetation recovery all contribute to shaping habitat for bird populations and communities (Knick et al. 2005, Reinkensmeyer et al. 2008).

Most studies of effects of fire on sagebrush birds have focused on short-term (<5 year) effects (Knick et al. 2005). Those studies have concluded that research into longer term effects was a high priority because bird species associated with unburned habitats may be absent or have depressed abundances until recovery of mature sagebrush habitat characteristics, which may take decades (Knick et al. 2005). Time required for habitat characteristics to recover depends on the fire return interval and on local characteristics of habitats influenced by topography, soils, and moisture conditions. The historic frequency of fires in sagebrush ecosystems continues to be debated (Miller and Tausch 2001, Baker 2011, Miller et al. 2011). There is consensus, however, that mountain big sagebrush communities, which occur on more mesic and higher elevation sites within the sagebrush biome, generally burned more frequently than the more xeric big sagebrush communities (Miller and Tausch 2001, Baker 2011, Miller et al. 2011). In mountain big sagebrush communities adjacent to forests, mean composite fire return intervals for 1-10 ha plots have been estimated as 10-35 years in California and Oregon (Miller and Rose 1999, Heyerdahl et al. 2006, Miller and Heyerdahl 2008) and as 37 and 32 years in Montana (Heyerdahl et al. 2006, Lesica et al. 2007). Where soils limit fuel loads and connectivity fire return intervals may be as much as 150 (Miller and Tausch 2001). Fire rotation was recently estimated as 150-300 years with livestock grazing under 20th century conditions (Baker 2011).

The pace at which recovery of sagebrush communities occurs is of principal interest in understanding dynamics of bird populations following fires. Mountain big sagebrush is not fire tolerant (West and Young 2000) so regeneration must take place from seed present in the seed bank, or from seed produced by mature individuals outside the fire perimeter or within unburned patches of habitat. Some portion of sub-surface mountain big sagebrush seeds remain viable for at least 2 years (Wijayratne and Pyke 2009), and recruitment has been observed following a fire in seed produced at least 4 years previously (Ziegenhagen and Miller 2009). The factors determining canopy recovery rates include amount and timing of precipitation, herbivory, and site specific environmental factors that mediate plant species competition (Miller et al. 2011). The frequency of climatic conditions unfavorable to recruitment likely contributes to the recruitment of sagebrush in the years immediately following fire and subsequent variation in shrub canopy recovery time (Maier et al. 2001). Canopy cover typically reaches levels similar to adjacent unburned areas within 25 to 35 years in situations where recruitment was high in the first years after the fire (Baker 2011). Ziegenhagen (2003), examining a series of burns ranging from 4 to 49 years of recovery found that median % canopy cover of mountain big sagebrush returned to 20-25% within 32-36 years after the fire event. In Montana, Lesica (2007) concluded that average time to full recovery of mountain big sagebrush canopy cover was 32 years, and in Idaho recovery time was estimated at 27 years (Sankey et al. 2008). Slower recovery trajectories may occur on sites with poor initial recruitment (Ziegenhagen and Miller 2008) and recovery could take up to 75-100 years for larger fires where recruitment from existing local seed failed (Welch and Criddle 2003). Thus, evidence from studies of plant communities indicates that effects of fire are usually not short, but can last for many decades, depending on characteristics of the fire event and local conditions.

Most information on effects of fire on sagebrush birds has examined short-term effects. More research has been conducted on Greater Sage-Grouse (*Centrocercus urophasianus*) than other species of birds, and generally fire has negative consequences for sage-grouse (Nelle et al. 2000, Knick et al. 2005, Beck et al. 2008). Short-term effects of fire on shrub-nesting passerines are also generally negative (Knick et al. 2005, Humple and Holmes 2006, Holmes 2007), except perhaps in cases where fires remove less than 50% of the shrub canopy (Petersen and Best 1987). Short-term effects on ground-nesting birds associated with habitats with lower shrub canopy cover, such as Horned Lark (*Eremophila alpestris*) and Vesper Sparrow (*Pooecetes gramineus*), are generally positive, suggesting that shrub recovery rates may dictate the structure of bird communities in sagebrush-dominated communities. The longer-term effects of fire, as sagebrush communities recover toward pre-burn levels of canopy cover, have yet to be studied in detail. Data are needed to help identify the longevity of avian responses to fire in recovering communities.

I employed a chronosequence approach, substituting space for time, and took advantage of multiple burns in mountain big sagebrush communities of the northwestern Great Basin that occurred between 1988 and 1999. My objectives were to evaluate how vegetation characteristics in those fires of different vintage compared with characteristics in unburned locations, to document changes in estimated population densities of songbirds across the chronosequence, and to examine the degree to which abundances had recovered as time since fire progressed.

METHODS

Study area

I quantified vegetation and bird abundances in mountain big sagebrush communities on Bald, Catnip, and Badger Mountains within the Sheldon National Wildlife Refuge (SNWR) in northwestern Great Basin (Figure 1). The SNWR includes 232,694 ha, most of which occurs as a mosaic of low sagebrush (*Artemisia arbuscula*) and big sagebrush, with the higher elevations supporting mountain big sagebrush communities. Refuge records indicate aggressive control of natural fires between 1935 and the early 1980's. Lightning strikes in this part of the Great Basin typically occur between June and September in conjunction with wet thunderstorms. A reduction of fine fuels as a result of livestock grazing, coupled with effective suppression, kept most lightning-induced fires very small during this period. Between 1984 and 2001 there was much variation in the land area burned annually by wildland fires, with little to none in most years, and large fires (>500 ha) in only several years. Of 27 documented wildfires during that period, size ranged from <1 ha to 15,378 ha with a median of 45 ha.

Domestic livestock have been excluded from the refuge since the early 1990's, although feral horses continue to graze portions of the landscape. The lack of managed livestock grazing and associated impacts on fuels and post-fire vegetation succession makes the SNWR an ideal location to study fire ecology in a relatively intact ecosystem. The refuge is also located within one of the least fragmented expanses of sagebrush communities remaining in the Intermountain West (Knick et al. 2003). I chose study areas on the refuge based on the distribution of mountain big sagebrush communities (Figure 1) and their overlap with mapped fires. The areas selected included a 914 ha fire that occurred in 1988 on Bald Mountain, a 2,727 ha fire that occurred on Catnip Mountain in 1996, and two large fires on Badger Mountain; an approximately 15,378 ha wildfire that occurred in 1999, and a 2,792 ha fire that occurred in 1994. Unburned areas on each mountain were included as reference sites. Unlike the other three fires that were ignited by lightning strikes, the Catnip Mountain fire began as a prescribed burn but escaped control and ended up burning over 1000 ha outside of the planned burn area.

To select sampling points I used ARCVIEW 3.3 (Environmental Systems Research Institute, Inc., Redlands, Calif.) and GIS coverages provided by the U.S. Fish and Wildlife Service that detailed vegetation community types and fire boundaries. I projected a sampling grid with 500 m spacing across each of the study landscapes by selecting two random numbers between 1 and 500 corresponding to the last 3 digits of east and north UTM coordinates. The boundary of the Bald and Badger mountain study areas are fairly discrete as determined by transitions between mountain big sagebrush and Wyoming big sagebrush. The boundary of the Catnip Mountain study area was arbitrarily determined in order to restrict the extent of unburned habitat for sampling due to logistical reasons and to ensure that the elevation of control sites was similar to burned sites. To set the Catnip Mountain Boundary I arbitrarily bounded the wildfire with a rectangle. Points that fell within 100 m of a fire perimeter were eliminated from the second stage sampling frame. Finally, I generated a random sample of grid intersections within each of the 4 burns and within unburned areas as defined above. A single sample of 74-75 points was selected for all burns except the Bald Mountain burn where only 30 potential points existed in the sampling frame. The first half of each sample was surveyed in 2007 and the second in 2008. Within the relatively small Bald Mountain burn I surveyed all 30 points each year, but only use data from half the sample in each year for analysis to avoid issues with pseudoreplication. Detailed maps of point count locations are provided (Appendix B).

Elevations of the sampling points ranged from 1,763 to 2,097 m at Bald Mountain, 1,812 to 2,216 m at Catnip Mountain, and 1,840 to 2,178 m at Badger Mountain. Despite their relatively close proximity (all are within approximately 32 km), and similar elevations, the mountains differ to some degree in plant composition and productivity. Badger Mountain is rockier and tends to have shallower soils. Both Badger and Catnip support stands of mountain mahogany (*Cercocarpus ledifolius*) trees with only a small number of western juniper (*Juniperus occidentalis*) trees, while Bald Mountain has western juniper but not mahogany. The mountain big sagebrush and mountain big sagebrush-bitterbrush communities on Sheldon support a great diversity of bunchgrasses; I recorded 11 species of deep rooted perennial grass within the study areas. Most of the sampling locations were characterized by a mixed understory of blue-bunch wheatgrass (*Pseudoregnaria spicata*), Idaho fescue (*Festuca idahoensis*), Thurber's needlegrass (*Achnatherum thurberiana*), and bottlebrush squirreltail (*Elymus elymoides*). Other fairly common species included*Achnatherum nevadense*, and *Poa cusickii*, with *Hesperostipa comata* and *Achnaterum hymenoides* occurring more frequently in localized areas of sandier soils.

Bird surveys

I conducted five-minute point count surveys between 20 May and 4 July in 2007 and between 24 May and 2 July in 2008 following standard protocols (Ralph et al. 1993).

I began surveys approximately 20 minutes after local sunrise and were completed them within 3.5 hours. I did not conduct surveys during periods of high winds or precipitation and visited each location 2 times with different observers and approximately 2 weeks between visits. I measured the distance from the observer to each bird detected with a laser rangefinder (Leica LRF900), and noted the type of detection (song, call, or visual). If a bird was not located visually, a distance was measured using the rangefinder to the habitat patch that the call or song was perceived to be coming from. Three observers conducted the majority of surveys in each year, with a smaller number of surveys conducted by a fourth observer. Six different observers completed 958 surveys of 479 points, with three of them participating in surveys during both years of study.

Vegetation Sampling

At each of the sampling points I measured vegetation along two 50 m transects. I recorded the species, height, and intercept of each shrub along the transect (Canfield 1941). I measured canopy rather than foliar cover, and excluded gaps within otherwise continuous shrub canopies that were greater than 20-cm. In addition, the relative vigor of each shrub was recorded on a scale of 1-4, corresponding to the proportion of the canopy with live vegetation (0-25%, 26-50%, 51-75%, and 76-100%) and averaged to create an index of shrub vigor for each point. Herbaceous vegetation and ground cover was measured every 5 m along these transects using a 0.2-m^2 frame (40 cm x50 cm). I modified Daubenmire's (1959) methods in several ways. First, I estimated cover on a continuous scale to the nearest percent rather than in cover classes, and second, I estimated total horizontal coverage when viewed from above as opposed to discrete vertical strata. Within each frame I estimated cover of bare ground, litter, annual grasses, perennial grasses, and forbs. I conducted all vegetation sampling during July of the same year in which the bird surveys occurred.

Statistical analysis

I used program DISTANCE v5.1 (Thomas et al. 2010) to estimate bird population densities from the count data for species that I detected at more than 25 locations. There are three critical assumptions in distance sampling:

1. Birds at the point are detected with certainty.
2. Birds are detected at their initial location.
3. Measurements of bird-to-observer distances are exact.

The first assumption is of much less concern in shrubland or grassland communities than it would be in forests where birds at the point but above the observer in the canopy may not be detected with 100% certainty. My use of a laser rangefinder should help reduce the possibility of bias associated with assumption three, although any systematic under-estimation of distance would result in an upward bias in the resultant density estimates. Assumption two is the most problematic as birds not initially within a distance facilitating detection could move closer to the observer during the 5-minute count period, which would also result in an upwards bias in the density estimate. I have no way of evaluating the extent of any bias imparted due to bird movement, although a 5-minute count period should perform better than longer count periods sometimes employed by researchers (Buckland 1996). While unadjusted counts of birds have been widely criticized as mere indices, it has also been pointed out that meeting all the assumptions of distance sampling, as well as controlling for all sources of bias in detection probability is difficult. T hese limitations should be recognized, and density estimates from program DISTANCE may best be thought of as indices themselves (Johnson 2008).

I used the Multiple Covariate Distance Sampling (MCDS) engine to include covariates of interest in the detection function model with the goal of reducing the potential for bias in density estimates (Marques et al. 2007). I chose several covariates that were likely to influence detection functions. For example, I included a categorical variable corresponding to observer because observer differences can influence detection probabilities (Diefenbach et al. 2003, Norvell et al. 2003). I also included time of day, which is known to influence song rates and bird activity (Shields 1977, Verner and Ritter 1986), and strata, which were defined by mountain and burn history. Including strata as a covariate allows investigation of potentially different detection functions among the communities being investigated in situations where data are too sparse to develop independent estimates of detection function. In some cases I included detection type (whether a bird was singing or not) because of its likely influence on detectability of birds, but following recommendations (Marquez et al. 2007) I did not use these models where insufficient non-singing detections produced problematic composite detection functions as determined by visual assessment. Where included, this covariate may reduce biases driven by risk of nest predation that influence song rates (Robertson et al. 2010). The MCDS engine only allows half-normal and hazard rate key functions to be used, and following Thomas et al. (2010) I did not fit every possible combination of key functions and adjustment terms but rather restricted models to half-normal key functions with cosine adjustment terms and hazard rate key functions with simple polynomial adjustment terms. In total there were 11 *a priori* models that I attempted to fit for each bird species, although for many species I were not able to estimate models by strata or with covariates due to limited detections (Appendix C).

I followed analysis guidelines suggested by Marques et al. (2007) and Thomas et al. (2010). To summarize, I first conducted an exploratory analysis for each species using both exact distances and short interval groupings to assess goodness of fit visually using quantile-quantile plots and histograms. Data truncation points (*w*) were selected for each species at distances where the probability of detection fell to between 10 and 20%. This reduced the need for additional adjustment terms to fit the model to the long tail of data, which can be problematic, especially for hazard-rate models with covariates (Marques et al. 2007) and because detections further away from the sampling point contribute little to the density estimate (Buckland et al. 2001). Following selection of a truncation distance, I further evaluated model fit both visually and using the χ^2 goodness-of-fit test (Buckland et al. 2004). Models with covariates were scaled using the truncation distance (w). Finally, I fit as many of the *a priori* models as possible and models were ranked based on their Akaike Information Criteria (AIC) scores (Appendix B).

As a way to examine the effects of time since fire in the context of a chronosequence I calculated ratios between density estimates for burned and unburned portions of each landscape, as well as for vegetation variables of interest. This scaled the data to the values found on the unburned areas for each mountain, and expressed recovery to pre-burn levels as a ratio. I calculated approximate 95% confidence intervals around these ratios using the Fieller method (Fieller 1940).

RESULTS

Model Selection

The number of detections within each species' truncation distance and therefore used for density estimates ranged from 2,448 for Brewer's Sparrow (*Spizella breweri*) to 33 for Spotted Towhee (*Pipilo maculatus*; Table 1). For 11 of the 12 species for which I fit models, a hazard rate detection function was selected as the best model based on AIC (Table C1). The majority of detection types for most species were songs, which typically generates a shoulder in the detection function, fitting the hazard rate function the best. The one exception was Sage Thrasher (*Oreoscoptus montanus*), a species in which both parents incubate (Reynolds et al. 1999), and in which mated males sing less frequently than unmated males (Gooding 1970). In no case was modeling separate detection functions for different burn histories supported by AIC, and in only one case (American Robin [*Turdus migratorius*]) was including strata as a covariate supported based on ΔAIC scores. For most species there were no competing models with $\Delta\text{AIC} < 2$ (Table C1), and in situations where models were within 2 ΔAIC units, density estimates from the competing models were similar and I used models with the lower score. The most frequently supported covariate in final models was whether or not a bird was singing (4 of 10 species), followed by observer (3 species), time (2 species), year (1 species), and strata (1 species). Because distance sampling is "pooling robust" (Buckland et al. 2001), density estimates did not vary much between models with and without covariates for a given species, but model precision was sometimes improved.

Density estimates

Using the best-ranked detection function model I generated density estimates by strata and year. While many species exhibited some degree of variation in densities between the two years of study, only Brewer's Sparrow showed consistent annual differences among the three mountains and burn histories with confidence intervals that did not overlap. Brewer's Sparrow densities were more than twice as great in 2007 than 2008 across the entire study area (Table 3.2). Thus, for Brewer's Sparrow I present density estimates for each year, but for other species I present only a single estimate in order to focus results on the patterns related to vegetation recovery and time since fire. Collectively I present 91 density estimates (Tables 3.2, 3.3), of which 83 were non-zero values. The median coefficient of variation for these was 21.5% with 1st and 3rd quartiles of 13.6 and 38.8%, respectively.

Six of the 12 species I examined had reduced densities in burned areas. Sage Sparrow (*Amphispiza belli*) occurred in relatively low densities and only occurred on unburned point counts (Table 3). Spotted Towhee was similarly restricted to unburned portions of the landscapes with the exception of three detections on the 1994 burn on Badger Mountain. Gray Flycatcher (*Empidonax wrighti*) density was lower on burned points, irrespective of time the number of years that had passed (Table 3.3). Scaling estimates of Gray Flycatcher density at burned points to density at unburned points for each mountain revealed no clear pattern of recovery of density even 20 years after fire (Figure 3.2). At 19-20 years of recovery for the Bald Mountain fire, Gray Flycatchers occurred at only 17% (0-45%) the density of adjacent unburned areas. Green-tailed Towhee (*Pipilo chlorusus*) occurred at significantly reduced density on burned points for all three mountains, except at the oldest burn on Bald Mountain where confidence intervals of estimates overlapped. Ratios of Green-tailed Towhee densities between burned and unburned habitats revealed a pattern of recovery associated time since fire, reaching approximately 75% of the density on adjacent unburned sites at the 19-20 year old burn (Figure 3.2). Both American Robin and Brown-headed Cowbird (*Molothrus ater*) also had higher density estimates at unburned portions of each mountain, although estimates were imprecise and confidence intervals overlapped (Table 3.3). Two additional species for which I did not estimate density also occurred only in unburned locations: Black-throated Sparrow (*Amphispiza bilineata*) was detected on 10 points and Loggerhead Shrike (*Lanius ludovicianus*) occurred on 12 points.

Two species, Horned Lark (*Eremophila alpestris*) and Vesper Sparrow (*Pooecetes gramineus*), occurred at higher densities in burned areas with the exception of the Bald Mountain (19 to 20 years of recovery) where estimates were similar for burned and unburned habitats. Confidence intervals also overlapped for estimates of Horned Lark densities at the Badger Mountain 1994 burn and adjacent unburned areas. Plotting the ratios as a chronosequence shows declining densities with time since fire for both species out to 20 years, with perhaps a steeper decline in Horned Lark during the earlier stages (<13 years) of habitat succession (Figure 3.2).

Four species showed no clear associations between burn history and estimated densities. Brewer's Sparrow density estimates had confidence intervals that overlapped for most comparisons, but results are suggestive that densities were reduced on the most recent burn (8-9 years recovery), roughly equal to unburned areas on the intermediate burns (11-14 years recovery), and increased relative to unburned areas at Bald Mountain

(19-20 years recovery; Table 3.2; Figure 3.2). Rock Wren (*Salpinctes obsoletus*) density varied among mountains, but was fairly uniform among burn histories within each mountain (Table 3.3). Western Meadowlark (*Sternella neglecta*) showed no patterns with respect to burn history, and Sage Thrasher had widely overlapping confidence intervals for between burned and unburned density estimates within each mountain.

Vegetation

Shrubs showed the strongest pattern relative to recovery time of any physiognomic vegetation group (Table 3.4). Total shrub cover, big sagebrush cover, and mean shrub height were similar between burned and unburned locations at Bald Mountain after 19 years of recovery, but were greater at unburned than burned sites for Catnip and Badger. Total shrub cover was similar for the unburned portions of all three mountains, and ratios of burned to unburned estimates plotted against years of recovery suggest a recovery horizon of about 20 years for this metric at these sites (Figure 4.3). In contrast, cover of bitterbrush was much lower at burned sites for all three mountains with no discernable pattern of recovery with time since fire at the temporal scale investigated (Table 4.4, Figure 4.3). Bunchgrass cover tended to be higher on the burned portions of each mountain, but differences were small and confidence intervals overlapped. Forb cover was inconsistent in terms of exhibiting a response to fire – it was significantly higher on the burned portion of Catnip Mountain – which is a mid-aged burn within those sampled - but was similar among burn histories for the other two mountains. The exotic Cheatgrass (*Bromus tectorum*) was a fairly minor component of the grass understory. It occurred at greater levels of cover on the burned sites at Badger Mountain (with average cover on the 1994 burn intermediate between the cover in the unburned areas and cover in the 1999 burn; Table 3.4). It was also slightly, but not significantly greater in cover at burned locations on Catnip Mountain, and was slightly but not significantly lower in the 1988 burn on Bald Mountain.

DISCUSSION

I found that the impact of fire on bird abundances in mountain big sagebrush habitats persists for at least two decades in multiple songbird species. Sage Sparrow, Black-throated Sparrow, and Loggerhead Shrike were relatively rare in these landscapes and occurred only in unburned habitats. Spotted Towhee was also virtually restricted to unburned habitats with only a few occurrences on burned sites. Gray Flycatcher and Green-tailed Towhee had reduced densities in burned portions of the landscape across all stages of the chronosequence out to 20 years. Similar results have been reported for short-term effects of fire on Green-tailed Towhee in Rocky Mountain shrublands (Jehle et al. 2006), and in mountain big sagebrush (Noson et al. 2006). Only Horned Lark and Vesper Sparrow showed increased densities in areas with reduced shrub canopy after fire, and both species declined to densities similar to those in unburned habitats within 20 years after fire. The direction of effects for these species are similar to what has been reported for short-term responses to fire (Knick et al. 2005), and is consistent with previous research that focused on physiognomic drivers of habitat use across multiple sites (Rotenberry and Wiens 1980, Rotenberry 1985, Vander Haegen et al. 2000).

Brewer’s Sparrow was unique among the species I investigated in that they appeared to occur in lower densities than unburned areas during the early stages of recovery, approximately equal densities during middle stages of recovery, and greater densities than unburned areas later in recovery. Previous research has shown strong negative short-term effects following fire (Knick et al. 2005), with abundance correlated with the amount of residual shrub cover at a fine scale (Holmes 2007). For burns along recovery trajectories similar to those I studied, recovery to pre-burn densities may occur at about 11-14 years. Although our chronosequence does not extend further than 20 years I presume that at some point further along the successional trajectory, perhaps when the oldest shrubs begin to senesce and canopy volume decreases, density would begin to drop again. In the more recently burned portions of our study area Brewer's Sparrow commonly nested in green rabbitbrush (*Chrysothamnus viscidiflorus*) and in bunches of great basin wild rye (*Leymus cinereus*), both of which were readily available where the sagebrush canopy was still in the earlier stages of recovery. Where those habitat elements are not available in a post-fire landscape the reduction in density in the years following fire may be greater. This pattern of response, suggests that maximum density is reached at some intermediate level following fire.

Short-term responses to fire by Sage Thrasher have been mixed in previous research (Knick et al. 2005), and patterns of abundance in this study were likewise not straightforward. Our results for Sage Thrasher should be interpreted cautiously as I noted a number of unmated males in burned areas over the course of this study. Mated males sing much less frequently (Gooding 1970), and therefore are less detectable on point count surveys. This phenomenon has been noted in numerous species (Gibbs and Wenny 1993), and coupled with a male-biased adult sex ratio has important implications for population estimates based on point count surveys (Newson et al. 2005). I generally make the assumption that singing birds are mated and breeding in the habitats I am comparing. Differential pairing success between unburned and successional habitats could lead to biased estimates of differences in density. I noted evidence of this for Sage Thrasher, but not for other common species.

I observed little to no effects of fire on understory vegetation. With the exception of increased forbs at the Catnip Mountain (11 to 12 years of recovery), there were no significant differences between burned and unburned sites at any of the study areas. Further investigation casts some doubt as to whether the increased forbs at Catnip Mountain can be attributed to the fire. Mean elevation was 100m (75 – 125m) higher for burned sampling points at Catnip. This is a relatively small difference, but when I controlled statistically for elevation, the difference in forb cover between the burned and unburned portions of Catnip Mountain was no longer significant. Bunchgrass cover was similar between burned and unburned sites for each mountain, providing support for Seefeldt's (2007) conclusion that the effects of fire on the herbaceous components of mountain big sagebrush communities are small and short-lived when invasive weeds are absent.

Total shrub canopy cover was approximately 30% in the unburned portions of all three landscapes, although the big sagebrush component of this canopy was variable. Shrub canopy cover, shrub height, and big sagebrush cover were similar between the burned and unburned at Bald Mountain (19-20 years recovery), but remained reduced in the other burns (8-14 years recovery). Bitterbrush cover remained significantly reduced even after 20 years of recovery. Recovery of the shrub canopy cover levels within 20 years at Bald Mountain was slightly faster than the 25 to 35 (Baker 2011), 32 (Lesica

2007), and 32-36 years (Ziegenhagen 2003) reported previously for mountain big sagebrush.

The observation that densities of numerous species of shrub-nesting birds remained suppressed even after shrub canopy cover recovered to the level of adjacent unburned areas suggests that canopy cover alone is not an effective metric with which to assess recovery in this community. Gray Flycatcher, a species with a strong affinity for unburned habitat in this study, tends to place its nest in shrubs with dead branches, perhaps to camouflage it from predators, and in many cases selects taller shrubs with a "lollipop" type profile that have a gap between the canopy and the ground (Sterling 1999, A. L. Holmes, unpublished data). Sagebrush shrubs do not typically achieve that type of structure within 20 years (R. Miller, pers. comm.). Loggerhead Shrikes, which were restricted to unburned areas have an affinity for taller shrubs (Woods and Cade 1996), and on our study site were most often observed in stands with tall bitterbrush, a feature missing even after 20 years of recovery in the burned portion of Bald Mountain.

Densities of some shrub-associated birds remained depressed for at least 2 decades even when the shrub canopy, as measured by canopy cover, had recovered. Only two of the species I studied, Horned Lark, and Vesper Sparrow, showed higher densities after fire. Because grass cover was similar among burned and unburned locations I conclude that differences are driven by shrub rather than understory characteristics.

The chronosequence approach carries with it several key assumptions that are seldom evaluated and as such has been criticized as a means of understanding long-term patterns of succession (Johnson and Miyanishi 2008). Most importantly, the approach requires that biotic and abiotic conditions have been similar over the time span of the successional stage being investigated, and in this case, that burned and unburned areas were not determined by inherent site differences. Rocky areas, for example, with low fuel loadings and poor horizontal connectivity of fuels can inhibit the spread of fire. In this case bare ground and rock cover were similar between burned and unburned portions of both mountains, suggesting that boundaries were not determined by environmental differences. Each of the fires that I studied was actively suppressed, and boundaries between burned and unburned areas included lines of suppression. In addition, each of the fires were large fires that occurred under extreme conditions: high fuel loads and hot and dry conditions that facilitated rapid spread into portions of the landscapes that may not have burned under average conditions, and more complete burns within the fire perimeters.

I caution that my results do not extend to lower elevation Wyoming big sagebrush (*A. tridentata* spp. *wyomingensis*) communities, which generally take much longer to recover from disturbance (Baker 2011, Miller et al. 2011) and are less resistant to invasions from cheatgrass and other invasive plants (Suring et al. 2005, Baker 2006, Chambers et al. 2007). Likewise, inference from this study is limited to these particular sites, and should not be generalized without caution. Fires that experience lower rates of initial shrub recruitment are likely to show the same general patterns of increases and decreases among the species investigated, but the rates of change will not necessarily be similar. Despite limitations to inference, results from this study when combined with findings of a previous synthesis of information on fire and sagebrush bird communities (Knick et al. 2005) suggest that there is little to no sustained benefit for most bird populations in mountain big sagebrush from prescribed burning, unless that management is being done to reduce juniper or piñon encroachment in efforts to prevent a shift in ecological states.

ACKNOWLEDGEMENTS

I am grateful to M. Halley, A. Hannuksela, M. Desrosier, J. Bolser, and B. Zyla for assistance with point count surveys. The staff at the Sheldon National Wildlife Refuge provided logistical support and housing. I am especially grateful to B. Day. M. Green, R. Miller, and K. Dugger provided helpful suggestions on the study design. Funding was provided by the U.S. Fish and Wildlife Service Migratory Bird Program and through a grant provided by the U. S. Forest Service Joint Fire Science Program. Additional support was provided to the senior author through the NSF Graduate Research Fellowship Program.

LITERATURE CITED

Baker, W. L. 2011. Pre-Euroamerican and recent fire in sagebrush ecosystems. In S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Beck, J. L., J. W. Connelly and K. P. Reese. 2008. Recovery of Greater Sage-Grouse Habitat Features in Wyoming Big Sagebrush following Prescribed Fire. Restoration Ecology 17(3): 393-403

Blaisdell, J. P., Murray, R. B. and E. D. McArthur, 1982. Managing intermountain rangelands – sagebrush-grass ranges. General Technical Report INT-134., U.S. Department of Agriculture Forest Service, Intermountain Research Station.

Buckland, S. T. 2006. Point transect surveys for songbirds: robust methodologies. The Auk 123: 345-357.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. Introduction to Distance Sampling. Oxford University Press.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388-394.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117–145.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43-63.

Diefenbach, D. R., D. W. Brauning, and J. A. Mattice. 2003. Variability in grassland bird counts related to observer differences and species detection rates. Auk 120:1168–1179.

Fieller, E. C. 1940. The biological standardization of Insulin, Supplement to Journal of the Royal Statistical Society 7:1-64.

Gibbs, J. P. and D. G. Wenny. 1993. Song output as a population estimator: effect of male pairing status. Journal of Field Ornithology. 64:316–322.

Gooding, J. W. 1970. Breeding biology of the Sage Thrasher. Master's Thesis. Central Washington State College, Ellensburg.

Heyerdahl, E. K, R. F.Miller, and R. A. Parsons. 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. Forest Ecology and Management 230:107-118

Holmes, A. L. 2007. Short term effects of a prescribed burn on songbirds and vegetation in mountain big sagebrush. Western North American Naturalist 67(2):292-298

Holmes, A.L., and R. F. Miller. 2010. State-and-Transition Models for Assessing Grasshopper Sparrow Habitat Use. Journal of Wildlife Management 74: *in press*

Humple, D., and A. L. Holmes. 2006. Effects of a fire on a breeding population of Loggerhead Shrike in sagebrush steppe habitat. Journal of Field Ornithology 77:21-28.

Jehle, G., J. A. Savidge, and N. B. Kotliar. 2006. Green-tailed Towhee response to prescribed fire in mountain shrubland. The Condor 108(3): 634-646

Johnson, D. H. 2008. In Defense of Indices: The case of bird surveys. Journal of Wildlife Management 72: 857-868.

Johnson, E. A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11: 419-431.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for the avifauna of sagebrush habitats. Condor 105:611-634.

Knick, S. T., A. L. Holmes, and R. Miller. 2005. The role of fire in structuring sagebrush habitats and bird communities. Studies in Avian Biology 30:63-75.

Lesica, P, S. V. Cooper, and G. Kudray. 2007. Recovery of Big Sagebrush Following Fire in Southwest Montana. Rangeland Ecology & Management 60:261-269.

Maier, A.M., B. L. Perryman, R. A. Olson, and A. L. Hild. 2001. Climatic influences on recruitment of 3 subspecies of Artemisia tridentata. Journal of Range Management 54:699–703.

Marques, F. F. C. and S. T. Buckland (2004) Covariate models for the detection function. Advanced Distance Sampling (eds S. T. Buckland, D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers & L. Thomas), pp. 31–47. Oxford University Press,Oxford.

Marques, T. A., L. Thomas, S. G. Fancy and S. T. Buckland. 2007. Improving estimates of bird density using multiple covariate distance sampling. The Auk 127: 1229-1243.

Miller, R. F., and E. K. Heyerdahl. 2008. Fine scale variation of historical fire regimes in semi-arid shrubland and woodland: An example from California, USA. International Journal of Wildland Fire 17:245–254.

Miller, R. F., S. T. Knick, et al. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Miller, R. F. and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

Miller, R. F. and R. J. Tausch. 2001. The role of fire in pinyon and juniper woodlands: a descriptive analysis. Tall Timbers Research Station Miscellaneous Publication No. 11:15–30.

Nelle, P. J., K. P. Reese, and J. W. Connelly. 2000. Long-term effects of fire on sage grouse habitat. Journal of Range Management 53:586-591.

Newson, S.E., Woodburn, R.J.W., Noble, D.G., Baillie, S.R. & Gregory, R.D. 2005. Evaluating the breeding bird survey for producing national population size and density estimates. Bird Study 52: 42–54.

Norvell, R. E., F. P. Howe, and J. R. Parrish. 2003. A seven-year comparison of relative abundance and distance-sampling methods. Auk 120:1013–1028.

Noson, A. C., R. A. Schmitz, and R. F. Miller. 2006. Influence of fire and juniper encroachment on birds in high elevation sagebrush steppe. Western North American Naturalist 66:343–353.

Petersen, K. L., and L. B. Best. 1987. Effects of prescribed burning on nongame birds in a sagebrush community. Wildlife Society Bulletin 15:317–329.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Field methods for monitoring landbirds. USDA Forest Service Publication, PSW-GTR 144, Albany, CA.

Reinkensmeyer, D.P., R.F. Miller, R.G. Anthony, V.E. Marr and C.M. Duncan. 2008. Winter and early spring bird communities in grasslands, shrubsteppe, and juniper woodlands in central Oregon. Western North American Naturalist 68: 25-35

Reynolds, T. D., T. D. Rich and D. A. Stephens. 1999. Sage Thrasher (Oreoscoptes montanus), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/463 doi:10.2173/bna.463

Robertson, B. A., R. L. Hutto, and J. J. Fontaine. 2010. Evaluating food availability and nest predation risk as sources of bias in aural bird surveys. Journal of Field Ornithology 81: 420-429.

Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67:213–217.

Sankey, T., C. Moffet, and K. Weber, 2008. Postfire recovery of sagebrush communities: Assessment using SPOT-5 and very large-scale aerial imagery, Rangeland Ecology and Management, 61:598–604.

Seefeldt, S.S., Germino, M., Dicristina, K., 2007. Prescribed fires in *Artemisia tridentata* ssp. *vaseyana* steppe have minor and transient effects on vegetation cover and composition. Applied Vegetation Science 10, 249–256.

Shields, W.M. 1977. The effect of time of day on avian census results. Auk 94: 380–383.

Soule, P. T., P. A. Knapp, and H. D. Grissino-Mayer. 2004. Human agency, environmental drivers, and western juniper establishment during the late Holocene. Ecological Applications 14:96–112.

Sterling, J. C. 1999. Gray Flycatcher (*Empidonax wrightii*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/458 doi:10.2173/bna.458

Suring, L. H., M. J. Wisdom, R. J. Tausch, R. F. Miller, M. M. Rowland, L. Schueck, and C. W. Meinke. 2005. Modeling threats to sagebrush and other shrubland communities. Chapter 4 in Part II: regional assessment of habitats for species of conservation concern in the Great Basin. Pages 114–149 in M. J. Wisdom, M. M. Rowland, and L. H. Suring, editors. Habitat threats in the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Allen Press, Lawrence, Kansas.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5-14.

Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables. Conservation Biology 14:1145–1160.

Verner, J. and Ritter, L.V. 1986. Hourly variation in morning point counts of birds. Auk 103: 117–124.

Welch, B. L., and C. Criddle. 2003. Countering misinformation concerning big sagebrush.USDA Forest Service Research Paper RMRS-RP-40. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Wijayratne, U., Pyke, D.A., 2009, Investigating Seed Longevity of Big Sagebrush (Artemisia tridentata): U.S. Geological Survey Open-File Report 2009-1146, p. 26 (http://pubs.usgs.gov/of/2009/1146/pdf/ofr20091146.pdf, accessed 28 September, 2010.)

Wright, H. A., and A. W. Bailey. 1982. Fire ecology, United States and southern Canada. John Wiley and Sons, New York, NY.

Young, J. A., R. E. Eckert, and R. A. Evans. 1979. Historical perspectives regarding the sagebrush ecosystem. Pp. 1-13 in The sagebrush ecosystem: a symposium. Utah State University, College of Natural Resources, Logan, UT.

Ziegenhagen, L. L., 2003, Shrub Reestablishment Following Fire in the Mountain Big Sagebrush (Artemisia tridentata Nutt. ssp. vaseyana (Rydb.) Beetle) Alliance: M.S. Thesis, Oregon State University, Corvallis, OR.

Zeigenhagen, L. L. and R. F. Miller. 2009. Postfire Recovery of Two Shrubs in the Interiors of Large Burns in the Intermountain West, USA. Western North American Naturalist 69:195-205.

Table 3.1. Best detection function model by bird species (as ranked by AIC), number of detections (n), truncation distance (w), number of parameters (K), effective detection radius (EDR), and covariates included in the model. Species are ordered from highest to lower number of detections.

Species	Key function[1]	n	w	K	EDR	Covariates
Brewer's Sparrow	Haz (1)	2732	140	9	67	Sing, observer
Vesper Sparrow	Haz (1)	1123	210	9	129	Time, observer
Green-tailed Towhee	Haz (0)	716	170	8	119	Sing, observer
Sage Thrasher	HN (0)	530	189	2	189	Time
Gray Flycatcher	Haz (0)	429	150	3	103	Sing
Rock Wren	Haz (0)	404	240	2	160	-
Western Meadowlark	Haz (0)	188	220	3	160	Sing
American Robin	Haz (0)	83	190	8	121	Strata
Sage Sparrow	Haz (0)	60	140	3	111	Year
Brown-headed Cowbird	Haz (0)	59	150	2	101	-
Spotted Towhee	Haz (0)	33	200	2	146	-

[1] Haz = Hazard rate, HN = Half Normal; number in parentheses indicates number of adjustment terms. [2] Sing is a binary variable for whether a bird sang or was detected only through a call note or visually. Observer is a 6-level categorical variable indicating the surveyor.Strata is a 7-level categorical variable corresponding to the burn history and landscape.

Table 3.2. Estimated Brewer's Sparrow density (D) expressed as the number of individuals per km^2, coefficient of variation (CV) of the estimate, and 95% confidence intervals (95 low and 95 high) by year of count for each mountain's burned and unburned sites.

					95% CI	
Mountain	Year of count	Year of fire	D	CV	low	high
Bald	2007	1988	359.7	12.6	280.3	461.6
		not burned	262.7	11.2	210.6	327.7
	2008	1988	160.1	17.2	113.9	225.1
		not burned	94.3	12.3	73.9	120.3
Badger	2007	1999	164.2	12.7	127.9	210.7
		1994	202.1	10.0	166.0	246.2
		not burned	212.6	12.4	167.4	270.1
	2008	1999	70.7	14.0	53.7	93.0
		1994	112.4	13.3	86.5	146.1
		not burned	94.0	12.9	73.0	121.0
Catnip	2007	1996	265.9	9.4	220.1	320.0
		not burned	276.2	9.3	229.9	331.8
	2008	1996	107.38	11.4	85.8	134.4
		not burned	95.9	13.9	72.9	126.1

Table 3.3. Density estimates (D) in relation to fire histories expressed as the number of individuals per km^2, coefficient of variation of the estimate (CV), and 95% confidence intervals for each mountain. Count data from the two years are averaged because annual variation for these species was low.

					95% CI	
Species	Mountain	Burn history	D	CV	low	High
Gray Flycatcher	Bald	1988	2.2	71.9	0.6	8.3
		not burned	13.2	17.8	9.3	18.7
	Badger	1999	7.5	25.6	4.5	12.3
		1994	9.2	23.4	5.8	14.6
		not burned	22.1	12.0	17.4	27.9
	Catnip	1996	7.4	23.4	4.7	11.7
		not burned	25.3	11.4	20.2	31.7
Horned Lark	Bald	1988	4.3	51.3	1.6	11.6
		not burned	4.4	41.3	2.0	9.6
	Badger	1999	53.9	13.7	41.1	70.6
		1994	20.0	23.9	12.5	31.8
		not burned	10.1	31.1	5.5	18.4
	Catnip	1996	85.1	10.0	69.9	103.8
		not burned	37.0	15.0	27.5	49.7
Rock Wren	Bald	1988	2.1	51.2	0.8	5.6
		not burned	3.7	34.6	1.9	7.2
	Badger	1999	14.5	15.8	10.6	19.7
		1994	17.5	15.5	12.9	23.8
		not burned	17.4	14.1	13.2	22.9
	Catnip	1996	8.4	21.2	5.6	12.8
		not burned	5.8	22.7	3.7	9.1

Table 3.3. (Continued)

					95% CI	
Species	Mountain	Burn history	D	CV	low	High
American Robin	Bald	1988	1.7	72.7	0.4	7.0
		not burned	1.2	50.1	0.5	3.1
	Badger	1999	0.6	37.0	0.3	1.2
		1994	3.3	42.7	1.5	7.4
		not burned	4.5	32.4	2.4	8.4
	Catnip	1996	0.5	138.8	0.0	5.6
		not burned	1.3	41.9	0.6	2.9
Sage Thrasher	Bald	1988	5.4	21.1	3.6	8.3
		not burned	3.6	15.7	2.6	4.9
	Badger	1999	2.6	21.5	1.7	4.0
		1994	2.1	22.1	1.4	3.2
		not burned	4.5	13.9	3.4	5.9
	Catnip	1996	7.6	10.1	6.2	9.2
		not burned	9.2	9.6	7.6	11.1
Green-tailed Towhee	Bald	1988	17.9	25.7	10.8	29.6
		not burned	24.3	11.5	19.4	30.5
	Badger	1999	6.3	24.9	3.8	10.2
		1994	17.5	13.7	13.4	22.9
		not burned	35.3	9.3	29.4	42.3
	Catnip	1996	4.0	30.1	2.2	7.1
		not burned	13.6	17.4	9.7	19.2

Table 3.3. (Continued)

					95% CI	
Species	Mountain	Burn history	D	CV	low	High
Spotted Towhee	Bald	1988	0.0	-	-	-
		not burned	1.4	52.0	0.5	3.7
	Badger	1999	0.0	-	-	-
		1994	0.6	64.9	0.2	1.9
		not burned	2.6	43.1	1.1	5.9
	Catnip	1996	0.0	-	-	-
		not burned	2.0	51.6	0.8	5.3
Vesper Sparrow	Bald	1988	16.8	20.6	11.1	25.2
		not burned	19.4	13.8	14.8	25.5
	Badger	1999	33.3	8.1	28.4	39.0
		1994	28.7	8.7	24.2	34.1
		not burned	14.0	15.9	10.2	19.1
	Catnip	1996	27.0	9.1	22.6	32.3
		not burned	14.6	14.5	10.9	19.4
Sage Sparrow	Bald	1988	0.0	-	-	-
		not burned	0.4	86.3	0.1	2.0
	Badger	1999	0.0	-	-	-
		1994	0.0	-	-	-
		not burned	5.2	27.1	3.1	8.8
	Catnip	1996	0.0	-	-	-
		not burned	4.8	26.8	2.9	8.2

Table 3.3. (Continued)

Species	Mountain	Burn history	D	CV	95% CI low	95% CI High
Brown-headed Cowbird	Bald	1988	0.0	-	-	-
		not burned	7.0	41.4	3.2	15.5
	Badger	1999	1.7	74.1	0.4	6.2
		1994	5.0	37.5	2.4	10.2
		not burned	4.6	38.8	2.2	9.6
	Catnip	1996	0.8	74.1	0.2	3.1
		not burned	5.5	47.7	2.2	13.4
Western Meadowlark	Bald	1988	0.7	87.5	0.1	3.2
		not burned	6.7	18.9	4.7	9.7
	Badger	1999	2.5	25.8	1.5	4.2
		1994	1.4	39.5	0.7	3.1
		not burned	1.1	40.4	0.5	2.4
	Catnip	1996	1.9	29.6	1.0	3.3
		not burned	1.7	31.5	0.9	3.1

Table 3.4. Mean (95% CI) elevation, vegetation, and ground cover by burn history and location.

	Location			
	Bald 1988 (n=30)	Bald (n=75)	Catnip 1996 (n=75)	Catnip (n=74)
Elevation (m)	1951 (1932-1972)	1927 (1907 – 1945)	2065 (2050 – 2081)	1966 (1946-1986)
Shrub cover (%)	28.7 (24.8 – 32.7)	29.5 (27.0 – 31.9)	18.0 (16.5 – 19.5)	30.8 (28.3-33.3)
Big sagebrush cover (%)	10.8 (7.6 – 14.1)	9.3 (7.5 – 11.1)	8.1 (6.7 – 9.4)	16.7 (13.8-19.6)
Bitterbrush (%)	0.7 (0.05-1.4)	4.7 (3.3 – 6.0)	0.2 (0.1 – 1.1)	3.4 (2.1 – 4.6)
Shrub height (cm)	53.4 (49.7 – 57.1)	51.1 (47.9 – 54.4)	38.7 (37.1 – 40.3)	47.8 (44.0 – 51.7)
Bunchgrass (%)	19.2 (15.6 – 22.9)	14.4 (12.6 – 16.3)	10.5 (9.5 – 11.6)	9.1 (7.7 – 10.6)
Annual grass (%)	1.5 (0.7 – 2.3)	2.3 (1.5 – 3.0)	2.6 (1.7 – 3.5)	1.2 (0.3 – 2.1)
Bare ground (%)	50.5 (44.4 – 56.5)	40.4 (36.7 – 44.2)	56.1 (52.9 – 59.2)	53.3 (49.2 – 57.2)
Rock (%)	4.0 (2.0-5.9)	8.5 (6.1 – 10.9)	4.0 (2.7 – 5.4)	4.6 (3.4 – 5.8)
Forb (%)	6.6 (4.4 – 8.8)	6.4 (4.9 – 8.0)	8.5 (7.4 – 9.5)	4.7 (3.8 – 5.6)
Western juniper (#/ha)	0.05 (0-.12)	6.2 (1.7 – 10.6)	0	0
Mountain mahogany (#/ha)	0	0	0.9 (0 – 2.2)	4.8 (0.8 – 8.8)

Table 3.4. (Continued)

	Location		
	Badger 1999 (n = 75)	Badger 1994 (n=75)	Badger (n = 74)
Elevation (m)	1938 (1924-1952)	2008 (1993-2023)	1980 (1962-1999)
Shrub cover (%)	10.1 (8.8-11.3)	18.8 (17.0-20.6)	31.3 (28.9 – 33.7)
Big sagebrush cover (%)	1.7 (1.0 – 2.3)	8.2 (6.7-9.7)	16.1 (14.2-18.1)
Bitterbrush (%)	0.7 (0.2 – 1.1)	1.3 (0.7-1.9)	8.7 (7.0-10.4)
Shrub height (cm)	41.5 (39.3-43.7)	51.9 (49.7-54.1)	56.0 (53.4 – 58.6)
Bunchgrass (%)	11.4 (9.8-13.0)	16.1 (14.1-18.2)	13.3 (12.6 – 16.1)
Annual grass (%)	4.8 (3.1 – 6.5)	1.7 (1.1-2.3)	0.75 (0.4 – 1.1)
Bare ground (%)	54.0 (49.7-58.3)	49.3 (45.2-53.4)	43.9 (40.4-47.5)
Rock (%)	11.0 (8.0-13.9)	11.3 (8.1-14.4)	11.0 (8.5 – 13.5)
Forb (%)	4.3 (3.3-5.3)	4.4 (3.6-5.3)	4.5 (3.6-5.3)
Western juniper (#/ha)	0	0	0
Mountain mahogany (#/ha)	5.5 (1.6-9.4)	26.6 (4.6-48.6)	18.7 (1.3-36.2)

Figure 3.1. Location of Sheldon NWR in Nevada (inset) and detail of study areas. Shaded areas are mountain big sagebrush, mountain big sagebrush/bitterbrush, or mountain shrub with a sagebrush component. Each dot represents a point count location. The three sampling areas (clockwise from the left) are Bald, Catnip, and Badger Mountains.

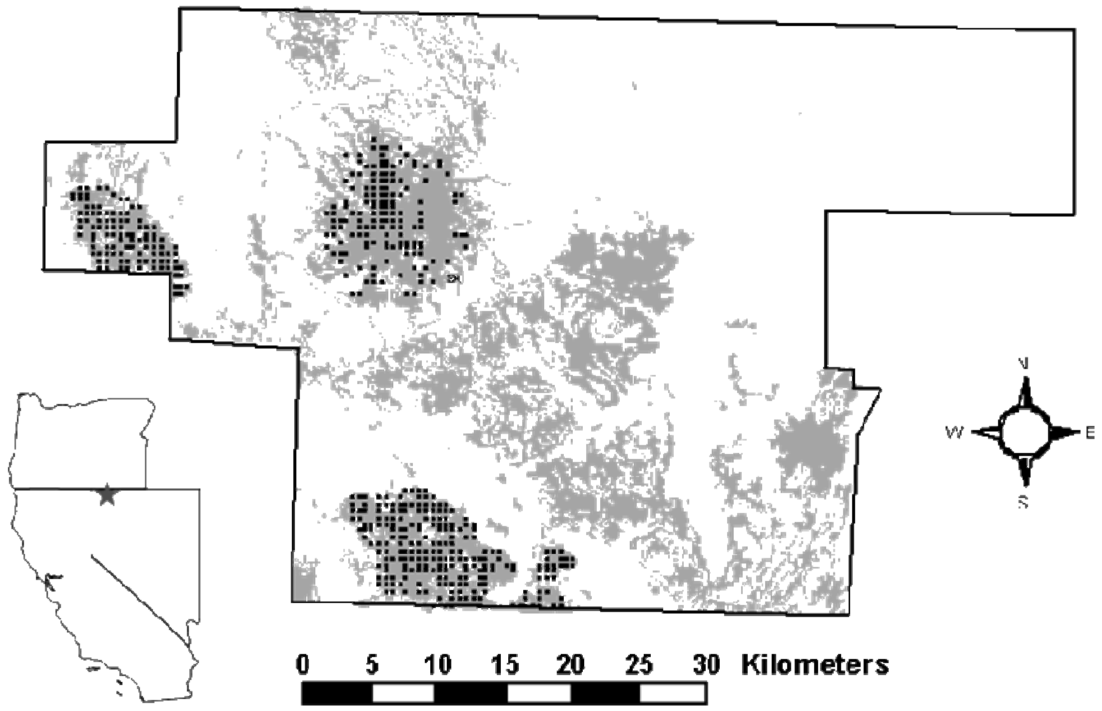
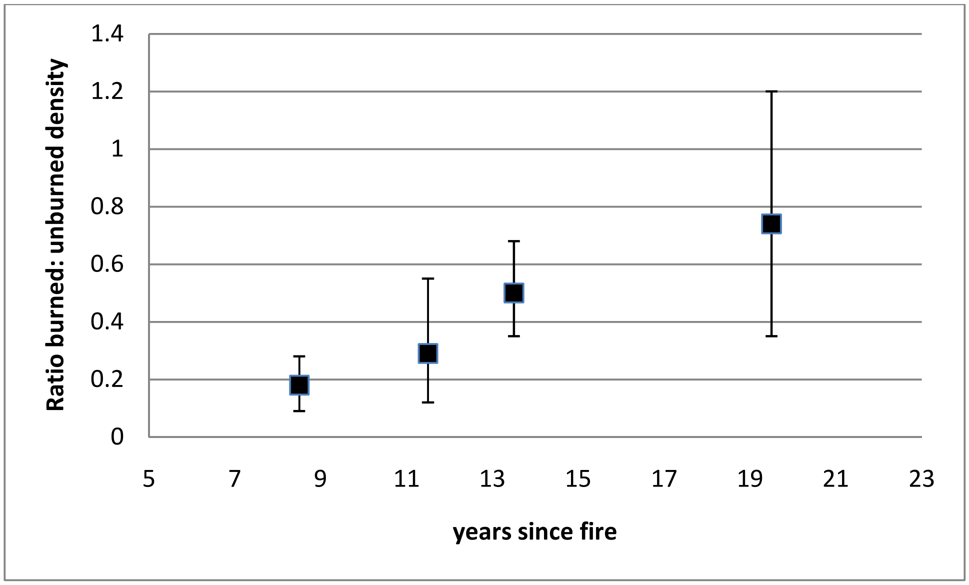


Figure 3.2. Ratios of bird densities (# per km^2) between burned and adjacent unburned habitats for four fires of different ages for a) Green-tailed Towhee, b) Gray Flycatcher, c) Vesper Sparrow, d) Horned Lark, and e) Brewer's Sparrow. Error bars are approximate 95% confidence intervals.

a) Green-tailed Towhee



b) Gray Flycatcher

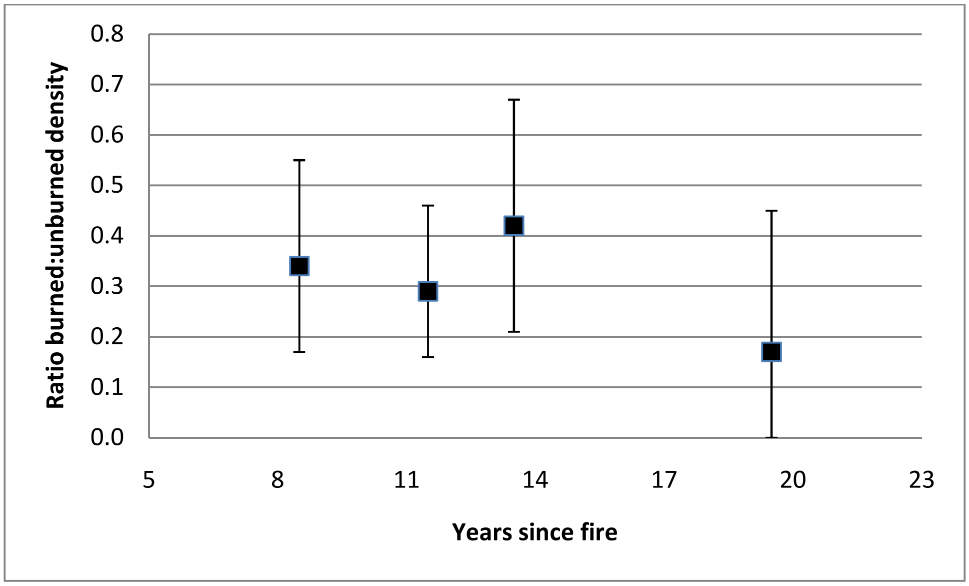
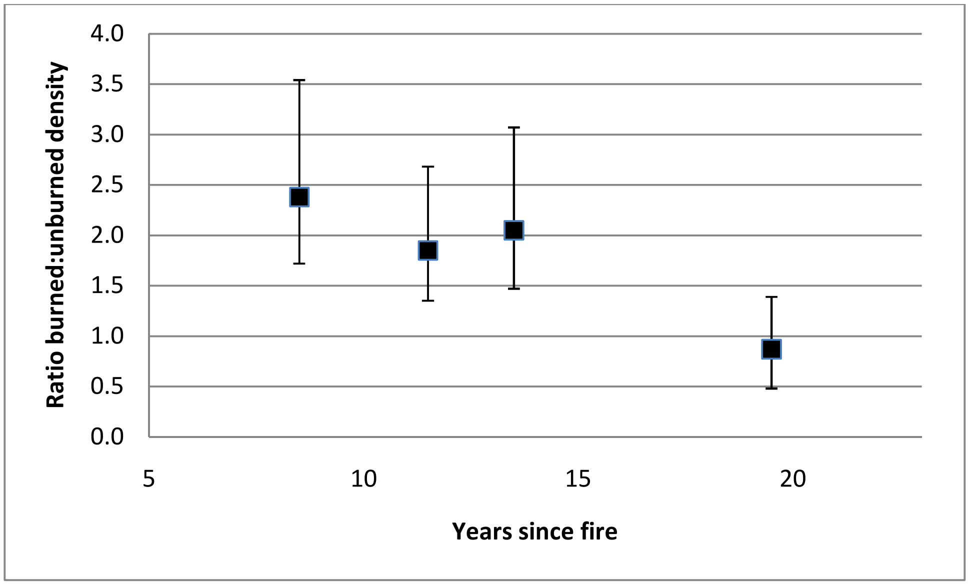


Figure 3.2 (Continued)

c) Vesper Sparrow



d) Horned Lark

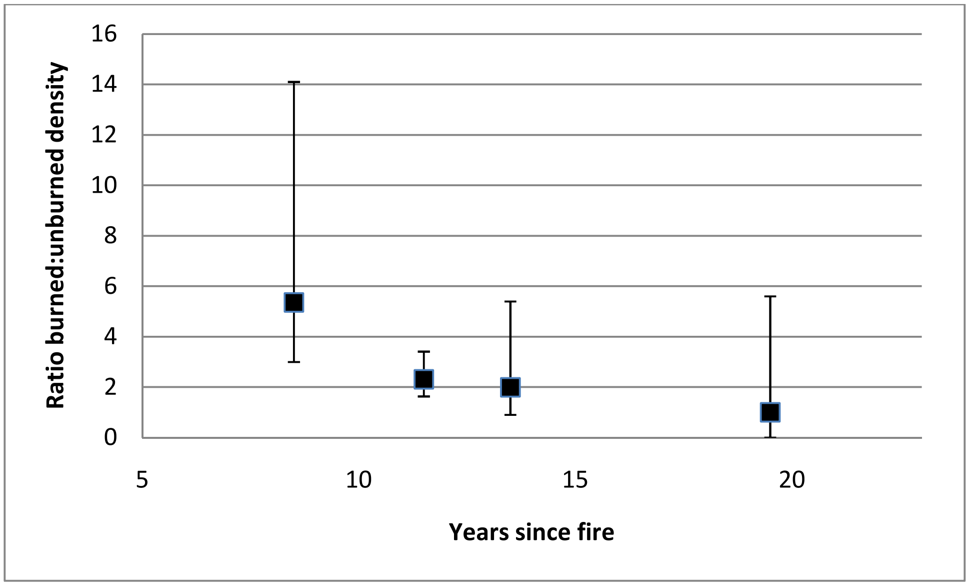


Figure 3.2 (Continued)

e) Brewer's Sparrow

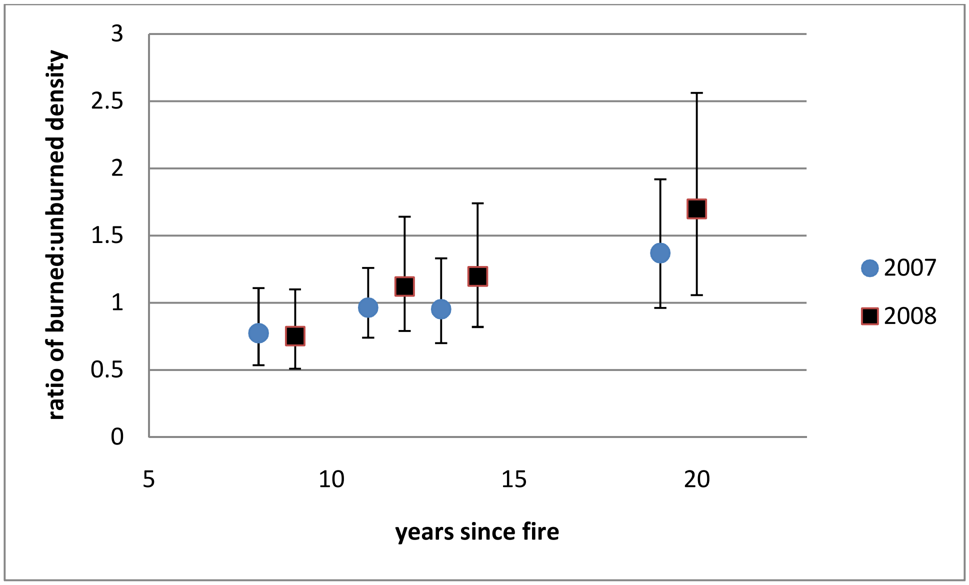
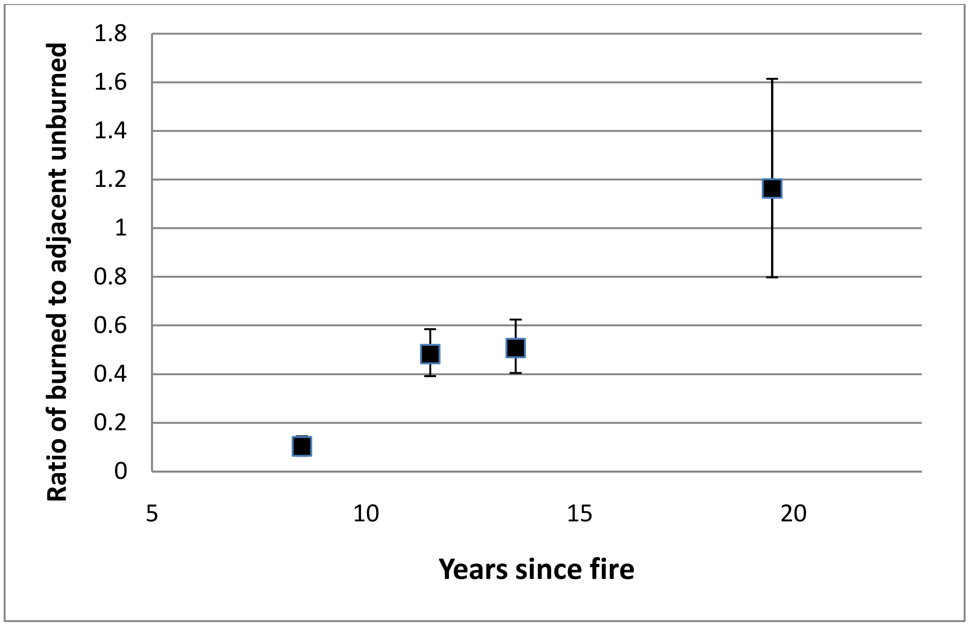
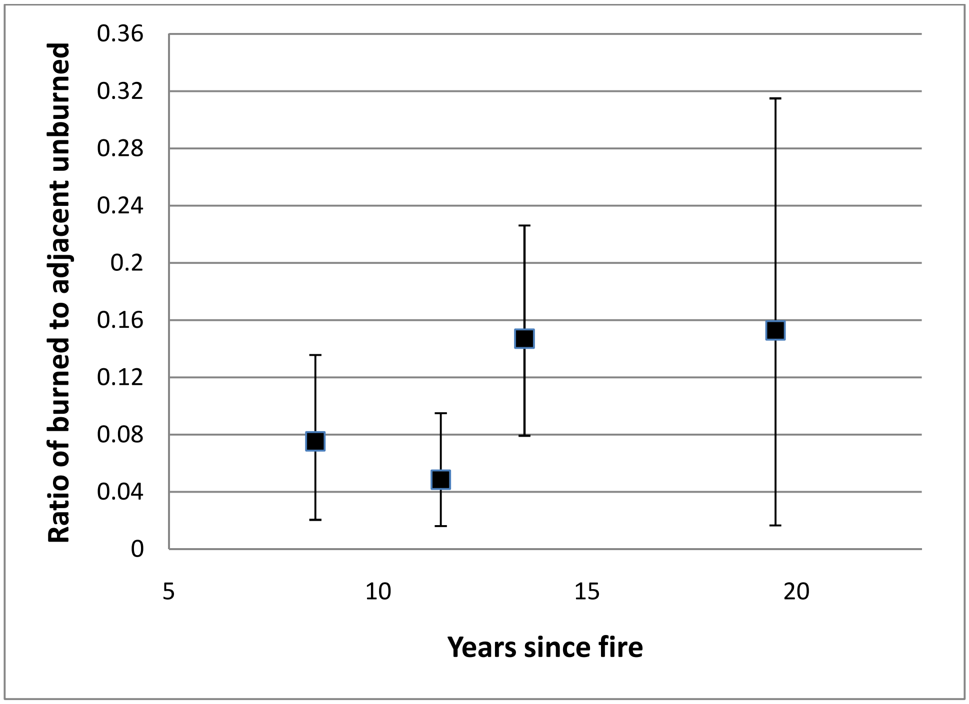


Figure 3.3. Ratios (95% CI) of big sagebrush cover (a) and bitterbrush cover (b) between burned and adjacent unburned areas in relation to the number of years since the fire occurred.

a) big sagebrush cover



b) bitterbrush cover



CHAPTER 4: BIRD DIVERSITY AND FIRE-MEDIATED COMMUNITY STRUCTURE IN MOUNTAIN BIG SAGEBRUSH

ABSTRACT

I investigated the role of fire as a natural disturbance in structuring breeding bird communities in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) habitat in the Great Basin of the western United States. I estimated diversity and abundance of birds breeding within the boundaries of 4 fires that varied in years of recovery from 8 to 20 years. Bird diversity was higher outside of fire perimeters for all 4 burns. Multiple Response Permutation Procedure analyses demonstrated that bird communities were different between burned and unburned sagebrush communities and that the magnitude of the effect diminished with years of recovery. Strong patterns of covariation in species distribution and abundance were captured in an ordination that distilled information on 12 species of birds into a 3-dimensional “species space” with synthetic axes. Patterns of abundance for individual species coupled with results from an indicator species analysis reveal affinities for early successional habitat (Vesper Sparrow [*Pooecetes gramineus*], Horned Lark [*Eremophila alpestris*]), or mature habitat (Gray Flycatcher [*Empidonax wrightii*], Green-tailed Towhee [*Pipilo Chlorurus*], Sage Sparrow [*Amphispiza belli*]). Brewer’s Sparrow (*Spizella breweri*) had a significant indicator value for later stages of canopy recovery, where they occurred at their greatest abundance. Bird community dynamics appeared to be a consequence of the differential response of species to changes in the structure of the shrub canopy resulting from secondary succession.

INTRODUCTION

Natural disturbances such as fires and floods play a major role in the structuring of biological communities (Sousa 1984, Pickett and White 1995). Evidence indicates that some communities reach a maximum diversity at some intermediate level of disturbance frequency or intensity (Connell 1978, Lubchenco 1978, Miller 1982). This phenomenon can arise from different mechanisms and occur both spatially and temporally (Roxburgh et al. 2004). With few exceptions, however, a hump-shaped response to disturbance has not been observed in vertebrate communities (Fuentes and Jaksic 1988). Alternatively, a disturbance regime that is similar to historic processes, or central tendencies within a historic range of variability, may maximize species diversity on a landscape because species generally adapt, through evolution, to specific disturbance regimes (Denslow 1985).

Bird diversity is positively correlated with the structural complexity of habitat (MacArthur and MacArthur 1961), and fire in big sagebrush (*Artemisia tridentata*) shrublands results in an immediate and relatively long-lasting structural simplification of habitat because the dominant shrubs are not fire tolerant. Fire and post-fire vegetation succession are known to influence the abundance of many species of birds that nest in big sagebrush ecosystems. Until recently (Holmes 2010, Chapter 3), however, the majority of research pertaining to fire had been limited to relatively short-term responses (< 5 years; reviewed in Knick et al. 2005). In general, species that rely on shrubs for nesting respond negatively and those that are associated with more open habitats respond positively. Short-term responses to disturbance may not accurately portray long-term effects due to vegetation dynamics, and potentially slow responses to disturbance by sagebrush songbirds due to lag effects and site fidelity (Rotenberry et al. 1995, Knick and Rotenberry 2002), necessitating longer-term research, or chronosequence approaches that substitute space for time. In chapter 3 I demonstrated that impacts of fire in mountain big sagebrush (*A.t.* ssp. *vaseyana*) had varying durations among different species, being fairly short-lived for some and persisting to at least 20 years in others.

Little direct evidence exists about historic fire regimes in sagebrush ecosystems, and ecologists have relied largely on proxy information to inform estimates about pre-settlement fire frequency (Miller and Tausch 2001). In mountain big sagebrush communities adjacent to forests, mean composite fire return intervals for 1-10 ha plots have been estimated as 10-35 years in California and Oregon (Miller and Rose 1999, Miller and Heyerdahl 2008) and as 37 and 32 years in Montana (Heyerdahl et al. 2006, Lesica et al. 2007) . Mean composite fire return interval estimates are typically generated from individual sites and can characterize local-scale variation in space and time. They are dependent upon sample size and generally decrease as larger areas are sampled. A second metric, natural fire rotation, has also been used to describe historic fire regimes in sagebrush ecosystems (Baker 2006, Baker 2011). Natural fire rotation does not directly consider spatial or temporal variation (Reed 2006, Miller et al. 2011), but instead estimates the probability that a location will burn within a year. Fire rotation estimates are computed for large areas and are driven primarily by large fires because smaller fires do not impact much of the landscape. Baker (2010), using both ignition rates and spread based on grazed 20th Century landscapes, estimated fire rotation in mountain big sagebrush communities ranged from 150 to 300 years. On average, more productive communities likely would have burned more frequently, and more xeric communities with sparser herbaceous vegetation and less horizontal fuel connectivity likely would have burned less frequently.

Following a fire, the canopy cover of mountain big sagebrush often reaches levels similar to adjacent unburned areas within 25 to 35 years (Harniss and Murray 1973, Lesica 2007, Ziegenhagen and Miller 2009, Nelle et al. 2000). Ziegenhagen (2003), examining a series of burns ranging from 4 to 49 years of recovery found that median % canopy cover of mountain big sagebrush returned to 20-25% within 32-36 years after the fire event. In Montana, Lesica (2007) concluded that average time to full recovery of mountain big sagebrush canopy cover was 32 years, and in Idaho recovery time was estimated as 27 years (Sankey et al. 2008). Slower recovery trajectories may occur on sites with poor initial recruitment (Ziegenhagen and Miller 2008) and recovery could take much longer for fires where recruitment from existing local seed failed (Welch and Criddle 2003).

The pace at which recovery shrub structure occurs in sagebrush is of great interest in attempting to understand dynamics of bird populations following disturbance. It also provides useful proxy information about the historic fire regime based on the assumption that the average frequency of large fires was not greater than the average time required for sagebrush to recover (Wright and Bailey 1982). Numerous bird species are considered sagebrush obligates (Greater Sage-Grouse [*Centrocercus urophasianus*], Sage Sparrow [*Amphispiza belli*], Sage Thrasher [*Oreoscoptus montanus*], Brewer’s Sparrow [*Spizella breweri*]) or near obligates (Gray Flycatcher [*Empidonax wrightii*], Green-tailed Towhee [*Pipilo chlorurus*]) and their preferences for particular canopy conditions likely reflect habitat conditions that existed under historic disturbance regimes under which they evolved. Thus, understanding the stage of post-fire habitat succession where individual species reach their maximum abundance, especially those that are obligates to sagebrush communities, may be informative in understanding historic patterns of disturbance.

The principal goal of this study is to explore bird diversity, and dynamics of bird communities as they relate to post-fire vegetation recovery in mountain big sagebrush, identify habitat features most strongly associated with gradients of community organization, and to identify species that may serve as indicators of different stages of secondary succession.

METHODS

Study area

The Sheldon National Wildlife Refuge (SNWR), located in northwestern Nevada, USA (Figure 4.1), includes over 230,000 ha of sagebrush and associated habitats, most of which occurs as a mosaic of low sagebrush (*Artemisia arbuscula*) and big sagebrush, with the higher elevations supporting the mountain big sagebrush subspecies. Domestic livestock have been excluded from the refuge since 1993. The lack of livestock grazing with its associated impacts on fuels and post-fire vegetation succession makes Sheldon an ideal location to study fire ecology in a relatively intact ecosystem. In addition, SNWR exists within one of the largest and least-fragmented areas of sagebrush shrublands within the sagebrush biome (Knick et al. 2003), minimizing landscape influences of anthropogenic habitat fragmentation (Vander Haegen et al. 2000, Knick and Rotenberry 2002). I chose study areas within the SNWR based on the distribution of mountain big sagebrush communities (Figure 1) and their overlap with mapped fires dating back to

1981. Three areas encompassing 4 large wildfires were selected. These included a 914 ha fire that occurred in 1988 on Bald Mountain, a 2,727 ha fire that occurred in 1996 on Catnip Mountain, and two burns on Badger Mountain; a 2,792 ha wildfire that occurred in 1994, and a 15,378 ha fire that occurred in 1999 (not all of which burned in mountain big sagebrush). The Catnip Mountain fire began as a prescribed burn but escaped control and burned over 1000 ha outside of the planned burn area, while the other 3 fires were ignited by lightning strikes.

For each mountain I projected a sampling grid with 500 m spacing and randomly selected 74 or 75 points within the burn perimeter and an equal number in unburned habitat, with the exception of the 1988 Bald Mountain burn where all of the 30 potential points were used. In total I selected 479 sampling locations. Elevations ranged from 1,763 to 2,097 m at Bald Mountain, 1,812 to 2,216 m at Catnip Mountain, and 1,840 to 2,178 m at Badger Mountain. Half of this sample was surveyed in 2007 and the other half in 2008. Additional details on the study area and selection of sampling points can be found in Chapter 3.

Bird densities

I conducted bird surveys during the nesting season between May 23rd and July 4th in 2007 and 2008. I followed standard point count protocols (Ralph et al. 1993) and did not conduct counts during inclement weather. I began counts 20 min after sunrise and continued for no more than 3.5 hrs, ensuring that surveys occurred during periods of peak bird activity. I recorded the method of detection (visual, song, or call) and distance to each bird. To facilitate distance estimation I used laser rangefinders (Leica LRF900).

When birds were not located visually, observers measured the distance to the center of the vegetation patch that the bird was thought to occupy. I surveyed each point two times during the breeding season, with repeat surveys occurring at least 12 days after the initial survey and conducted by a different observer.

Habitat sampling

I measured vegetation at each point count location using two 50 m transects. I recorded the species, height, and intercept of each shrub intercepted by transects (Canfield 1941). I also recorded relative vigor on a scale of 1-4, corresponding to the proportion of the canopy with live vegetation (0-25%, 26-50%, 51-75%, and 76-100%) and averaged to create an index of shrub vigor for each point. I measured herbaceous vegetation and ground cover every 5m along these transects using a 0.2-m^2 frame (40 cm x 50 cm). I modified Daubenmire's (1959) methods in several ways. First, I estimated cover on a continuous scale to the nearest percent rather than in cover classes, and second, I estimated total horizontal cover when viewed from above as opposed to for discrete vertical strata. Within each frame I estimated cover of bare ground, rock, litter, annual grasses, perennial grasses, and forbs. I conducted all vegetation sampling during July of the same year in which the bird surveys occurred for that location. Trees were counted within a variable radius plot; typically, I counted all trees within 50 m (facilitated by the use of a rangefinder), but at some points dense stands made that difficult and a smaller radius of 20 or 30 m was used.

Statistical analysis

To estimate species richness for each strata I generated sampling curves using a rarefaction analysis that randomly aggregates samples (point counts) and expresses diversity in terms of numbers of species using Ecosim software (Gotelli and Enstminger 2010). I used 1000 iterations to calculate 95% confidence intervals. Traditional rarefaction analyses control for differences in abundance (rather than number of samples) by repeatedly drawing a specified number of individuals from a community sample and using probability theory to derive an estimate of species richness and variance for a sample of a given number of individuals (Hurlbert 1971, Heck et al. 1975). One assumption of rarefaction is that the distribution of individuals is random with respect to one another. This assumption is not likely to be upheld in breeding bird communities due to territoriality and perhaps due to inter-species competition as well, but is not necessary if rarefaction is based on samples because they preserve the heterogeneity in the spatial distribution of individuals (Gotelli and Colwell 2001).

Detections of birds made flying over, but not directly using the habitat at a point count were not included. I also excluded non-breeding migrants and those species not well surveyed by this method (raptors, swallows, and Greater Sage-Grouse). The degree of overlap between confidence intervals of estimates is a relative measure of significance in evaluating differences in species diversity among burned and unburned areas for each mountain.

Community analyses were limited to 12 species for which I had previously generated estimates of densities (Chapter 3) using program DISTANCE v5.1 (Thomas et al. 2010). In summary, a series of *a priori* detection function models were ranked for each species by AIC and the best models were used to generate density estimates for each burn and adjacent unburned area. Here I use estimates at the level of individual points that are derived from those same models, and refer the reader to Chapter 3 for details on model development.

I conducted an Indicator Species Analysis (ISA: Dufrene and Legendre 1997) to identify bird species strongly associated with mature and successional vegetation phases. I classified the 1999 burn as early-stage, 1994 and 1996 burns as mid-stage, and the 1988 burn as late-stage canopy recovery. Unburned sites were classified as mature. The ISA generates an indicator value for each species in each group of interest between 0 and 100. This index is derived from data on both abundance and frequency. I used Monte Carlo simulations with 5000 randomizations to test for significance of indicator values, and P-values thus represent the probability of a similar or stronger value from randomized data.

I used Nonmetric Multidimensional Scaling (NMS; Mather 1976, Kruskal 1964) to ordinate point count survey stations in “species space”. NMS is an iterative multivariate ordination technique that uses ranked distances among sample units (McCune and Grace 2002). It is useful to explore patterns in community data and for visualizing structure in relation to habitat elements.

Data from both years were included. I first relativized species data by their annual maxima to reduce the influence of the single most abundant species (Brewer’s Sparrow) and amplify the signal of other widespread species that occur at much lower densities. As reported in Holmes (Chapter 3), most species densities did not differ significantly between the 2 years of surveys, but Brewer’s Sparrow was more than twice as abundant in 2007 than 2008. Despite the large difference between years the patterns of relative abundance among mountains and burn histories were similar. By relativizing by species annual maxima I remove any signal in the data associated with annual variation and focus the analysis on broader spatial patterns of community organization.

I used Euclidean (Pythagorean) distances as opposed to a proportional distance measure because variation in overall bird abundance can occur in this system without much change in the proportional representation of individual species. I assessed dimensionality by conducting a series of ordinations in the autopilot mode of PCORD (McCune and Mefford 2009). Ordinations were conducted with one, two, three, or four dimensional solutions. To evaluate whether the analyses were extracting stronger axes in species space than expected by chance, I conducted Monte Carlo tests using values obtained from 50 real runs and 50 runs with randomized data for each level of dimensionality. A three dimensional ordination was selected as the best solution because stress was significantly lower than expected by chance and because the small reduction in stress achieved at 4 dimensions did not justify the additional complexity. A final 3 dimensional ordination was performed using the starting point from the previous run and employing an additional 125 runs with a maximum of 500 iterations per run.

Correlations between scores on ordination axes and habitat elements at each point count were assessed using a matrix containing information on time since fire, elevation, and vegetation variables, and patterns of individual species abundances were assessed visually and through linear correlations with ordination axes scores. For the unburned areas where fire histories are unknown, but that have likely not burned in the past 75 years I coded the number of growing seasons since fire as 30 years. This reflects the assumption that vegetation structure stabilizes as shrub cover reaches an asymptote along the recovery trajectory and is based on data from these study sites (Chapter 3) as well as information published in the literature (Lesica 2007, Sankey et al. 2008, Ziegenhagen and Miller 2008, Baker 2011). The fires included in this study appear to be on a shrub canopy cover recovery trajectory of about 20-30 years, in line with published estimates for other mountain big sagebrush communities, but I elected to use the larger number because certain attributes of shrubs that may be important to nesting birds such as accumulation of dead branches around the base or elongate “tree-like” structure typically take 30-35 years (Rick Miller, pers. comm.).

To test for differences in bird communities between unburned and burned portions of each of the study areas I employed pair-wise comparisons of the relativized density matrix using Multi-response Permutation Procedures (MRPP; Mielke 1984, Mielke and Berry 2001). This method tests a null hypothesis of no treatment effect between 2 or more groups of entities. Euclidean distances were used to calculate a distance matrix and average within-group distances are calculated to index dispersion of the groups in species space. The chance-corrected within-group agreement (A) provides a measure of effect size where if heterogeneity within groups equals expectation by chance, then $A = 0$, and when all items are identical within groups then $A = 1$ (McCune and Grace 2002). Indicator species analysis, MRPP and NMS were carried out using PCORD version 6.9 beta (McCune and Mefford 2009).

RESULTS

Species diversity

Bird species richness was greater on unburned portions of all 3 mountains. At Bald Mountain, scaled to a sample size of 30 point counts, mean species richness was 18 (95% CI = 16, 20) for the unburned points and 12 (no CI for full sample) for burned points. Species accumulation curves based on sample rarefaction (Figure 4.2) show that only a few additional species are added in the unburned portion of Bald Mountain given the larger sample (a total of 20 species). At Catnip Mountain species accumulated at a steeper initial rate on the burned than the unburned areas (Figure 4.2) with confidence intervals that only overlap for smaller sample sizes. In total 19 species were recorded on the unburned portions of the mountain and 13 were recorded within the area burned in 1996. At Badger Mountain differences were not as large, with 16 species in total occurring within the boundaries of the 1999 burn, 17 within the 1994 burn, and 20 species in mature, unburned areas (Figure 4.2).

Indicator species analysis

At least one species had significant indicator values for 3 of the 4 stages of canopy recovery (Table 4.1). No species occurred at their maximum abundance or frequency on the 1994 or 1996 burns which made up the middle recovery stage grouping of sample points. Horned Lark, Vesper Sparrow, and Rock Wren (*Salpinctes obsoletus*) had significant indicator values within the early canopy recovery conditions present in the 1999 burn. For Rock Wren, which occurred at similar densities for all the strata at Badger Mountain, but lower densities on Catnip and Bald Mountains (Chapter 3), this appears to be an artifact of the small sample size as point counts from the other stages of succession on Badger Mountain were grouped with points from Catnip and Bald where Rock Wren were less abundant. The Badger 1999 fire is the only fire classified as early successional. Gray Flycatcher, Green-tailed Towhee, Spotted Towhee, and Sage Sparrow had significant indicator values for mature, unburned habitat, and Brewer's Sparrow had a significant indicator value for late-stage canopy recovery. Once again, these results should be interpreted with caution since only the 1988 fire was classified as late-stage canopy recovery.

Community analyses

The chance-corrected statistic of within group agreement for pair-wise comparisons between burned and unburned habitats decreased (indicating a smaller magnitude of effect) with the number of years of recovery. Values of the A-statistic dropped from 0.076 for the 1999 burn, 0.049 for the 1996 burn, 0.034 for the 1994 burn, and 0.028 for the 1988 burn. All of these A-statistic values were significant ($P < 0.0001$).

The Monte Carlo test of 3 dimensional ordinations show that the ordination extracted stronger gradients in the species abundance data than would be expected by chance. The final stress for the 3 dimensional NMS ordination was <0.00001 and final stability was 15.49. Axes in the solution are free from correlation with each other (orthogonality ($100*(1-R^2)$) for pairs of axes ≥ 99.6). Coefficients of determination for the correlations between ordination distances and distances in the original 12 dimensional space were 0.374 for the first axis, 0.297 for the 2nd axis and 0.191 for the third with a total R^2 for the 3 dimensional solution of 0.863.

To facilitate visualization of community structure in relation to years since fire, the ordination was rotated rigidly to maximize the correlation with the first axis (Figure 4.3). Multiple bird species showed moderate to strong correlations with each of the 3 axes of the best ordination (Table 4.2, Figure 4.3). The two most abundant ground nesting species, which had high indicator values for the early stages of post fire habitat, Horned Lark and Vesper Sparrow, were negatively correlated with axis 1. Shrub nesting birds that had significant indicator values for mature canopy conditions (Green-tailed Towhee, Gray Flycatcher, and Sage Sparrow) were positively correlated with axis 1 (Table 4.2, Figure 4.3).

Axis 1 was most strongly correlated with the number of years of recovery ($r = 0.52$), but was also positively correlated with other variables associated with recovery including shrub cover, sagebrush cover, and shrub height. It was negatively correlated with cover of green rabbitbrush which can increase following fire (Table 4.3). Axes 2 and 3 were not strongly correlated with any of the habitat variables.

DISCUSSION

The chronosequence approach carries with it several key assumptions that are seldom evaluated and as such has been criticized as a means of understanding long-term patterns of succession (Johnson and Miyanishi 2008). Most importantly, the approach requires that biotic and abiotic conditions have been similar over the time span of the successional stage being investigated, and in this case, that burned and unburned areas were not determined by inherent site differences. Rocky areas, for example, with low fuel loadings and poor horizontal connectivity of fuels can inhibit the spread of fire. In this case bare ground and rock cover were similar between burned and unburned portions of both mountains, suggesting that boundaries were not determined by environmental differences. Each of the fires that I studied was actively suppressed, and boundaries between burned and unburned areas included lines of suppression. In addition, each of the fires were large fires that occurred under extreme conditions: high fuel loads and hot and dry conditions that facilitated rapid spread into portions of the landscapes that may not have burned under average conditions, and more complete burns within the fire perimeters.

I found strong patterns in bird species diversity and community structure that were related to fire histories and post-fire vegetation succession for sites that ranged from 8 and 20 years of recovery. Sites that hadn't burned in at least 70 years supported the most species; bird diversity was greater in unburned than burned habit for all 4 burns I studied. Among the burned sites, however, diversity did not increase with the number of years of recovery. It is possible this is an artifact of the chronosequence, in that inherent site differences between the mountains studied influence post fire habitats. Badger Mountain had more mountain mahogany and more rocky areas (both within and outside of burns). Some of these mahogany patches were only partially killed during the fires on Badger Mountain, providing refugia for species associated with trees such as Blue-gray Gnatcatcher (*Polioptila caerulea*) and Western scrub-jay (*Aphelocoma californica*).

Indicator species analysis identified Horned Lark and Vesper Sparrow as being associated with early stages of recovery, while Gray Flycatcher, Green-tailed Towhee, and Sage Sparrow had significant indicator values for mature, unburned habitats. Brewer's Sparrow was most strongly associated with late-stages of canopy recovery.

These results are consistent with short term responses to fire that have previously reported for these species (Knick et al. 2005). Gradients of individual species abundances that were responsible for the observed structure are similar to previous multivariate analyses of shrub-steppe bird habitat associations (Rotenberry and Knick 2002, Knick et al. 2003). Since no strong differences in grass cover existed as a function of burn history (Chapter 3), it appears that the entire suite of species are responding to shrub structure.

MRPP analysis revealed that the magnitude of fires effects on bird communities decreased with years of recovery – the oldest burns were less different from adjacent unburned habitats than were more recent fires. The community ordination captured 86% of the information on the 12 species of birds with 3 synthetic axes – all of which contributed to describe patterns of spatial co-variation in bird species distribution. The first axis was correlated principally with variables associated with the progression of secondary vegetation succession such as increases in big sagebrush and overall shrub cover, increases in shrub height, and decreases in green rabbitbrush cover. Those species with high indicator values for early successional and for mature canopy conditions were all correlated with the first ordination axis. Most bird species also were correlated with one or both of the other 2 axes which also describe structure in the bird community, but a lack of relationships between these axes and the habitat variables I measured makes interpretation difficult.

I did not observe a hump-shaped relationship between diversity and time since disturbance, even when estimates are scaled to reference sites within each mountain. It is possible that 20 years is simply not enough time to have reached a maximum diversity and that observed pattern represents only the initial part of a hump shaped relationship, but with only 4 fires there are really too few data points to explore this in depth. If fire is absent for extended periods mountain big sagebrush communities can transition into juniper or pinyon woodlands if a seed source is nearby (Miller and Tausch 2001). Initial phases of woodland expansion likely favor greater avian diversity as a function of added structure and heterogeneity. Woodland birds initially complement the assemblage of birds associated with sagebrush habitats. As tree canopy cover increases, as is common in recent woodland expansions (Miller 2005), however, the shrub layer declines due to competitive exclusion. There is a commensurate decline in most sagebrush associated birds (Knick et al. 2003) although Green-tailed Towhee density showed a curvilinear response to the amount of juniper the surrounding landscape (Noson et al. 2006). Diversity of bird communities in mature juniper woodlands that approximate pre-settlement conditions was greater than mountain big-sagebrush shrublands in central Oregon, primarily as a result of cavity nesting birds (Reinkensmeyer et al. 2008).

In this study, patterns of covariation among bird species reveal strong community structure in mountain big sagebrush habitat. Community dynamics appeared to be a consequence of the differential response of species to changes in the structure of the shrub canopy resulting from secondary succession. Periodic fire in mountain big sagebrush will increase habitat value for Horned Lark and Vesper Sparrow, and may “prime the pump” for increased habitat use by Brewer’s Sparrow at later stages of canopy recovery. Evidence for increased use by Brewer’s Sparrow in late-stage succession comes only from the single fire that occurred in 1988, so results are inconclusive, but suggest additional exploration is warranted. Mature areas within managed landscapes should be protected to provide refugia for the other species in this community that rely on more mature conditions. Gray Flycatcher seems like a good candidate for monitoring as an indicator of mature habitat in mountain big sagebrush without a woodland component.

The presence of cheatgrass (*Bromus tectorum*) and likelihood of conversion to a less desirable ecological state, whether gradual or sudden, should also be considered in mountain big sagebrush when making management decisions surrounding prescribed fire and fire suppression. Our results indicate a gradual return to pre-fire abundance and composition in bird communities following fire, but I caution that these results do not extend to lower elevation, more xeric big sagebrush communities. Although I suspect that patterns of habitat use would likewise follow post-fire recovery of shrub structure, recovery in those systems proceeds at a much slower pace and is more susceptible to interactions with invasive species such as cheatgrass.

ACKNOWLEDGEMENTS

Funding for this research was provided through grants from the United States Forest Service Joint Fire Sciences Program and the United States Fish and Wildlife Service Migratory Birds Program. Logistical support for data collection was provided by the staff at the Sheldon National Wildlife Refuge. I am grateful to Justin Bosler, Michelle Desrosiers, Matt Halley, Adam Hannuksela, Sallie Herman, and Ben Zyla for assistance with data collection.

LITERATURE CITED

Baker, W. L. 2006. Fire and Restoration of Sagebrush Ecosystems. Wildlife Society Bulletin 34(1): 177-185.

Baker, W. L. 2011. Pre-Euroamerican and recent fire in sagebrush ecosystems. In S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distances sampling. Oxford University Press, Oxford, United Kingdom.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39: 388-394.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Denslow, J. S. 1985. Disturbance-mediated coexistence of species. - In: Pickett, S. T. A. and White, P. S. (eds), The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp. 307-323.

Douglas, M. E. and J. A. Endler. 1982. Quantitative matrix comparisons in ecological and evolutionary investigations. Journal of Theoretical Biology 99: 777-795.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Fuentes, E., and F. M. Jaksic. 1988. The hump-backed species diversity curve: why has it not been found among land animals? Oikos 53: 139-143

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Gotelli, N. J. and G. L. Entsminger. 2010. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. (http://garyentsminger.com/ecosim.htm. Accessed October 30, 2010)

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242: 344–34

Heck, K. L., Jr., G. van Belle and D. Simberloff. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56: 1459-1461.

Harniss, R. O., and R. B. Murray. 1973. Thirty years of vegetal change following burning of sagebrush-grass range. Journal of Range Management 26:322 - 325.

Heyerdahl, E. K, R. F.Miller, and R. A. Parsons. 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. Forest Ecology and Management 230:660–678.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577-585.

Johnson, E. A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11: 419-431.

Knick, S.T., Dobkin, D.S., Rotenberry, J.T., Schroeder, M.A., Vander Haegen, M., Van Riper, C., 2003, Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats: The Condor, v. 105, no. 4, p. 611-634.

Knick, S. T., A. L. Holmes, and R. Miller. 2005. The role of fire in structuring sagebrush habitats and avian communities. Studies In Avian Biology 30: 63-75.

Knick, S.T., Rotenberry, J.T., 2000, Ghosts of habitats past- Contribution of landscape change to current habitats used by shrubland birds: Ecology, v. 81, no. 1, p. 220-227

Knick, S. T., and Rotenberry, J. T., 2002. Effects of habitat fragmentation on birds breeding in intermountain shrubsteppe. Studies in Avian Biology 25:130-140.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:1-27.

Lesica, P, S. V. Cooper, and G. Kudray. 2007. Recovery of Big Sagebrush Following Fire in Southwest Montana. Rangeland Ecology & Management 60:261-269.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preferences and algal competitive abilities. American Naturalist 112: 23-29.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley & Sons, London. 532 pp.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B. and M. J. Mefford. 2009. PC-ORD. Multivariate Analysis of Ecological Data. Version 6.91 beta MjM Software, Gleneden Beach, Oregon, U.S.A.

Mielke, P.W., Jr. 1984. Meteorological applications of permutation techniques based on distance functions. Pp. 813-830 in P.R. Krishnaiah and P.K. Sen, eds., Handbook ofStatistics, Vol. 4. Elsevier Science Publishers.

Mielke, P. W., Jr. and K. J. Berry. 2001. Permutation Methods: A Distance Function Approach. Springer Series in Statistics. 344pp.

Miller, R. F., and E. K Heyerdahl. 2008. Fine scale variation of historical fire regimes in semi-arid shrubland and woodland: An example from California, USA. International Journal of Wildland Fire 17:245–254.

Miller, R. F., S. T. Knick, et al. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Miller, R. F. and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550-559.

Miller, R. F. and R. J. Tausch. 2001. The role of fire in pinyon and juniper woodlands: a descriptive analysis. Tall Timbers Research Station Miscellaneous Publication No. 11:15–30.

Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. American Naturalist 120: 533-536.

Nelle, P. J., K. P. Reese, and J. W. Connelly. 2000. Long-term effects of fire on sage grouse habitat. Journal of Range Management 53:586-591.

Noson, A. C., R. A. Schmitz, and R. F. Miller. 2006. Influence of fire and juniper encroachment on birds in high elevation sagebrush steppe. Western North American Naturalist 66:343–353

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.

Ralph , C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Field methods for monitoring landbirds. USDA Forest Service Publication, PSW-GTR 144, Albany, CA.

Reed, W. J. 2006. A note on fire frequency concepts and definitions. Canadian Journal of Forest Research 36:1884–1888.

Reinkensmeyer, D. P., R. F. Miller, R. G. Anthony, and V. E. Marr. 2007. Avian community structure along a mountain big sagebrush successional gradient. Journal of Wildland Management 71:1056-1066.

Rotenberry, J. T., R. J. Cooper, J. M. Wunderle, and K. G. Smith. 1995. When and how are populations limited: the roles of insect outbreaks, fire, and other natural perturbations. Pp. 55–84 in T. E. Martin, and D. M Finch (editors). Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York, NY.

Roxburgh, S. H., K. Shea, and B. Wilson. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85:359-371

Saab, V. A., Powell, H. D. W., 2005. Fire and avian ecology in North America: processes influencing pattern. Stud. Avian Biol. 30, 1–13.

Sankey, T., C. Moffet, and K. Weber, 2008. Postfire recovery of sagebrush communities: Assessment using SPOT-5 and very large-scale aerial imagery, Rangeland Ecology and Management, 61:598–604.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual review of ecology and systematic 15: 353-391.

Thomas L, S. T. Buckland, E. A. Rexstad, J. L. Laake, and S. Strindberg. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables. Conservation Biology 14:1145–1160.

Welch, B. L., and C. Criddle. 2003. Countering misinformation concerning big sagebrush.USDA Forest Service Research Paper RMRS-RP-40. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Wiens, J. A., and J. T. Rotenberry. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. Journal of Applied Ecology 22:655–668.

Wright, H.A. & Bailey, A.W., 1982. Fire Ecology: United States and Southern Canada. John Wiley & Sons, New York.

Ziegenhagen, L. L., 2003. Shrub Reestablishment Following Fire in the Mountain Big Sagebrush (Artemisia tridentata Nutt. ssp. vaseyana (Rydb.) Beetle) Alliance: M.S. Thesis, Oregon State University, Corvallis, OR.

Zeigenhagen, L. L. and R. F. Miller. 2009. Postfire Recovery of Two Shrubs in the Interiors of Large Burns in the Intermountain West, USA. Western North American Naturalist 69:195-205.

Table 4.1. Indicator values for species grouped by recovery stage where they occurred at their maximum abundance. No species occurred at their greatest abundance on burns in the middle-stages of recovery. P-values are the odds that an indicator value from random groupings of data were equal to or greater than the observed values from monte carlo tests using 5000 randomizations.

Recovery stage	Species	IV (observed)	IV (random)	P
Early	Horned Lark	26.4	14.8	0.0022
	Vesper Sparrow	32.6	22.9	0.0004
	Rock Wren	21.1	14.4	0.0162
Late	Brewer's Sparrow	36.1	27	0.0002
Mature	Gray Flycatcher	35.6	15.4	0.0002
	American Robin	4.7	5.2	0.5112
	Sage Thrasher	19.9	17.9	0.1484
	Green-tailed Towhee	32.1	18.7	0.0004
	Spotted Towhee	8.6	3.2	0.0124
	Sage Sparrow	17	4.2	0.0002
	Brown-headed Cowbird	6.7	4.5	0.0996
	Western Meadowlark	10.4	8.5	0.1480

Table 4.2. Linear correlation coefficients (r) between bird indices and ordination axes

	Axis		
Species	1	2	3
Gray Flycatcher	0.697	-0.158	0.483
Horned Lark	-0.539	-0.398	0.085
Rock Wren	-0.07	0.513	0.431
American Robin	0.121	0.393	0.002
Sage Thrasher	0.117	-0.767	0.193
Green-tailed Towhee	0.534	0.427	-0.033
Spotted Towhee	0.316	0.264	-0.354
Brewer’s Sparrow	0.25	-0.254	-0.38
Vesper Sparrow	-0.677	0.062	0.13
Sage Sparrow	0.344	-0.213	0.221
Brown-headed Cowbird	0.161	0.183	-0.332
Western Meadowlark	0	-0.056	-0.405

Table 4.3. Linear correlations between habitat variables and ordination axes.

	Axis		
Habitat variable	1	2	3
Years since fire	0.522	-0.007	-0.036
Elevation	-0.14	-0.021	0.153
Shrub cover	0.323	0.046	-0.04
Shrub height	0.208	0.145	-0.031
Shrub vigor	-0.048	0.071	0.099
Big sagebrush cover	0.274	-0.008	0.121
Low sagebrush cover	0.141	-0.032	-0.105
Green rabbitbrush cover	-0.217	-0.004	-0.08
Bunchgrass cover	0.046	0.127	-0.112
Annual grass	-0.089	0.011	-0.058
Forb cover	-0.088	-0.07	-0.038
Bare ground	-0.121	-0.124	0.106
Rock cover	0.03	0.124	0.009
Litter cover	0.178	0.012	-0.043
Mahogany density	0.079	0.11	0.071
Juniper density	-0.003	0.036	-0.155

Figure 4.1. Location of Sheldon NWR in Nevada (inset) and detail of study areas. Shaded areas are mountain big sagebrush, mountain big sagebrush/bitterbrush, or mountain shrub with a sagebrush component. Each dot represents a point count location. The three sampling areas (clockwise from the left) are Bald, Catnip, and Badger Mountains.

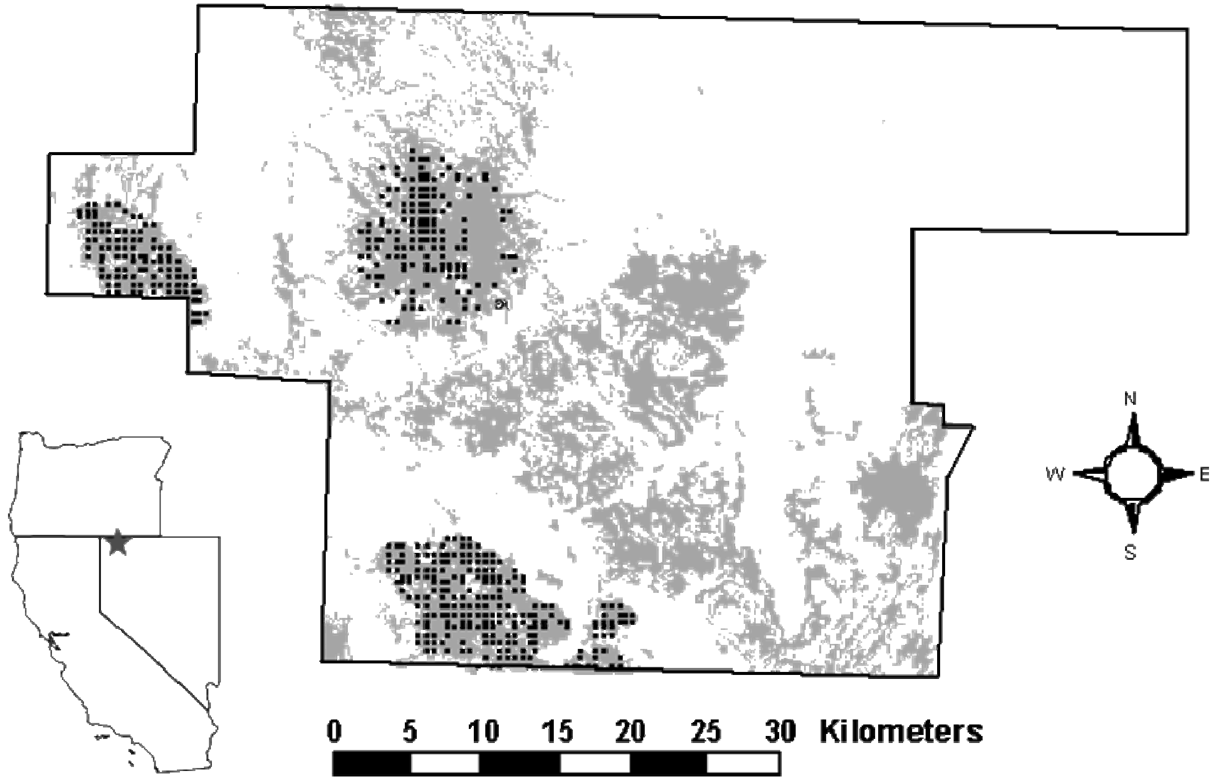
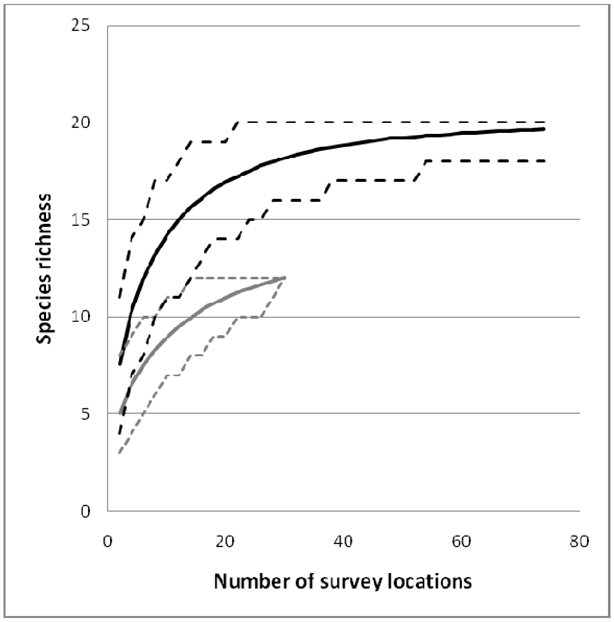


Figure 4.2. Species rarefaction curves based on aggregate samples (point counts) between burned and unburned mountain big sagebrush communities on Sheldon National Wildlife Refuge 2007-2008. Black lines are for unburned areas and gray lines for burned areas. Dashed lines show 95% confidence intervals: a) Bald Mountain 1988 burn at 19-20 years of vegetation recovery, b) Catnip Mountain 1996 burn at 11-12 years of recovery, c) Badger Mountain 1994 burn at 13-14 years of recovery, and d) Badger Mountain 1999 burn at 8 to 9 years of recovery.

a)



b)

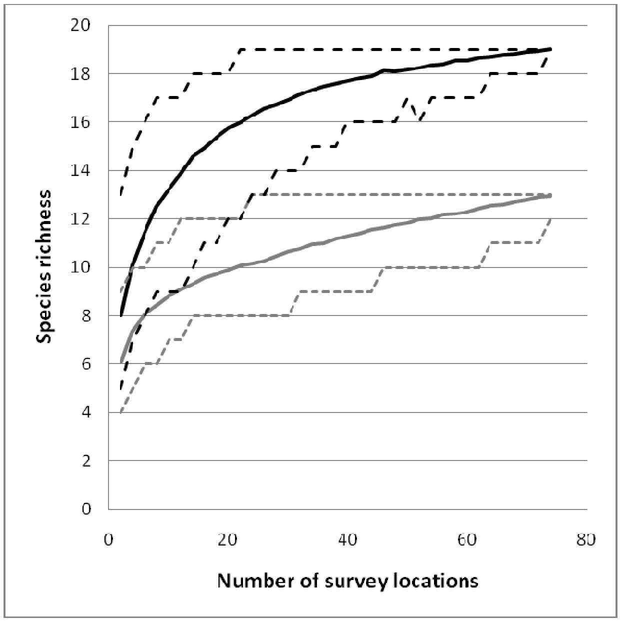
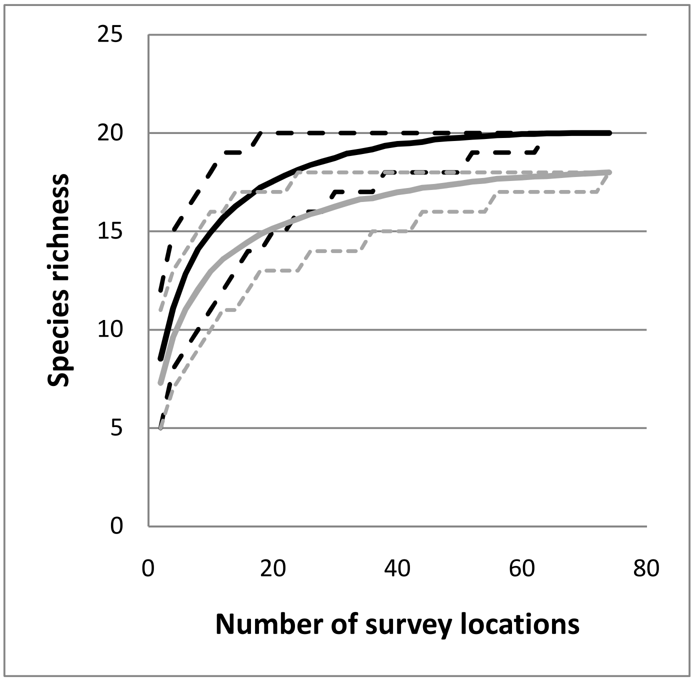


Figure 4.2 (Continued).

c)



d)

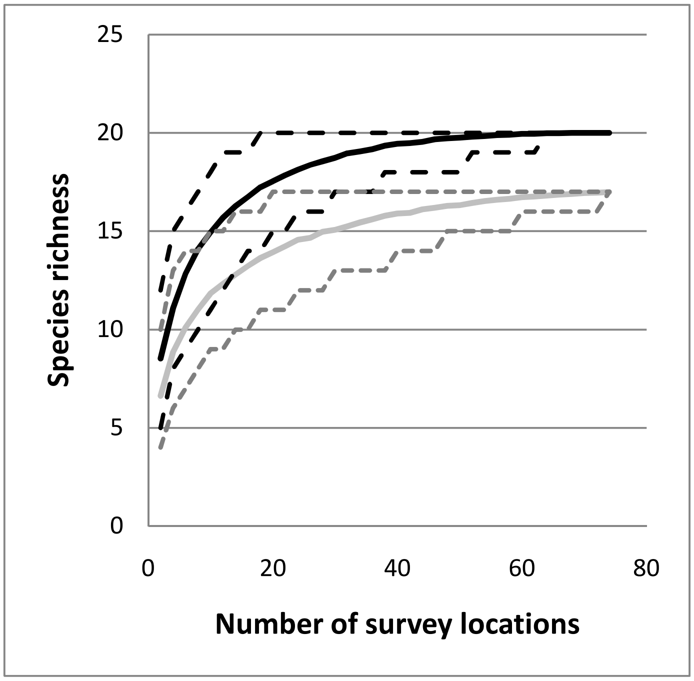


Figure 4.3. Species abundances overlaid on ordination of sampling points in species space. The x axis corresponds to ordination axis 1, and the y axis to ordination axis 2. Symbol size corresponds to species abundance, relativized to each species annual maxima. Open symbols correspond to sampling points in unburned habitats, and shaded symbols correspond to points in one of the burns. The ordination was rigidly rotated to maximize the correlation between the first axis and time-since fire – indicated by the vector labeled “fireyrs”.

Figure 4.3 (Continued)

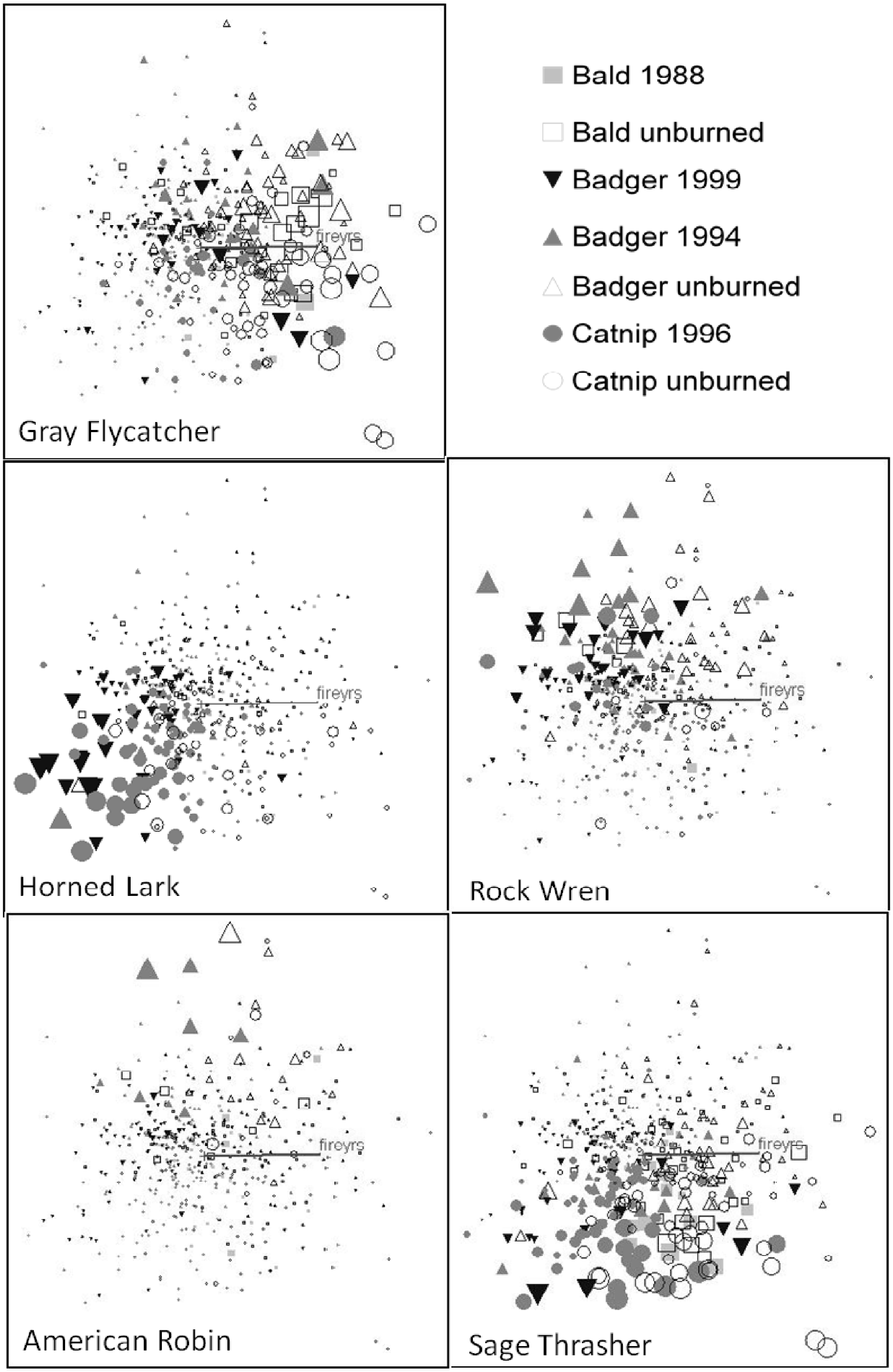
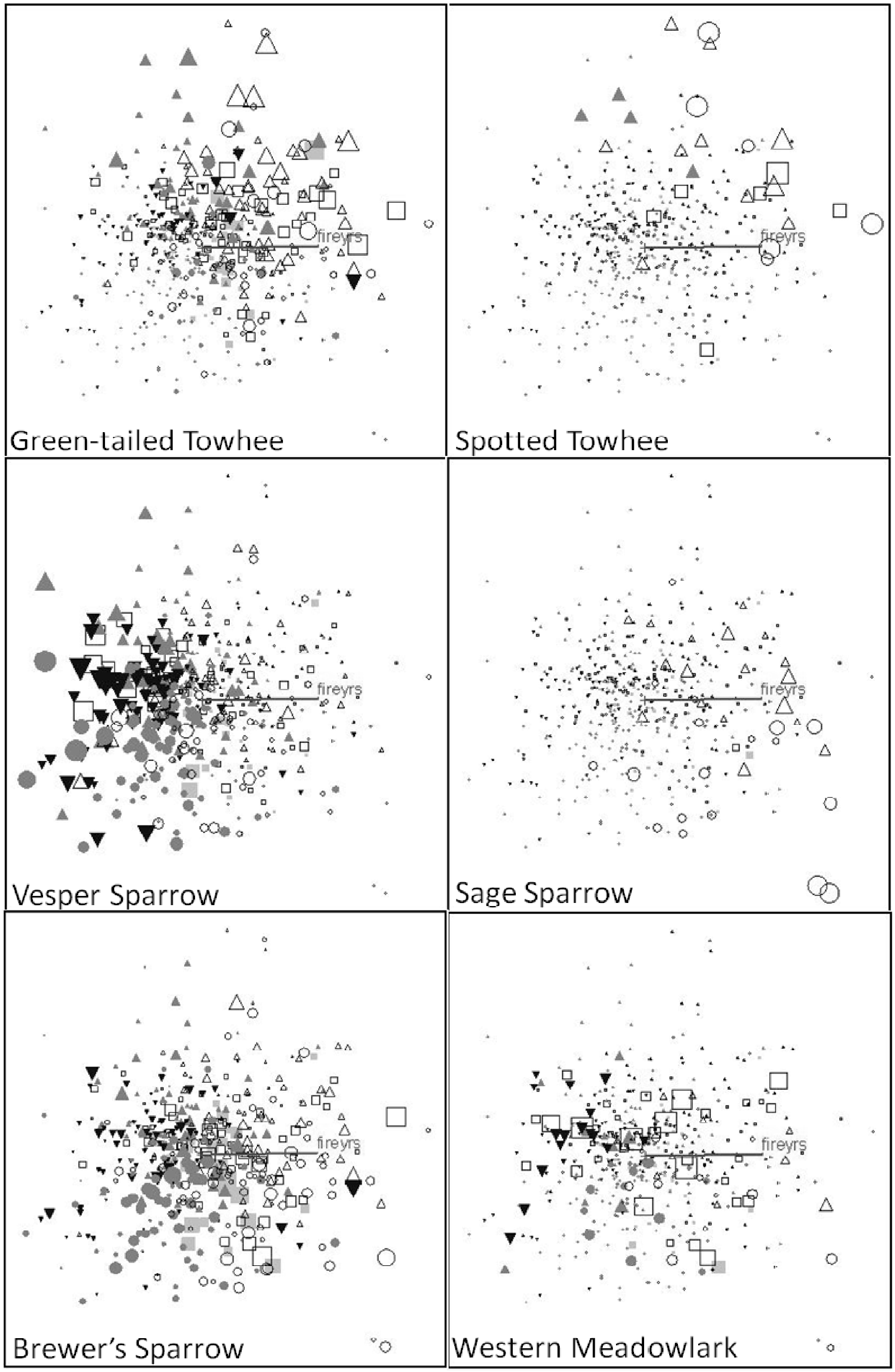


Figure 4.3 (Continued)



CHAPTER 5: CONCLUSIONS

In this dissertation I researched the abundance of small mammals and birds in relation to post-fire vegetation succession in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) habitats. I further explored species diversity and community structure in the bird community through a series of community analyses. This work represents some of the most extensive research on vertebrate densities and community organization in this type of vegetation community, and contributes to the collective knowledge about its fire ecology in general, and several species of management and conservation concern in particular.

Shrub cover and structure were strongly influenced by the amount of recovery time the different burns I studied had experienced. In contrast, cover and structure of understory vegetation appeared to be independent of disturbance histories at the temporal scale that our chronosequence of study plots investigated. Post-fire grass and forb cover were a function of pre-burn condition. With the exception of Belding's Ground Squirrel, patterns of mammal abundance were not related strongly to phases of vegetation succession, suggesting that shrub cover, within the range expressed on our study sites, is not an important determinant of the other species distribution or abundance.

In contrast, the bird community was organized along a gradient of recovery time that correlated strongly with shrub canopy recovery rates. Individual species had different patterns of density in relation to fire histories, with several species demonstrating increased density in the early phases of shrub canopy recovery that waned on sites that were further along. Others showed effects that persisted for at least two decades based on our chronosequence.

My research, which included spatially extensive vegetation sampling and photo documentation, will provide a baseline for the Sheldon National Wildlife Refuge from which to measure vegetation change into the future. It also provides insight into when and where to use prescribed burning or to suppress fires by elucidating the timeline that each bird species is expected to recover to pre-burn levels.

LITERATURE CITED

Baker, W. L. 2011. Pre-Euroamerican and recent fire in sagebrush ecosystems. In S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Beck, J. L., J. W. Connelly and K. P. Reese. 2008. Recovery of Greater Sage-Grouse Habitat Features in Wyoming Big Sagebrush following Prescribed Fire. Restoration Ecology 17(3): 393-403

Blaisdell, J. P., Murray, R. B. and E. D. McArthur, 1982. Managing intermountain rangelands – sagebrush-grass ranges. General Technical Report INT-134., U.S. Department of Agriculture Forest Service, Intermountain Research Station.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L Laake, D. L. Borchers and L. Thomas. 2001. Introduction to Distance Sampling: Estimating abundance of biological populations. Oxford University Press. 448 pages.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388-394.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117–145.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

d'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63-87.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43-63.

DeBano, L. F., Neary, D. G., and P. F. Ffolliott. 1998. Fire's Effects on Ecosystems. John Wiley & Sons, Inc. New York, N.Y.

Denslow, J. S. 1985. Disturbance-mediated coexistence of species. - In: Pickett, S. T. A. and White, P. S. (eds), The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp. 307-323.

Diefenbach, D. R., D. W. Brauning, and J. A. Mattice. 2003. Variability in grassland bird counts related to observer differences and species detection rates. Auk 120:1168–1179.

Dobkin, D. S., and J. D. Sauder. 2004. Shrubsteppe landscapes in jeopardy. Distributions, abundances, and the uncertain future of birds and small mammals in the Intermountain West. High Desert Ecological Research Institute, Bend, OR.

Douglas, M. E. and J. A. Endler. 1982. Quantitative matrix comparisons in ecological and evolutionary investigations. Journal of Theoretical Biology 99: 777-795.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Feldhamer, G. A. 1979. Vegetative and edaphic factors affecting abundance and distribution of small mammals in Southeast Oregon. The Great Basin Naturalist, 39:207-218.

Fieller, E. C. 1940. The biological standardization of Insulin, Supplement to Journal of the Royal Statistical Society 7:1-64.

Fuentes, E., and F. M. Jaksic. 1988. The hump-backed species diversity curve: why has it not been found among land animals? Oikos 53: 139-143

Gano, K., and W. H. Rickard. 1982. Small mammals of a bitterbrush-cheatgrass community. Northwest Science, 56:1-7.

Germano, D. J., and D. N. Lawhead. 1986. Species diversity and habitat complexity: Does vegetation organize vertebrate communities in the Great Basin? Great Basin Naturalist 46:711-720.

Gibbs, J. P. and D. G. Wenny. 1993. Song output as a population estimator: effect of male pairing status. Journal of Field Ornithology. 64:316–322.

Gooding, J. W. 1970. Breeding biology of the Sage Thrasher. Master's Thesis. Central Washington State College, Ellensburg.

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Gotelli, N. J. and G. L. Entsminger. 2010. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. (http://garyentsminger.com/ecosim.htm. Accessed October 30, 2010)

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242: 344–34

Hansen, C. G., 1956. An ecological survey of the vertebrate animals on Steen's Mountain, Harney County, Oregon. Ph.D. dissertation, Oregon State College, Corvallis, 199pp.

Heck, K. L., Jr., G. van Belle and D. Simberloff. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56: 1459-1461.

Hedlund, J. D. and W. H. Rickard. 1981. Wildfire and the short-term response of small mammals inhabiting a sagebrush-bunchgrass community. Murrelet, 62(1): 10-14.

Harniss, R. O., and R. B. Murray. 1973. Thirty years of vegetal change following burning of sagebrush-grass range. Journal of Range Management 26:322 - 325.

Heyerdahl, E. K, R. F.Miller, and R. A. Parsons. 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. Forest Ecology and Management 230:660–678.

Holmes, A. L. 2007. Short term effects of a prescribed burn on songbirds and vegetation in mountain big sagebrush. Western North American Naturalist 67(2):292-298

Holmes, A.L., and R. F. Miller. 2010. State-and-Transition Models for Assessing Grasshopper Sparrow Habitat Use. Journal of Wildlife Management 74: *in press*

Humple, D., and A. L. Holmes. 2006. Effects of a fire on a breeding population of Loggerhead Shrike in sagebrush steppe habitat. Journal of Field Ornithology 77:21-28.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577-585.

Jehle, G., J. A. Savidge, and N. B. Kotliar. 2006. Green-tailed Towhee response to prescribed fire in mountain shrubland. The Condor 108(3): 634-646

Johnson, E. A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11: 419-431.

Johnson, K. H., R. A. Olson, and T. D. Whitson. 1996. Composition and diversity of plant and small mammal communities in tebuthiuron-treated sagebrush (Artemisia tridentata). Weed Technology 10:404–416.

Kerley, G. I. H. 1992. Ecological correlates of small mammal community structure in the semi-arid Karoo, South Africa. Journal of Zoology 227:17–27.

Koehler, D. K., and S. H. Anderson. 1991. Habitat use and food selection of small mammals near a sagebrush/crested wheatgrass interface in southeastern Idaho. Great Basin Naturalist 51:249–255.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for the avifauna of sagebrush habitats. Condor 105:611-634.

Knick, S. T., A. L. Holmes, and R. Miller. 2005. The role of fire in structuring sagebrush habitats and bird communities. Studies in Avian Biology 30:63-75.

Knick, S.T., Rotenberry, J.T., 2000, Ghosts of habitats past- Contribution of landscape change to current habitats used by shrubland birds: Ecology, v. 81, no. 1, p. 220-227

Knick, S. T., and Rotenberry, J. T., 2002. Effects of habitat fragmentation on birds breeding in intermountain shrubsteppe. Studies in Avian Biology 25:130-140.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:1-27.

Lesica, P, S. V. Cooper, and G. Kudray. 2007. Recovery of Big Sagebrush Following Fire in Southwest Montana. Rangeland Ecology & Management 60:261-269.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preferences and algal competitive abilities. American Naturalist 112: 23-29.

Maier, A. M., B. L. Perryman, R. A. Olson, and A. L. Hild. 2001. Climatic influences on recruitment of 3 subspecies of Artemisia tridentata. Journal of Range Management 54:699–703.

Marques, F.F.C. & Buckland, S.T. (2004) Covariate models for the detection function. Advanced Distance Sampling (eds S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas), pp. 31–47. Oxford University Press,Oxford.

Marques, T.A., L. Thomas, S.G. Fancy and S.T. Buckland. 2007. Improving estimates of bird density using multiple covariate distance sampling. The Auk 127: 1229-1243.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley & Sons, London. 532 pp.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B. and M. J. Mefford. 2009. PC-ORD. Multivariate Analysis of Ecological Data. Version 6.91 beta MjM Software, Gleneden Beach, Oregon, U.S.A.

McGee, J. M. 1982. Small mammal populations in an unburned and early fire successional sagebrush community. J. of Range Management 35:177-180.

Mielke, P.W., Jr. 1984. Meteorological applications of permutation techniques based on distance functions. Pp. 813-830 in P.R. Krishnaiah and P.K. Sen, eds., Handbook ofStatistics, Vol. 4. Elsevier Science Publishers.

Mielke, P. W., Jr. and K. J. Berry. 2001. Permutation Methods: A Distance Function Approach. Springer Series in Statistics. 344pp.

Miller, R. F., and E. K Heyerdahl. 2008. Fine scale variation of historical fire regimes in semi-arid shrubland and woodland: An example from California, USA. International Journal of Wildland Fire 17:245–254.

Miller, R. F., S. T. Knick, et al. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, CA.

Miller, R. F. and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

Miller, R. F. and R. J. Tausch. 2001. The role of fire in pinyon and juniper woodlands: a descriptive analysis. Tall Timbers Research Station Miscellaneous Publication No. 11:15–30.

Miller, R. F., and P. F. Wigand. 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44:465-474.

Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. American Naturalist 120: 533-536.

Nelle, P. J., K. P. Reese, and J. W. Connelly. 2000. Long-term effects of fire on sage grouse habitat. Journal of Range Management 53:586-591.

Newson, S.E., Woodburn, R.J.W., Noble, D.G., Baillie, S.R. & Gregory, R.D. 2005. Evaluating the breeding bird survey for producing national population size and density estimates. Bird Study 52: 42–54.

Norvell, R. E., F. P. Howe, and J. R. Parrish. 2003. A seven-year comparison of relative abundance and distance-sampling methods. Auk 120:1013–1028.

Noson, A. C., R. A. Schmitz, and R. F. Miller. 2006. Influence of fire and juniper encroachment on birds in high elevation sagebrush steppe. Western North American Naturalist 66:343–353.

Olson, R. A., B. L. Perryman, S. Petersburg, and T. Naumann. 2003. Fire effects on small mammal communities in Dinosaur National Monument. Western North American Naturalist 63(1): 50-55.

Ostoja, S. M. 2009. Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. Diversity and Distributions 15: 863-870.

Paige, C., and S. A. Ritter. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, ID.

Parmenter, R. R., and J. A. MacMahon. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: The role of shrubs. Oecologia 59:145–156.

Parmenter, R. R., T. L. Yates, D. R. Anderson, K. P. Burnham, J. L. Dunnum, A. B. Franklin, M. T. Friggens, B. C. Lubow, M. Miller, G. S. Olson, C. A. Parmenter, J. Pollard, E. Rexstad, T. M. Shenk, T. R. Stanley, and G. C. White. 2003. Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. Ecological Monographs 73:1–26.

Peters, E. F., and S. C. Bunting. 1994. Fire conditions pre- and post-occurrence of annual grasses on the Snake River Plain. Pages 31-36 in S. B. Monsen and S. G. Kitchen, compilers. Proceedings—ecology and management of annual grasslands. USDA Forest Service, Intermountain Research Station, General Technical Report INT-GTR-313. Ogden, Utah.

Petersen, K. L., and L. B. Best. 1987. Effects of prescribed burning on nongame birds in a sagebrush community. Wildlife Society Bulletin 15:317–329.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.

Pierson, F. B., P. R. Robichaud, C.A. Moffet, K.E. Spaeth, S.P. Hardegree, P.E. Clark, and C. J. Williams. 2008. Fire effects on rangeland hydrology and erosion in a steep sagebrush dominated landscape, Hydrological Processes 22: 2916-2929.

Price, M. V., N. M. Waser. and T.A. Bass. 1984. Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65(2): 353–356.

Ralph , C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Field methods for monitoring landbirds. USDA Forest Service Publication, PSW-GTR 144, Albany, CA.

Rau B. M., R. R. Blank, J. C. Chambers, and D. W. Johnson. 2007. Prescribed fire in a Great Basin sagebrush ecosystem: dynamics of soil extractable nitrogen and phosphorus. Journal of Arid Environments 71: 362–375.

Rau, B. M., J. C. Chambers, R. R. Blank, and D. W. Johnson. 2008. Prescribed fire, soil, and plants: Burn effects and interactions in the central Great Basin. Rangeland Ecology & Management 61:169-181.

Reed, W. J. 2006. A note on fire frequency concepts and definitions. Canadian Journal of Forest Research 36:1884–1888.

Reinkensmeyer, D.P., R.F. Miller, R.G. Anthony, V.E. Marr and C.M. Duncan. 2008. Winter and early spring bird communities in grasslands, shrubsteppe, and juniper woodlands in central Oregon. Western North American Naturalist 68: 25-35

Reynolds, T. D., T. D. Rich and D. A. Stephens. 1999. Sage Thrasher (Oreoscoptes montanus), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/463 doi:10.2173/bna.463

Robertson, B. A., R. L. Hutto, and J. J. Fontaine. 2010. Evaluating food availability and nest predation risk as sources of bias in aural bird surveys. Journal of Field Ornithology 81: 420-429.

Rogers, L. E., and J. D. Hedlund. 1980. A comparison of small mammal populations occupying three distinct shrub-steppe communities in eastern Oregon. Northwest Science, 54:183-186.

Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: Habitats and environmental complexity. Ecology 50:558–572.

Rotenberry, J. T., R. J. Cooper, J. M. Wunderle, and K. G. Smith. 1995. When and how are populations limited: the roles of insect outbreaks, fire, and other natural perturbations. Pp. 55–84 in T. E. Martin, and D. M Finch (editors). Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York, NY

Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67:213–217.

Roxburgh, S. H., K. Shea, and B. Wilson. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85:359-371

Saab, V. A., Powell, H. D. W., 2005. Fire and avian ecology in North America: processes influencing pattern. Stud. Avian Biol. 30, 1–13.

Sankey, T., C. Moffet, and K. Weber, 2008. Postfire recovery of sagebrush communities: Assessment using SPOT-5 and very large-scale aerial imagery, Rangeland Ecology and Management, 61:598–604.

Schreiber, R. K. 1978. Bioenergetics of the Great Basin pocket mouse, Perognathus parvus. Acta Theriologica, 23: 469-487.

Seefeldt, S.S., Germino, M., Dicristina, K., 2007. Prescribed fires in *Artemisia tridentata* ssp. *vaseyana* steppe have minor and transient effects on vegetation cover and composition. Applied Vegetation Science 10, 249–256.

Shenbrot, G., B. Krasnov, and S. Burdelov. 2010. Long-term study of population dynamics and habitat selection of rodents in the Negev Desert. Journal of Mammalogy 91:776-786.

Shields, W.M. 1977. The effect of time of day on avian census results. Auk 94: 380–383.

Small, R. J., and B. J. Verts. 1983. Responses of a population of Perognathus parvus to removal trapping. Journal of Mammalogy, 64:139-143.

Soule, P. T., P. A. Knapp, and H. D. Grissino-Mayer. 2004. Human agency, environmental drivers, and western juniper establishment during the late Holocene. Ecological Applications 14:96–112.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual review of ecology and systematic 15: 353-391.

Sterling, J. C. 1999. Gray Flycatcher (*Empidonax wrightii*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/458 doi:10.2173/bna.458

Stout, J., A. L. Farris, and V. L. Wright. 1971. Small mammal populations of an area in Northern Idaho severely burned in 1967. Northwest Science. 45:219-226.

Suring, L. H., M. J. Wisdom, R. J. Tausch, R. F. Miller, M. M. Rowland, L. Schueck, and C. W. Meinke. 2005. Modeling threats to sagebrush and other shrubland communities. Chapter 4 in Part II: regional assessment of habitats for species of conservation concern in the Great Basin. Pages 114–149 in M. J. Wisdom, M. M. Rowland, and L. H. Suring, editors. Habitat threats in the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Allen Press, Lawrence, Kansas.

Tevis, L. Jr. 1956. Effect of a slash burn on forest mice. Journal of Wildlife Management 20:405-409.

Thibault, K. M., S. K. Ernest, E. P. White, J. H. Brown, J. R. Goheen. 2010. Long-term insights into the influence of precipitation on community dynamics in desert rodents. Journal of Mammalogy: 91:787-797.

Thomas L, S. T. Buckland, E. A. Rexstad, J. L. Laake, and S. Strindberg. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables. Conservation Biology 14:1145–1160.

Verner, J. and Ritter, L.V. 1986. Hourly variation in morning point counts of birds. Auk 103: 117–124.

Welch, B. L., and C. Criddle. 2003. Countering misinformation concerning big sagebrush.USDA Forest Service Research Paper RMRS-RP-40. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Wiens, J. A., and J. T. Rotenberry. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. Journal of Applied Ecology 22:655–668.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. Ecology 67:365–376.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. Pp. 4-10 in E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller (editors). Proceedings Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. GTR INT-276, USDA, Forest Service, Intermountain Research Station, Ogden, UT.

Wijayratne, U., and D. A. Pyke. 2009. Investigating Seed Longevity of Big Sagebrush (Artemisia tridentata): U.S. Geological Survey Open-File Report 2009-1146, (http://pubs.usgs.gov/of/2009/1146/pdf/ofr20091146.pdf, accessed 28 September, 2010.).

Wright, H. A., and A. W. Bailey. 1982. Fire ecology, United States and southern Canada. John Wiley and Sons, New York, NY.

Young, J. A., R. E. Eckert, and R. A. Evans. 1979. Historical perspectives regarding the sagebrush ecosystem. Pp. 1-13 in The sagebrush ecosystem: a symposium. Utah State University, College of Natural Resources, Logan, UT.

Ziegenhagen, L.L., 2003. Shrub Reestablishment Following Fire in the Mountain Big Sagebrush (Artemisia tridentata Nutt. ssp. vaseyana (Rydb.) Beetle) Alliance: M.S. Thesis, Oregon State University, Corvallis, OR.

Zeigenhagen, L. L. and R. F. Miller. 2009. Postfire Recovery of Two Shrubs in the Interiors of Large Burns in the Intermountain West, USA. Western North American Naturalist 69:195-205.

Zou, J., J. T. Flinders, H. L. Black, and S. G. Whisenant. 1989. Influence of experimental habitat manipulations on a desert rodent population in southern Utah. Great Basin Naturalist 48:435–448.

APPENDICES

APPENDIX A: SUPPLEMENTARY INFORMATION ON SMALL MAMMAL CAPTURES AND DENSITY MODELS

Table A1. Detection function model sets for each mammal species, resolution of the model is specified as either global or at the strata level. For all models without covariates all 3 key functions (Negative exponential, Half-normal, and hazard rate) were estimated and the key funcion with the lowest AIC value was selected. For models with covariates the negative exponential function was not estimated. The number in parenthesis following the key function in the table corresponds with the number of adjustment terms. For half normal models a cosine adjustment was used, while for hazard-rate and negative exponential models simple polynomial adjustments were used.

Species	Model	covariates	Key function	k	ΔAIC	EDR
Peromyscus	global	-	NE (2)	3	0.00	38.3
	global	Shrub cover	Haz (2)	5	1.72	43.2
	global	Stratum	Haz (2)	13	18.29	41.6
	global	Year	HN (2)	4	18.55	56.3
	strata	-	Variable	21	33.19	-
Perognathus	Global	-	NE (2)	3	0.00	30.8
	global	Year	Haz (2)	5	6.34	25.6
	strata	-	Haz (0-1)	11	7.74	-
	global	Shrub cover	HN (2)	4	18.26	50.5
	global	Stratum	Haz (1)	11	50.87	72.3
Lemmiscus	Global	-	NE (2)	3	0.00	23.6
	Global	Shrub cover	Haz (1)	4	0.28	21.7
	Global	Year	HN (1)	3	6.10	36.9
Tamius	Global	Detection type	Haz (0)	2	0.00	14.1
	global	Det type/shrub	Haz (0)	4	4.71	12.5
	Strata	-	Haz (0)/HN	7	8.20	-
	Global	-	Haz (0)	2	9.32	11.4
	Global	Stratum	Haz (0)	6	11.36	12.3
	Global	Time	Haz (0)	3	12.96	14.0
Spermophilus	Global	Det. Type	Haz (2)	5	0.00	68.3
	Global	Det. Type/shrub	Haz (2)	6	1.44	65.9
	Global	-	Haz (0)	2	38.92	58.2
	Strata	-	Haz / HN	7	40.99	-
	Global	Shrub cover	Haz (0)	3	41.27	57.5
	Global	time	Haz (0)	3	41.27	57.7
	Global	stratum	Haz (0)	6	42.97	59.3

Table A2. Trapping web capture totals for nocturnal mammals (excluding juvenile age class individuals) in mountain big sagebrush communities on Badger Mountain, Sheldon National Wildlife Refuge, during June 2006 and June 2007.

Burn	Year	#	PEMA	PEPA	ONLE	LECU	MIMO	SOVA	DIOR	NECI
1999	2006	1	22	21	1	2	0	0	0	0
		2	33	2	0	4	2	0	1	0
		3	26	17	0	0	0	0	0	0
	2007	1	18	6	0	4	0	0	0	0
		2	19	12	0	0	0	0	0	1
		3	6	15	0	0	0	0	0	0
1994	2006	1	24	7	3	0	0	0	0	0
		2	13	21	1	0	0	0	0	0
		3	25	12	2	12	0	0	0	0
	2007	1	15	1	0	0	0	0	0	0
		2	11	11	7	1	0	0	0	0
		3	19	5	0	0	0	0	0	0
control	2006	1	11	8	0	0	0	0	0	0
		2	22	29	2	0	0	0	0	0
		3	12	5	0	0	0	0	0	0
	2007	1	12	17	0	0	0	0	0	0
		2	5	4	0	0	0	0	0	0
		3	6	13	0	0	0	0	0	0

[1] PEMA = *Peromyscus maniculatus*, PEPA = *Perognathus parvus*, ONLE = *Onychomys leucogaster*, LECU = *Lemmiscus curtatus*, MIMO = *Microtus montanus*, DIOR = *Dipodomys ordii*, NECI = *Neotoma cinera*

Table A3. Total number of detections of diurnal small mammals on Bald and Badger Mountains, Sheldon National Wildlife Refuge, during June in 2006-2008. Each plot contained 2.4 km of transect and was surveyed annually.

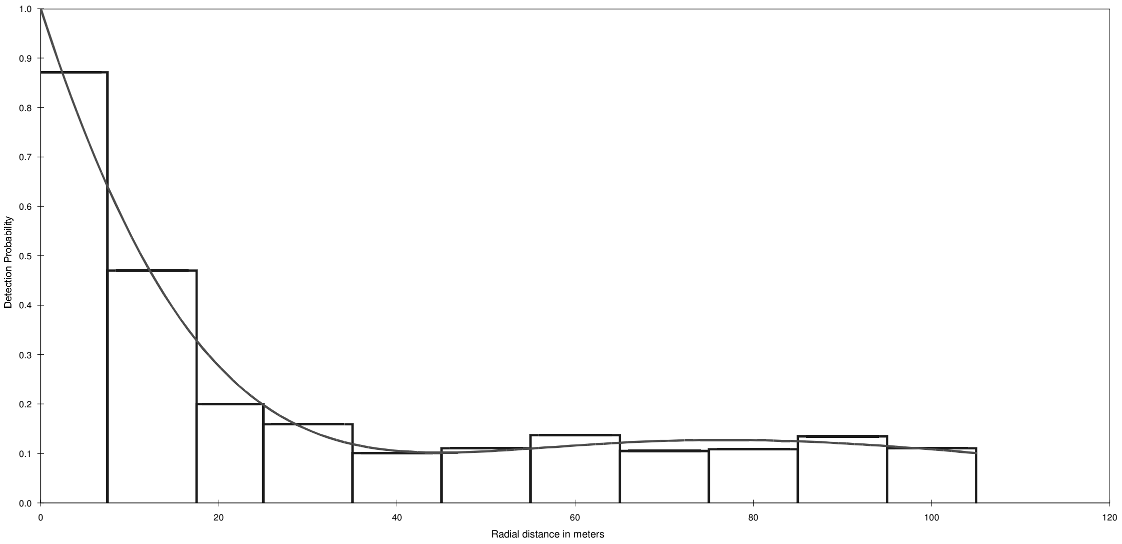
			Species					
Mountain	Year burned	Plot	TAMI	SPBE	SPTO	SPLA	MAFL	SYNU
Badger	1999	1	0	36	4	0	4	0
		2	6	28	0	2	1	0
		3	9	0	10	0	5	0
Badger	1994	1	4	12	7	0	0	0
		2	11	35	5	4	8	0
		3	6	17	8	1	1	2
Bald	1988	1	2	24	1	0	1	0
		2	3	28	0	0	0	2
		3	10	10	0	5	0	0
Badger	unburned	1	13	1	0	2	1	2
		2	12	4	0	1	1	2
		3	3	1	0	1	0	0
Bald	unburned	1	4	5	0	1	3	1
		2	4	1	0	0	0	1
		3	2	1	0	1	0	0

TAMI = Tamius minimus, SPBE = Spemophilus beldingii, SPTO = Spermophilus townsendi, SPLA = Spermophilus lancelata, MAFL = Marmota flaviventris, SYNU = Sylvus nutalli

Figure A1. Select program DISTANCE model output for *Permomyscus maniculatus*.

```
Effort        :    30.00000
 # samples     :    30
 Width         :    105.0000
 Left          :       0.0000000
 # observations:   598

 Model
    Negative Exponential key, k(y) = Exp(-y/A(1))
    Simple polynomial adjustments of order(s) :  2, 4


              Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      18.04        1.324
    A( 2)     -5.871        1.704
    A( 3)      38.93        10.24
    h(0)     0.13653E-02  0.20090E-03      14.71      0.10242E-02  0.18200E-02
    p        0.13287      0.19551E-01      14.71      0.99674E-01  0.17711
    EDR       38.274       2.8159           7.36       33.131       44.215
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


         A( 1)   A( 2)   A( 3)
 A( 1)  1.000   0.770  -0.937
 A( 2)  0.770   1.000  -0.777
 A( 3) -0.937  -0.777   1.000




  Cell          Cut          Observed     Expected   Chi-square
   i           Points         Values       Values      Values
 -----------------------------------------------------------------
   1     0.000        7.50          20        17.25        0.438
   2      7.50        17.5          48        45.83        0.103
   3      17.5        25.0          26        32.95        1.467
   4      25.0        35.0          39        36.55        0.164
   5      35.0        45.0          33        34.85        0.098
   6      45.0        55.0          45        42.89        0.104
   7      55.0        65.0          67        56.91        1.787
   8      65.0        75.0          60        71.54        1.862
   9      75.0        85.0          71        82.67        1.647
  10      85.0        95.0          99        88.30        1.297
  11      95.0        105.          90        88.25        0.035
 -----------------------------------------------------------------
 Total Chi-square value =     9.0013  Degrees of Freedom =  7.00

Probability of a greater chi-square value, P = 0.25256

 The program has limited capability for pooling.  The user should
 judge the necessity for pooling and if necessary, do pooling by hand.
```

Figure A1. (Continued)



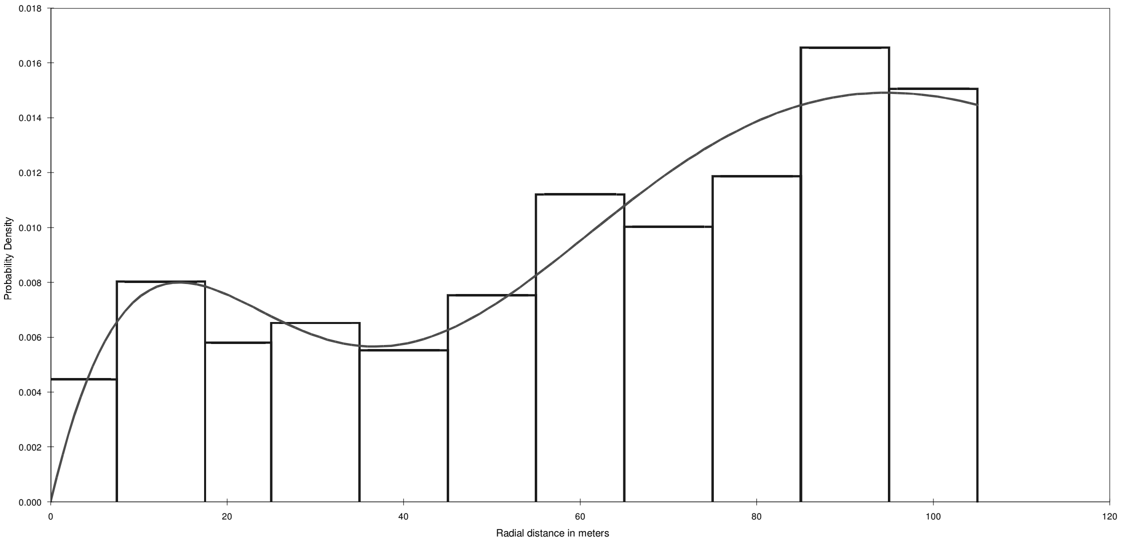
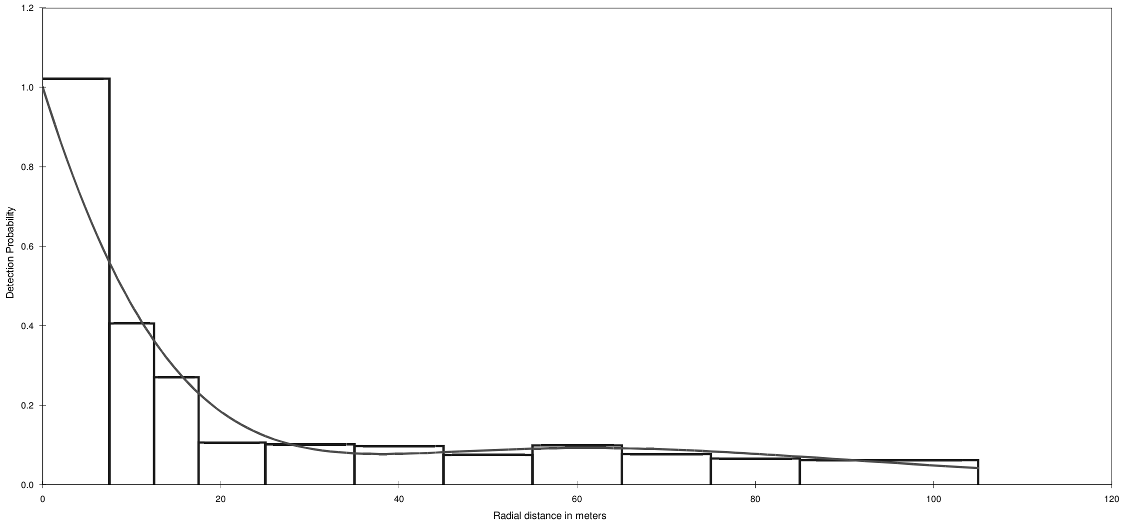


Figure A2. Select program DISTANCE model output for *Perognathus parvus*.

```
Effort        :    30.00000
 # samples     :    30
 Width         :    105.0000
 Left          :       0.0000000
 # observations:   281

 Model
    Negative Exponential key, k(y) = Exp(-y/A(1))
    Simple polynomial adjustments of order(s) :  2, 4


              Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      14.06        1.002
    A( 2)     -9.505        3.316
    A( 3)      81.38        24.83
    h(0)     0.21057E-02  0.40819E-03      19.39      0.14428E-02  0.30733E-02
    p        0.86150E-01  0.16700E-01      19.39      0.59027E-01  0.12574
    EDR       30.819       2.9871           9.69       25.477       37.281
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


         A( 1)   A( 2)   A( 3)
 A( 1)  1.000   0.788  -0.902
 A( 2)  0.788   1.000  -0.774
 A( 3) -0.902  -0.774   1.000



  Cell           Cut           Observed     Expected   Chi-square
   i            Points          Values       Values      Values
 -----------------------------------------------------------------
   1     0.000         7.50          17        11.50         2.629
   2      7.50         12.5          12        13.22         0.112
   3      12.5         17.5          12        12.77         0.046
   4      17.5         25.0          10        15.59         2.007
   5      25.0         35.0          18        16.46         0.144
   6      35.0         45.0          23        18.56         1.063
   7      45.0         55.0          22        25.55         0.493
   8      55.0         65.0          35        32.54         0.187
   9      65.0         75.0          32        36.42         0.537
  10      75.0         85.0          31        36.46         0.818
  11      85.0         105.          69        61.94         0.805
 -----------------------------------------------------------------
 Total Chi-square value =     8.8410  Degrees of Freedom =  7.00

Probability of a greater chi-square value, P = 0.26428

 The program has limited capability for pooling.  The user should
 judge the necessity for pooling and if necessary, do pooling by hand.
```

Figure A2. (Continued)



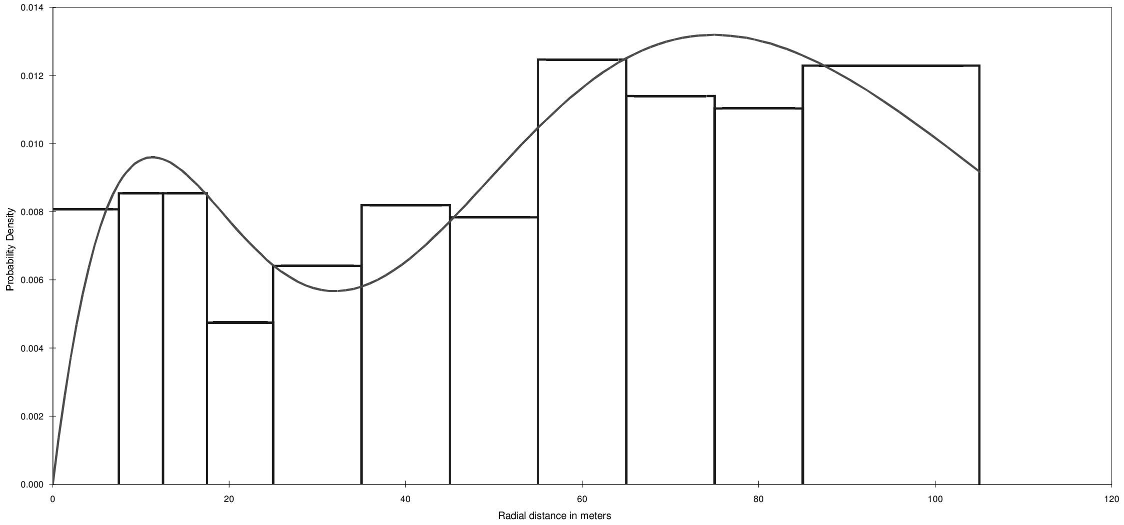
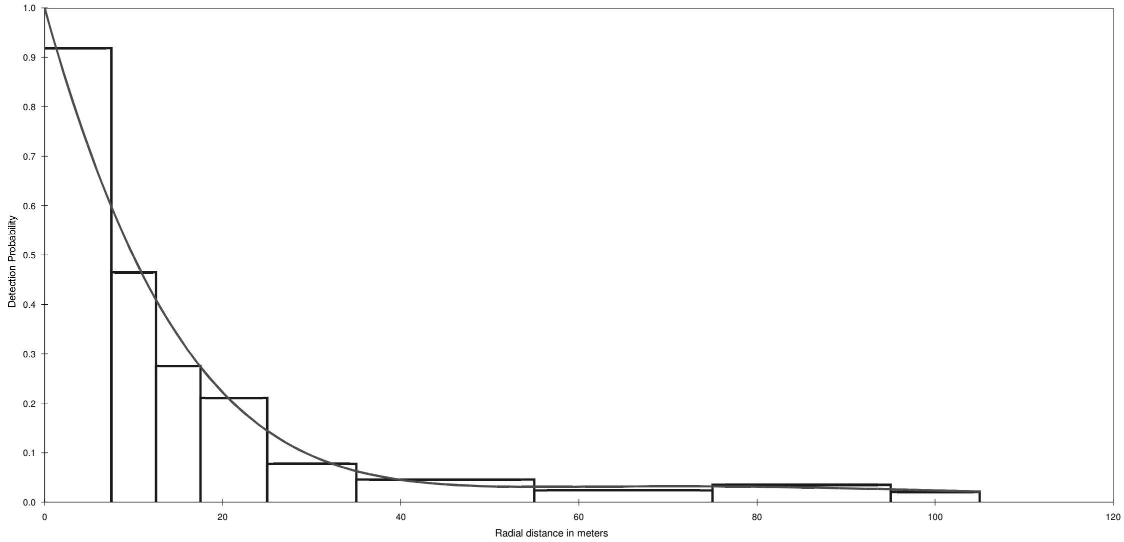


Figure A3. Select program DISTANCE model output for *Lemmiscus curtatus*.

```
Effort        :    30.00000
 # samples     :    30
 Width         :    105.0000
 Left          :       0.0000000
 # observations:   108

 Model
    Negative Exponential key, k(y) = Exp(-y/A(1))
    Simple polynomial adjustments of order(s) :  2, 4


              Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      15.54        2.177
    A( 2)     -6.253        2.023
    A( 3)      23.62        11.89
    h(0)     0.35840E-02  0.81662E-03      22.79      0.22942E-02  0.55988E-02
    p        0.50616E-01  0.11533E-01      22.79      0.32401E-01  0.79071E-01
    EDR       23.623       2.6913          11.39       18.860       29.588
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


         A( 1)   A( 2)   A( 3)
 A( 1)  1.000   0.646  -0.933
 A( 2)  0.646   1.000  -0.778
 A( 3) -0.933  -0.778   1.000



  Cell          Cut           Observed     Expected   Chi-square
   i           Points          Values       Values      Values
 -----------------------------------------------------------------
   1     0.000        7.50          10         7.83        0.602
   2      7.50        12.5           9         9.51        0.027
   3      12.5        17.5           8         9.70        0.299
   4      17.5        25.0          13        12.28        0.042
   5      25.0        35.0           9        11.02        0.369
   6      35.0        55.0          16        13.36        0.524
   7      55.0        75.0          12        15.87        0.944
   8      75.0        95.0          23        19.28        0.717
   9      95.0        105.           8         9.16        0.146
 -----------------------------------------------------------------
 Total Chi-square value =     3.6703  Degrees of Freedom =  5.00

Probability of a greater chi-square value, P = 0.59779

 The program has limited capability for pooling.  The user should
 judge the necessity for pooling and if necessary, do pooling by hand.
```

Figure A3. (Continued).



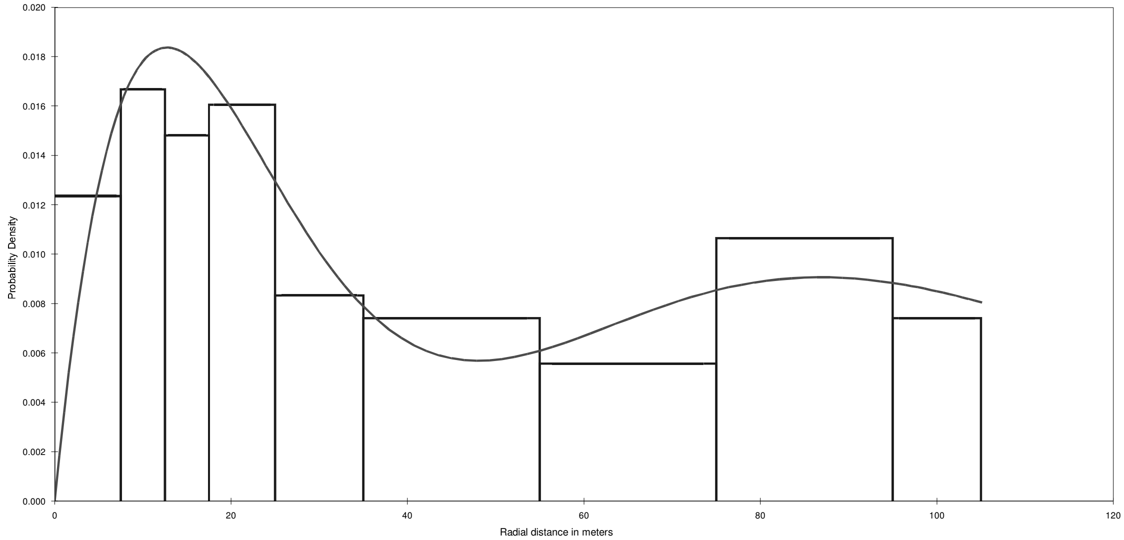
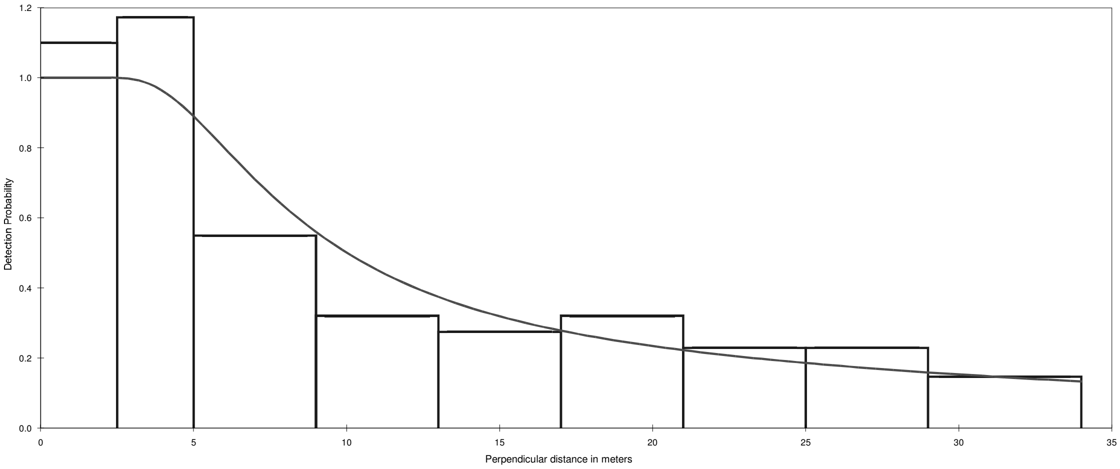


Figure A4. Select program DISTANCE output for *Tamius minimus*.

```
Effort        :    36.00000
 # samples     :    15
 Width         :    34.00000
 Left          :       0.0000000
 # observations:    77

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))

    s = A(1) * Exp(fcn(A(3)))
    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the power parameter.
    Parameter A(3) is the coefficient of level C of factor covariate DET_TYPE.


              Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      7.518       0.7725
    A( 2)      1.822        4.345
    A( 3)      1.784        1.552
    f(0)     0.70932E-01  0.69452E-02       9.79      0.58386E-01  0.86172E-01
    p        0.41465      0.40600E-01       9.79      0.34131      0.50374
    ESW       14.098       1.3804           9.79       11.605       17.127
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


        A( 1)   A( 2)   A( 3)
 A( 1)  1.000   0.386  -0.364
 A( 2)  0.386   1.000  -0.649
 A( 3) -0.364  -0.649   1.000



  Cell          Cut           Observed     Expected   Chi-square
   i           Points          Values       Values      Values
 -----------------------------------------------------------------
   1     0.000        2.50          15       13.65        0.133
   2      2.50        5.00          16       13.16        0.615
   3      5.00        9.00          12       15.63        0.844
   4      9.00        13.0           7        9.97        0.886
   5      13.0        17.0           6        7.02        0.148
   6      17.0        21.0           7        5.42        0.462
   7      21.0        25.0           5        4.43        0.072
   8      25.0        29.0           5        3.75        0.417
   9      29.0        34.0           4        3.97        0.000
 -----------------------------------------------------------------
 Total Chi-square value =     3.5777  Degrees of Freedom =  5.00

Probability of a greater chi-square value, P = 0.61167

 The program has limited capability for pooling.  The user should
 judge the necessity for pooling and if necessary, do pooling by hand.
```

Figure A4. (Continued).

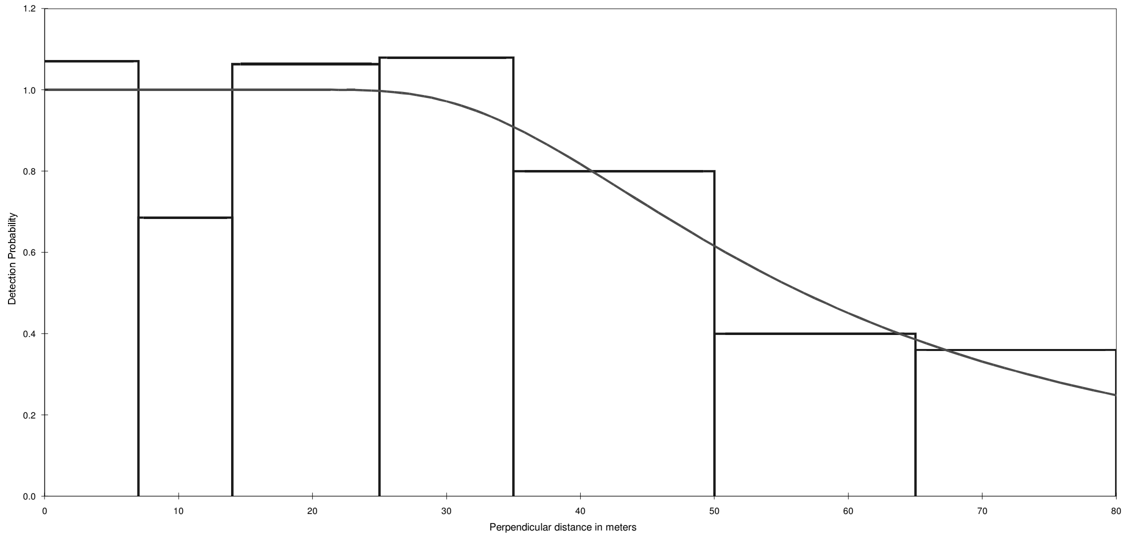


```
                        Estimate      %CV     df     95% Confidence Interval
                         ------------------------------------------------------
Stratum: 1. BD88
Hazard/Cosine
                m        3.0000
                f(0)    0.65099E-01   25.04    11.53 0.37950E-01  0.11167
                p       0.45180       25.04    11.53 0.26338      0.77502
                ESW      15.361       25.04    11.53  8.9549       26.351
Stratum: 2. BDUN
Hazard/Cosine
                m        3.0000
                f(0)    0.69417E-01   30.46     7.69 0.34754E-01  0.13865
                p       0.42370       30.46     7.69 0.21213      0.84628
                ESW      14.406       30.46     7.69  7.2123       28.774
Stratum: 3. BR94
Hazard/Cosine
                m        3.0000
                f(0)    0.66826E-01   19.35    19.22 0.44753E-01  0.99787E-01
                p       0.44012       19.35    19.22 0.29475      0.65720
                ESW      14.964       19.35    19.22  10.021       22.345
Stratum: 4. BR99
Hazard/Cosine
                m        3.0000
                f(0)    0.70414E-01   23.85    12.49 0.42270E-01  0.11730
                p       0.41770       23.85    12.49 0.25075      0.69581
                ESW      14.202       23.85    12.49  8.5254       23.657
Stratum: 5. BRUN
Hazard/Cosine
                m        3.0000
                f(0)    0.78054E-01   17.26    23.06 0.54761E-01  0.11126
                p       0.37681       17.26    23.06 0.26436      0.53710
                ESW      12.812       17.26    23.06  8.9883       18.261

Note: Detection function was modelled globally, and estimated separately in
      each straum, given the covariate values of the observations in the strata.
```

Figure A5. Select program DISTANCE output for *Spermophilus beldingii*.

```
Effort        :    36.00000
 # samples     :    15
 Width         :    80.00000
 Left          :       0.0000000
 # observations:   194

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))
    Cosine adjustments of order(s) :  2, 3

    s = A(1) * Exp(fcn(A(3)))
    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the power parameter.
    Parameter A(3) is the coefficient of level C of factor covariate DET_TYPE.
    Parameter A(4) is the coefficient of the adjustment term of order  2.
    Parameter A(5) is the coefficient of the adjustment term of order  3.


              Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      10.41       0.9398
    A( 2)      2.504        5.286
    A( 3)      1.770       0.2731
    A( 4)    -0.2352       0.2140
    A( 5)    -0.2566       0.1697
    f(0)     0.14632E-01  0.12450E-02       8.51      0.12375E-01  0.17301E-01
    p        0.85427      0.72686E-01       8.51      0.72249       1.0000
    ESW       68.342       5.8149           8.51       57.800       80.806
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


        A( 1)   A( 2)   A( 3)   A( 4)   A( 5)
 A( 1)  1.000   0.266  -0.861   0.362   0.124
 A( 2)  0.266   1.000  -0.352   0.845  -0.689
 A( 3) -0.861  -0.352   1.000  -0.411  -0.053
 A( 4)  0.362   0.845  -0.411   1.000  -0.693
 A( 5)  0.124  -0.689  -0.053  -0.693   1.000
```

Figure A5. (Continued).



```
                        Estimate      %CV     df     95% Confidence Interval
                          ------------------------------------------------------
Stratum: 1. BD88
Hazard/Cosine
                m        5.0000
                f(0)    0.12429E-01   14.06    59.43 0.93948E-02  0.16442E-01
                p        1.0057       14.06    59.43 0.76023       1.0000
                ESW      80.459       14.06    59.43  60.819       106.44
Stratum: 2. BDUN
Hazard/Cosine
                m        5.0000
                f(0)    0.32238E-01   41.45     5.85 0.12091E-01  0.85953E-01
                p       0.38774       41.45     5.85 0.14543       1.0000
                ESW      31.019       41.45     5.85  11.634       82.704
Stratum: 3. BR94
Hazard/Cosine
                m        5.0000
                f(0)    0.16982E-01   15.57    57.48 0.12456E-01  0.23152E-01
                p       0.73608       15.57    57.48 0.53992       1.0000
                ESW      58.886       15.57    57.48  43.193       80.281
Stratum: 4. BR99
Hazard/Cosine
                m        5.0000
                f(0)    0.12862E-01   14.70    61.38 0.96011E-02  0.17230E-01
                p       0.97187       14.70    61.38 0.72548       1.0000
                ESW      77.749       14.70    61.38  58.038       104.15
Stratum: 5. BRUN
Hazard/Cosine
                m        5.0000
                f(0)    0.14976E-01   59.92     4.87 0.35655E-02  0.62900E-01
                p       0.83469       59.92     4.87 0.19873       1.0000
                ESW      66.775       59.92     4.87  15.898       280.47

Note: Detection function was modelled globally, and estimated separately in
      each straum, given the covariate values of the observations in the strata.
```

APPENDIX B: DETAILED STUDY AREA MAPS

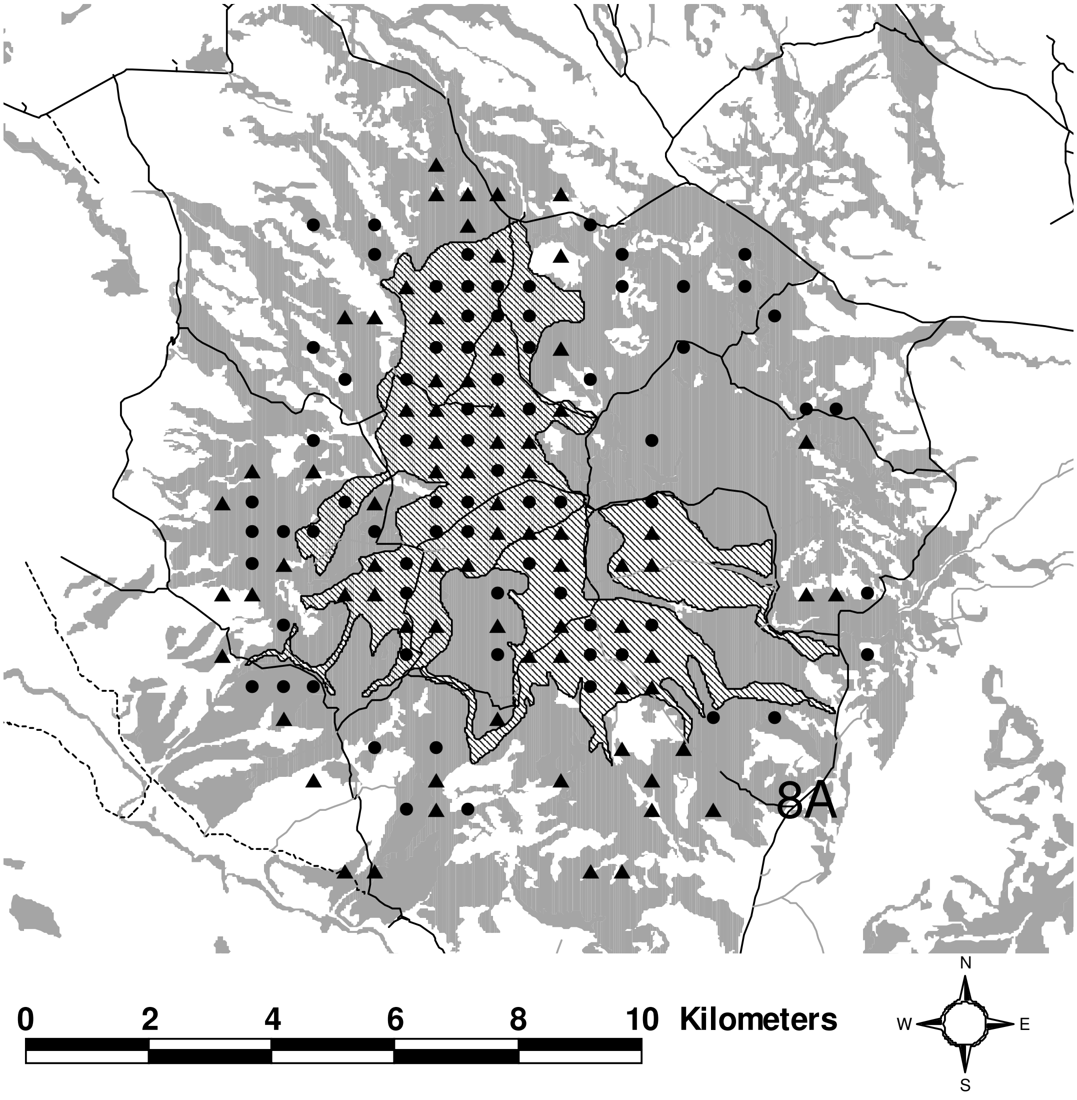


Figure B1. Detail of Catnip Mountain study area. Shading shows mountain big sagebrush, mountain big sagebrush-bitterbrush, or mountain shrub vegetation. Circles are point count locations for 2007, triangles are point count locations for 2008. The hatched area burned in 1996.

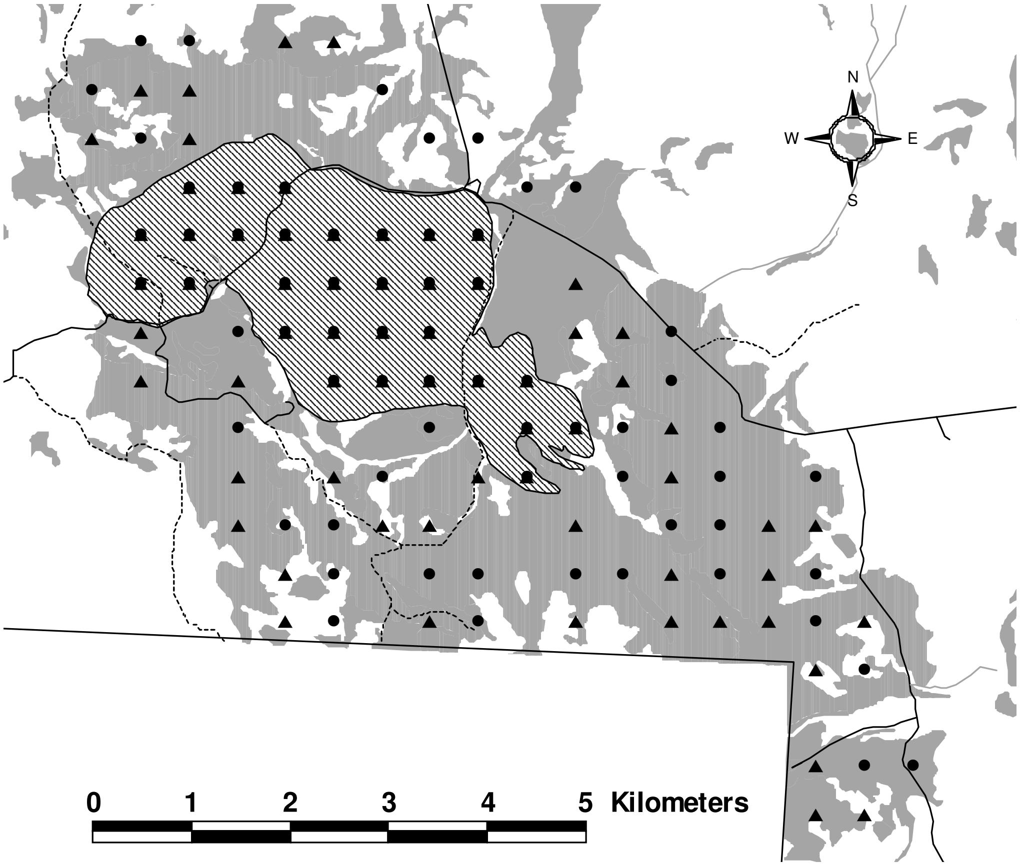


Figure B2. Detail of Bald Mountain study area. Shading shows mountain big sagebrush, mountain big sagebrush-bitterbrush, or mountain shrub vegetation. Circles are point count locations for 2007, triangles are point count locations for 2008. The hatched area burned in 1988.

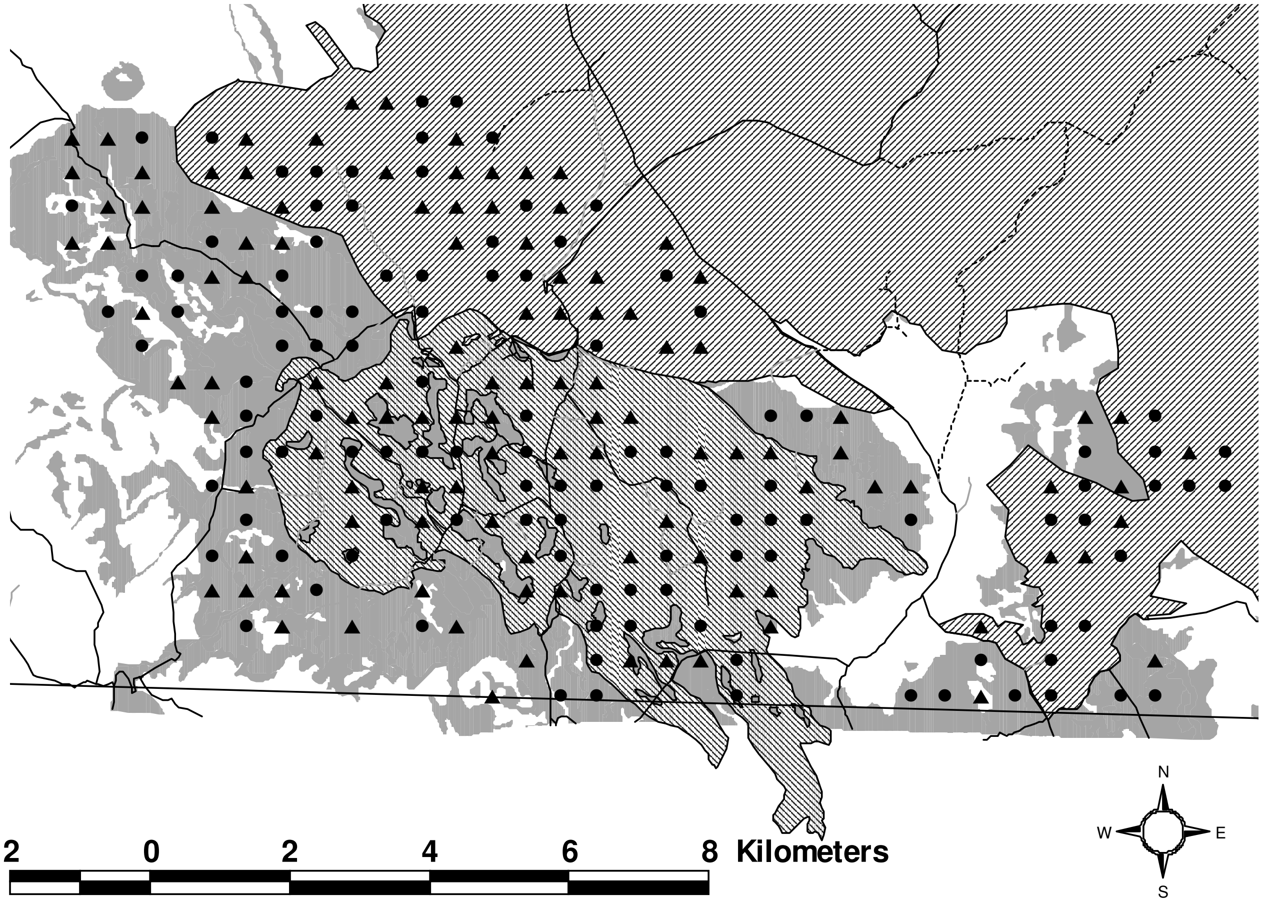


Figure B3. Detail of Badger Mountain study area. Shading shows mountain big sagebrush, mountain big sagebrush-bitterbrush, or mountain shrub vegetation. Circles are point count locations for 2007, triangles are point count locations for 2008. The hatched areas burned in 1999 (upper area) and 1994 (lower area).

APPENDIX C. SUPPLEMENTARY INFORMATION ON MODEL SELECTION AND FINAL BIRD DENSITY MODELS

The following pages show select output from program DISTANCE including the parameter estimates and where covariates are included, the calculated probability of detection for each strata. For models with covariates, the calculated probability of detection is calculated based on covariate values for each point count. For covariates which are factors, parameter estimates corresponding to the last level of a given factor are part of the intercept. Histograms for each species are the probability of detection plotted against radial distance and the probability density plotted against radial distance.

Glossary of terms

Data items:

n - number of observed objects (single or clusters of animals)
k - number of samples
K - point transect effort, typically K=k
ER - encounter rate (n/L or n/K or n/T)
W - width of line transect or radius of point transect
x(i) - distance to i-th observation
s(i) - cluster size of i-th observation

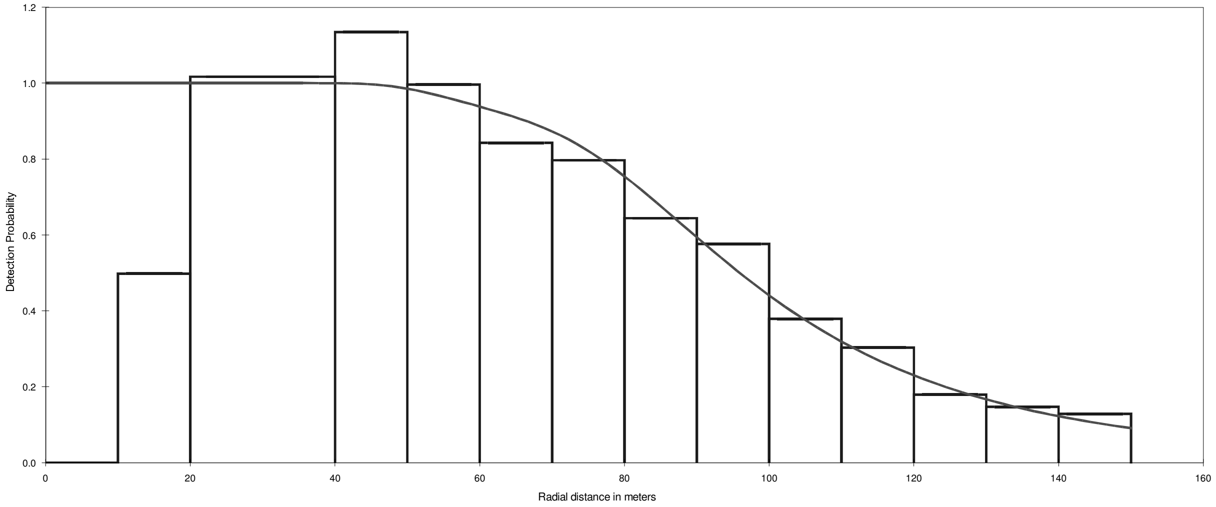
Parameters or functions of parameters:

m - number of parameters in the model
A(I) - i-th parameter in the estimated probability density function(pdf)
h(0) - 2*PI/v
v - PI*W*W*p, is the effective detection area for point transects
p - probability of observing an object in defined area
EDR - for point transects, effective detection radius = W*sqrt(p)
D - estimate of density of animals

Figure C1. Select program DISTANCE model output for Gray Flycatcher.

```
Effort        :    479.0000
 # samples     :   479
 Width         :    150.0000
 Left          :       0.0000000
 # observations:   429

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))

    s = A(1) * Exp(fcn(A(3)))
    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the power parameter.
    Parameter A(3) is the coefficient of level N of factor covariate SING.


             Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate      Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      93.34       0.6732
    A( 2)      4.566        3.074
    A( 3)    -0.4209       0.8991E-01
    h(0)     0.18724E-03  0.71378E-05       3.81      0.17373E-03  0.20180E-03
    p        0.47473      0.18097E-01       3.81      0.44047      0.51165
    EDR       103.35       1.9699           1.91       99.551       107.30
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


        A( 1)   A( 2)   A( 3)
 A( 1)  1.000   0.151  -0.359
 A( 2)  0.151   1.000  -0.023
 A( 3) -0.359  -0.023   1.000
```

Figure C1. (Continued)



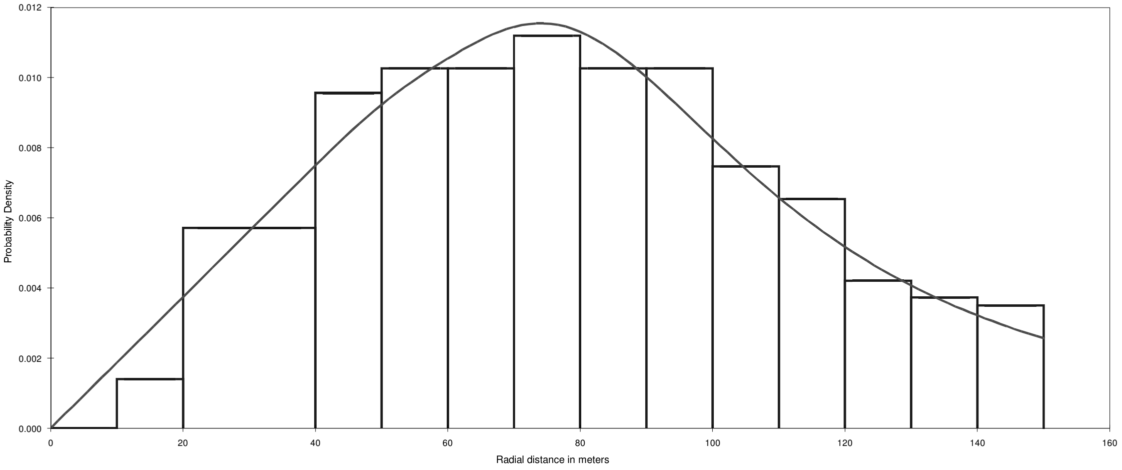


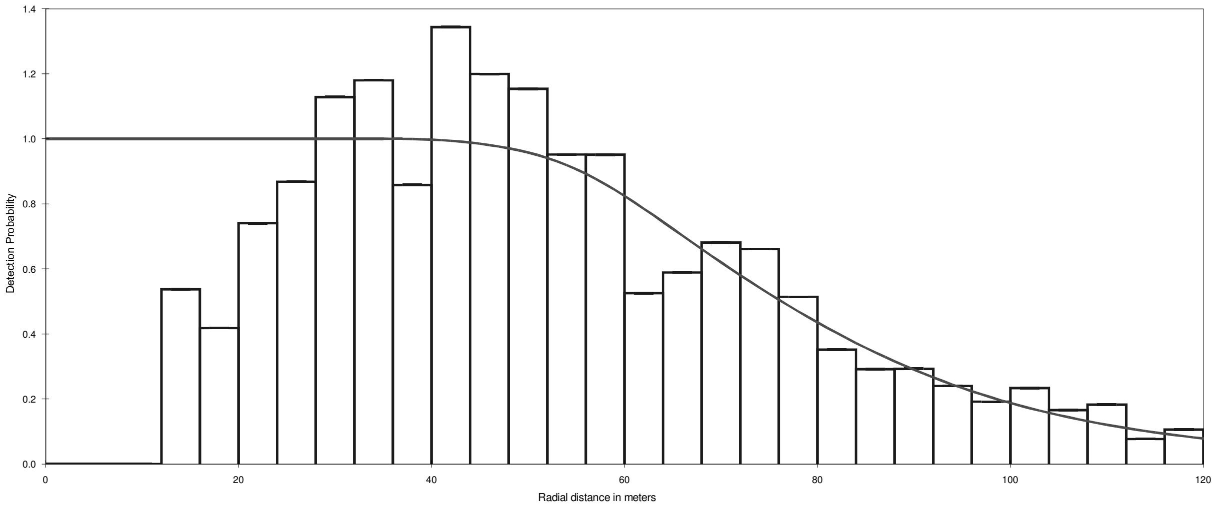
Figure C1. (Continued).

```
                        Estimate      %CV     df     95% Confidence Interval
                       ------------------------------------------------------
Stratum: 1. BR94
Hazard/Polynomial
                m       3.0000
                h(0)   0.18070E-03   10.98    47.66 0.14498E-03  0.22521E-03
                p      0.49191       10.98    47.66 0.39469      0.61309
                EDR     105.20        5.49    47.66  94.213       117.48
Stratum: 2. BR99
Hazard/Polynomial
                m       3.0000
                h(0)   0.20719E-03   14.54    33.76 0.15441E-03  0.27801E-03
                p      0.42902       14.54    33.76 0.31973      0.57565
                EDR     98.249        7.27    33.76  84.769       113.87
Stratum: 3. BRUN
Hazard/Polynomial
                m       3.0000
                h(0)   0.18565E-03    7.40   111.22 0.16036E-03  0.21493E-03
                p      0.47880        7.40   111.22 0.41358      0.55431
                EDR     103.79        3.70   111.22  96.458       111.69
Stratum: 4. BD88
Hazard/Polynomial
                m       3.0000
                h(0)   0.16915E-03   30.94     4.97 0.77618E-04  0.36863E-03
                p      0.52549       30.94     4.97 0.24113       1.0000
                EDR     108.74       15.47     4.97  73.164       161.60
Stratum: 5. BDUN
Hazard/Polynomial
                m       3.0000
                h(0)   0.18274E-03    9.34    67.52 0.15171E-03  0.22011E-03
                p      0.48643        9.34    67.52 0.40384      0.58591
                EDR     104.62        4.67    67.52  95.308       114.83
Stratum: 6. CP96
Hazard/Polynomial
                m       3.0000
                h(0)   0.18913E-03   13.10    36.74 0.14520E-03  0.24635E-03
                p      0.47000       13.10    36.74 0.36082      0.61220
                EDR     102.83        6.55    36.74  90.065       117.41
Stratum: 7. CPUN
Hazard/Polynomial
                m       3.0000
                h(0)   0.18837E-03    7.10   124.13 0.16370E-03  0.21676E-03
                p      0.47189        7.10   124.13 0.41009      0.54300
                EDR     103.04        3.55   124.13  96.051       110.54

Note: Detection function was modelled globally, and estimated separately in
      each straum, given the covariate values of the observations in the strata.
```

Figure C2. Select program DISTANCE model output for Horned Lark.

```
Effort        :    479.0000
 # samples     :   479
 Width         :    120.0000
 Left          :       0.0000000
 # observations:   677

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))

    s = A(1) * Exp(fcn(A(3)) + fcn(A(4)) + fcn(A(5)) + fcn(A(6)) + fcn(A(7)) +
fcn(A(8)))
    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the power parameter.
    Parameter A(3) is the coefficient of level N of factor covariate SING.
    Parameter A(4) is the coefficient of level AH of factor covariate INITIALS.
    Parameter A(5) is the coefficient of level AMH of factor covariate INITIALS.
    Parameter A(6) is the coefficient of level BZ of factor covariate INITIALS.
    Parameter A(7) is the coefficient of level JEB of factor covariate INITIALS.
    Parameter A(8) is the coefficient of level MD of factor covariate INITIALS.


             Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      95.83        1.208
    A( 2)      5.493        2.887
    A( 3)    -0.3365       0.4470E-01
    A( 4)     0.1102       0.1887
    A( 5)    -0.2134       0.7787E-01
    A( 6)    -0.3234       0.7077E-01
    A( 7)    -0.3583E-01   0.6322E-01
    A( 8)    -0.7672E-01   0.6785E-01
    h(0)     0.29460E-03  0.90322E-05       3.07      0.27739E-03  0.31287E-03
    p        0.47146      0.14455E-01       3.07      0.44392      0.50070
    EDR       82.395       1.2631           1.53       79.952       84.913
  ---------  -----------  -----------  --------------  ----------------------

 Sampling Correlation of Estimated Parameters

        A( 1)   A( 2)   A( 3)   A( 4)   A( 5)   A( 6)   A( 7)   A( 8)
 A( 1)  1.000  -0.003  -0.462  -0.230  -0.625  -0.757  -0.658  -0.731
 A( 2) -0.003   1.000   0.045  -0.021   0.020   0.052   0.014  -0.003
 A( 3) -0.462   0.045   1.000  -0.021   0.096   0.257  -0.125   0.139
 A( 4) -0.230  -0.021  -0.021   1.000   0.175   0.189   0.220   0.200
 A( 5) -0.625   0.020   0.096   0.175   1.000   0.497   0.517   0.506
 A( 6) -0.757   0.052   0.257   0.189   0.497   1.000   0.550   0.577
 A( 7) -0.658   0.014  -0.125   0.220   0.517   0.550   1.000   0.589
 A( 8) -0.731  -0.003   0.139   0.200   0.506   0.577   0.589   1.000
```

Figure C2. (Continued)



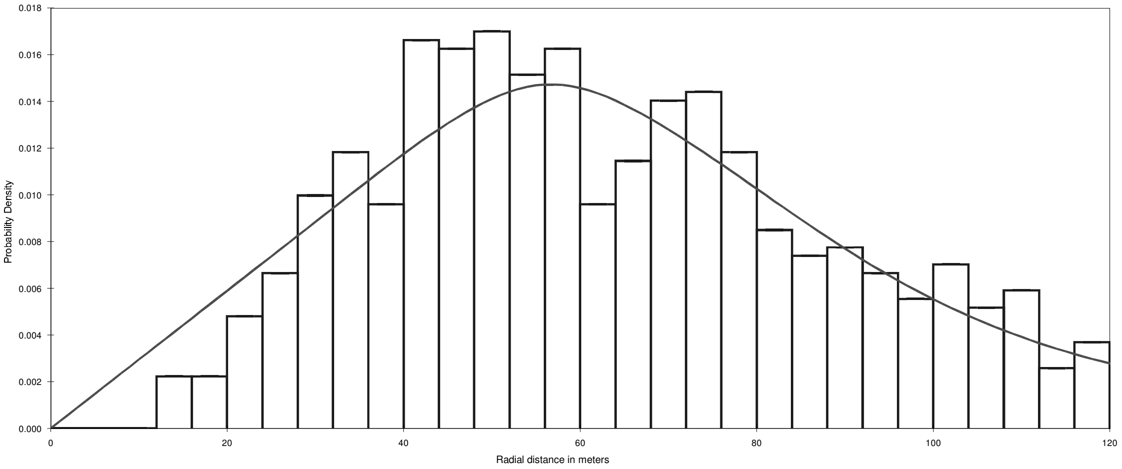


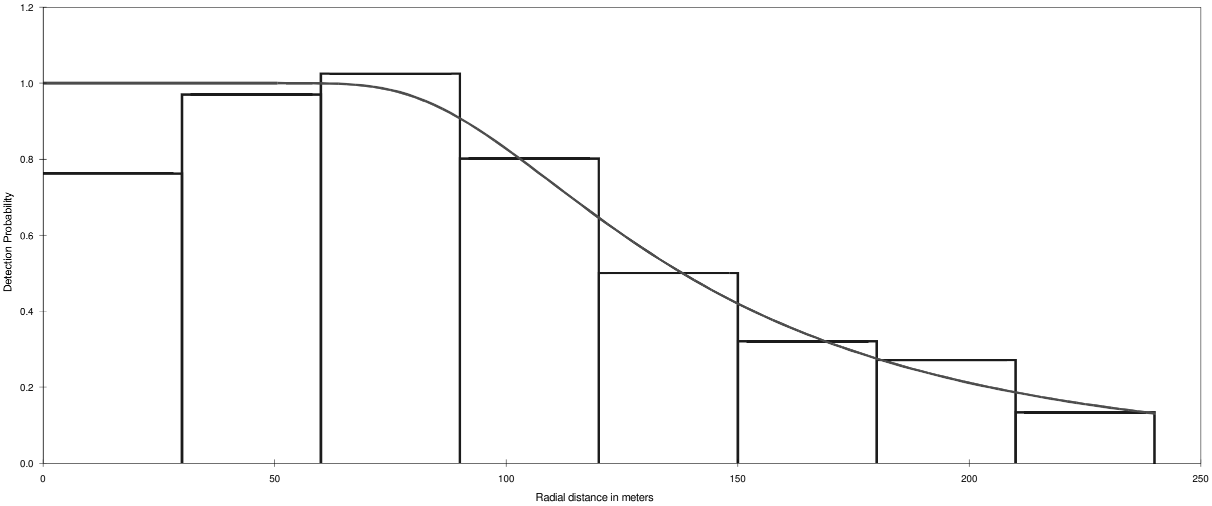
Figure C2. (continued)

```
Estimate      %CV     df     95% Confidence Interval
                        ------------------------------------------------------
 Stratum: 1. BR94
 Hazard/Polynomial
                m       8.0000
                h(0)   0.29412E-03   10.26    63.24 0.23975E-03  0.36083E-03
                p      0.47222       10.26    63.24 0.38492      0.57931
                EDR     82.462        5.13    63.24  74.435       91.353
 Stratum: 2. BR99
 Hazard/Polynomial
                m       8.0000
                h(0)   0.30036E-03    6.24   167.00 0.26559E-03  0.33969E-03
                p      0.46240        6.24   167.00 0.40887      0.52294
                EDR     81.600        3.12   167.00  76.728       86.782
 Stratum: 3. BRUN
 Hazard/Polynomial
                m       8.0000
                h(0)   0.31619E-03   14.98    29.65 0.23320E-03  0.42870E-03
                p      0.43926       14.98    29.65 0.32397      0.59558
                EDR     79.532        7.49    29.65  68.259       92.667
 Stratum: 4. BD88
 Hazard/Polynomial
                m       8.0000
                h(0)   0.23339E-03   25.62     6.92 0.12840E-03  0.42425E-03
                p      0.59509       25.62     6.92 0.32737       1.0000
                EDR     92.570       12.81     6.92  68.415       125.25
 Stratum: 5. BDUN
 Hazard/Polynomial
                m       8.0000
                h(0)   0.31584E-03   21.44    12.85 0.19967E-03  0.49961E-03
                p      0.43974       21.44    12.85 0.27799      0.69560
                EDR     79.576       10.72    12.85  63.147       100.28
 Stratum: 6. CP96
 Hazard/Polynomial
                m       8.0000
                h(0)   0.29395E-03    4.80   269.77 0.26748E-03  0.32303E-03
                p      0.47250        4.80   269.77 0.42996      0.51925
                EDR     82.486        2.40   269.77  78.684       86.472
 Stratum: 7. CPUN
 Hazard/Polynomial
                m       8.0000
                h(0)   0.28416E-03    7.04   119.57 0.24722E-03  0.32661E-03
                p      0.48877        7.04   119.57 0.42524      0.56179
                EDR     83.895        3.52   119.57  78.248       89.949

 Note:Detection function was modelled globally, and estimated separately in
      each straum, given the covariate values of the observations in the strata.
```

Figure C3. Select program DISTANCE model output for Rock Wren.

```
Effort        :    479.0000
# samples     :   479
Width         :    240.0000
Left          :       0.0000000
# observations:   404

Model
   Hazard Rate key, k(y) = 1 - Exp(-(y/A(1))**-A(2))


             Point        Standard    Percent Coef.        95 Percent
 Parameter   Estimate       Error      of Variation     Confidence Interval
 ---------  -----------  -----------  --------------  ----------------------
   A( 1)      121.6        10.29
   A( 2)      2.887        0.4078
   h(0)     0.79402E-04  0.68202E-05       8.59      0.67086E-04  0.93979E-04
   p        0.43729      0.37561E-01       8.59      0.36947      0.51757
   EDR       158.71       6.8160           4.29       145.86       172.68
 ---------  -----------  -----------  --------------  ----------------------


Sampling Correlation of Estimated Parameters


        A( 1)   A( 2)
A( 1)  1.000   0.792
A( 2)  0.792   1.000
```

Figure C3. (Continued)



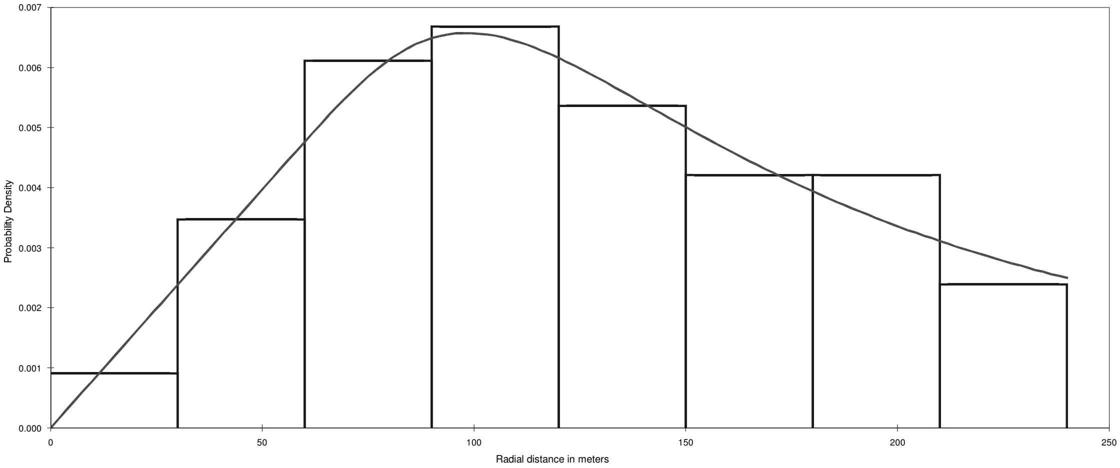
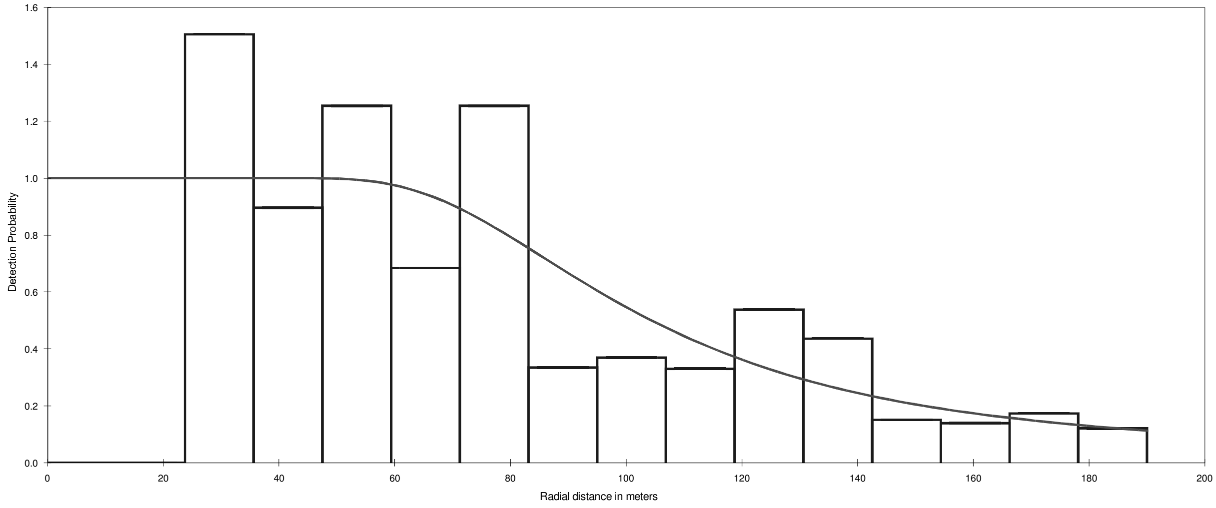


Figure C4. Select program DISTANCE model output for American Robin.

```
Effort        :    479.0000
 # samples     :   479
 Width         :    190.0000
 Left          :       0.0000000
 # observations:    83

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))

s = A(1) * Exp(fcn(A(3))+ fcn(A(4))+ fcn(A(5))+ fcn(A(6))+ fcn(A(7))+ fcn(A(8)))

    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the power parameter.
    Parameter A(3) is the coefficient of level BD88 of factor covariate

REGION_LABEL.
    Parameter A(4) is the coefficient of level BDUN of factor covariate
REGION_LABEL.
    Parameter A(5) is the coefficient of level BR94 of factor covariate
REGION_LABEL.
    Parameter A(6) is the coefficient of level BR99 of factor covariate
REGION_LABEL.
    Parameter A(7) is the coefficient of level BRUN of factor covariate
REGION_LABEL.
    Parameter A(8) is the coefficient of level CP96 of factor covariate
REGION_LABEL.


              Point         Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      133.2        6.560
    A( 2)      3.941        7.089
    A( 3)    -0.3829       0.5001
    A( 4)    -0.2481       0.3239
    A( 5)    -0.5440       0.2992
    A( 6)     0.6016        2.267
    A( 7)    -0.3412       0.2717
    A( 8)    -0.6209       0.6112
    h(0)     0.13623E-03  0.14422E-04      10.59      0.11039E-03  0.16812E-03
    p        0.40667      0.43051E-01      10.59      0.32955      0.50186
    EDR       121.17       6.4133           5.29       109.05       134.63
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


         A( 1)   A( 2)   A( 3)   A( 4)   A( 5)   A( 6)   A( 7)   A( 8)
 A( 1)  1.000   0.023  -0.480  -0.741  -0.804  -0.113  -0.885  -0.390
 A( 2)  0.023   1.000   0.058   0.090   0.045  -0.269   0.064   0.164
 A( 3) -0.480   0.058   1.000   0.363   0.390   0.035   0.431   0.199
 A( 4) -0.741   0.090   0.363   1.000   0.603   0.055   0.665   0.308
 A( 5) -0.804   0.045   0.390   0.603   1.000   0.073   0.717   0.325
 A( 6) -0.113  -0.269   0.035   0.055   0.073   1.000   0.077  -0.002
 A( 7) -0.885   0.064   0.431   0.665   0.717   0.077   1.000   0.360
 A( 8) -0.390   0.164   0.199   0.308   0.325  -0.002   0.360   1.000
```

Figure C4. (Continued)



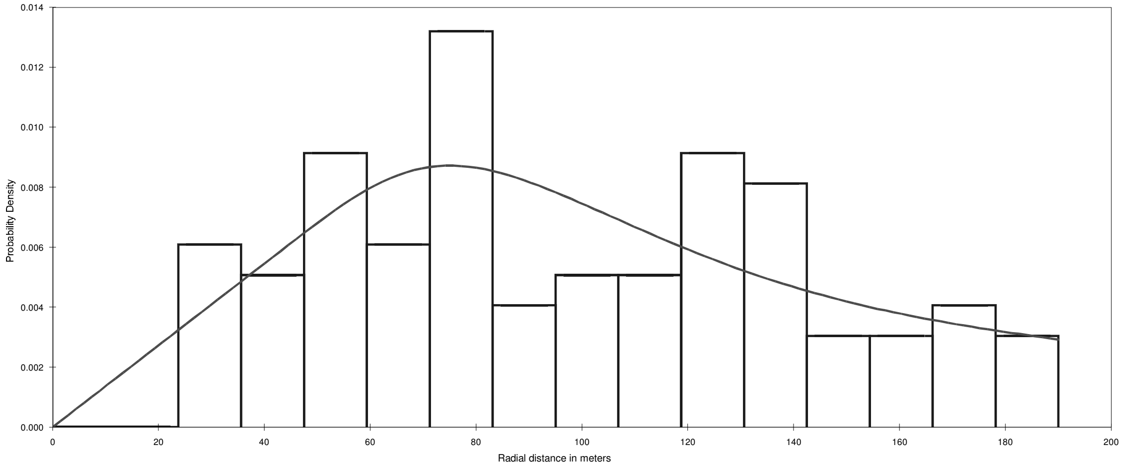


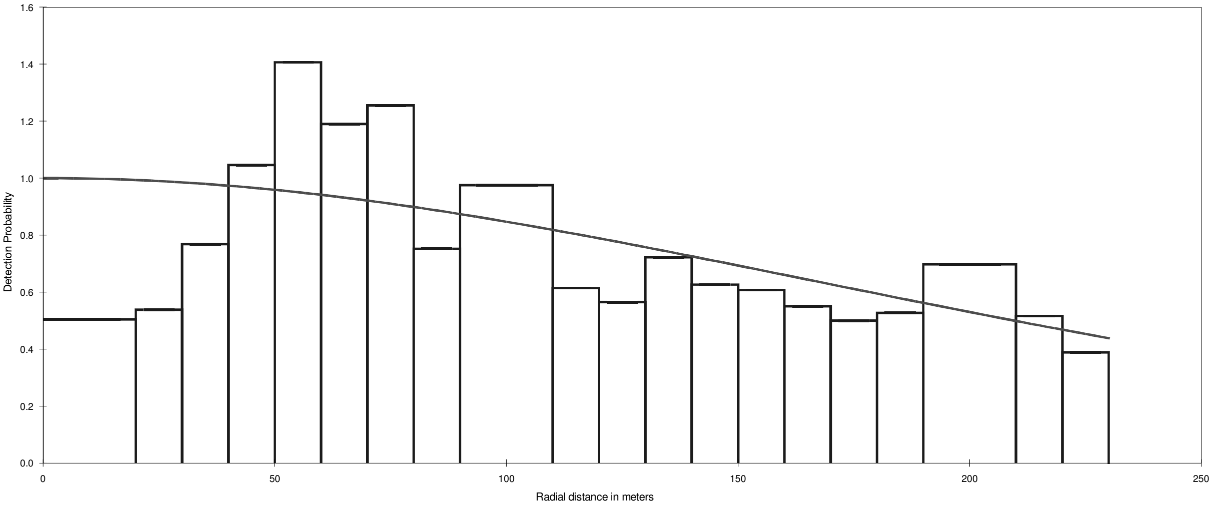
Figure C4. (Continued)

```
                    Estimate      %CV     df     95% Confidence Interval
                        ------------------------------------------------------
 Stratum: 1. BR94
 Hazard/Polynomial
                m       8.0000
                h(0)   0.20660E-03   23.73    13.55 0.12485E-03  0.34187E-03
                p      0.26817       23.73    13.55 0.16206      0.44375
                EDR     98.391       11.87    13.55  76.289       126.90
 Stratum: 2. BR99
 Hazard/Polynomial
                m       8.0000
                h(0)   0.55933E-04    9.19     9.04 0.45464E-04  0.68811E-04
                p      0.99051        9.19     9.04 0.80513       1.0000
                EDR     189.10        4.59     9.04  170.46       209.77
 Stratum: 3. BRUN
 Hazard/Polynomial
                m       8.0000
                h(0)   0.14534E-03   15.28    26.20 0.10637E-03  0.19861E-03
                p      0.38118       15.28    26.20 0.27895      0.52086
                EDR     117.31        7.64    26.20  100.28       137.22
 Stratum: 4. BD88
 Hazard/Polynomial
                m       8.0000
                h(0)   0.15595E-03   55.20     3.61 0.34998E-04  0.69487E-03
                p      0.35526       55.20     3.61 0.79730E-01   1.0000
                EDR     113.25       27.60     3.61  51.653       248.29
 Stratum: 5. BDUN
 Hazard/Polynomial
                m       8.0000
                h(0)   0.12477E-03   27.78     8.13 0.66652E-04  0.23356E-03
                p      0.44404       27.78     8.13 0.23721      0.83121
                EDR     126.61       13.89     8.13  92.132       173.99
 Stratum: 6. CP96
 Hazard/Polynomial
                m       8.0000
                h(0)   0.23737E-03   96.22     1.81 0.49775E-05  0.11320E-01
                p      0.23339       96.22     1.81 0.48941E-02   1.0000
                EDR     91.791       48.11     1.81  10.394       810.63
 Stratum: 7. CPUN
 Hazard/Polynomial
                m       8.0000
                h(0)   0.86607E-04   18.37    12.65 0.58364E-04  0.12852E-03
                p      0.63969       18.37    12.65 0.43108      0.94925
                EDR     151.96        9.19    12.65  124.59       185.34

 Note: Detection function was modelled globally, and estimated separately in
```

Figure C5. Select program DISTANCE model output for Sage Thrasher.

```
Effort        :    479.0000
 # samples     :   479
 Width         :    230.0000
 Left          :       0.0000000
 # observations:   530

 Model
    Half-normal key, k(y) = Exp(-y**2/(2*s**2))

    s = A(1) * Exp(fcn(A(2)))
    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the coefficient of covariate TIME.


              Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      867.2        84.84
    A( 2)    -0.2349E-02   0.8944E-03
    h(0)     0.56106E-04  0.14664E-05       2.61      0.53299E-04  0.59062E-04
    p        0.67385      0.17612E-01       2.61      0.64013      0.70935
    EDR       188.80       2.4673           1.31       184.02       193.71
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


         A( 1)   A( 2)
 A( 1)  1.000  -0.992
 A( 2) -0.992   1.000
```

Figure C5. (Continued)



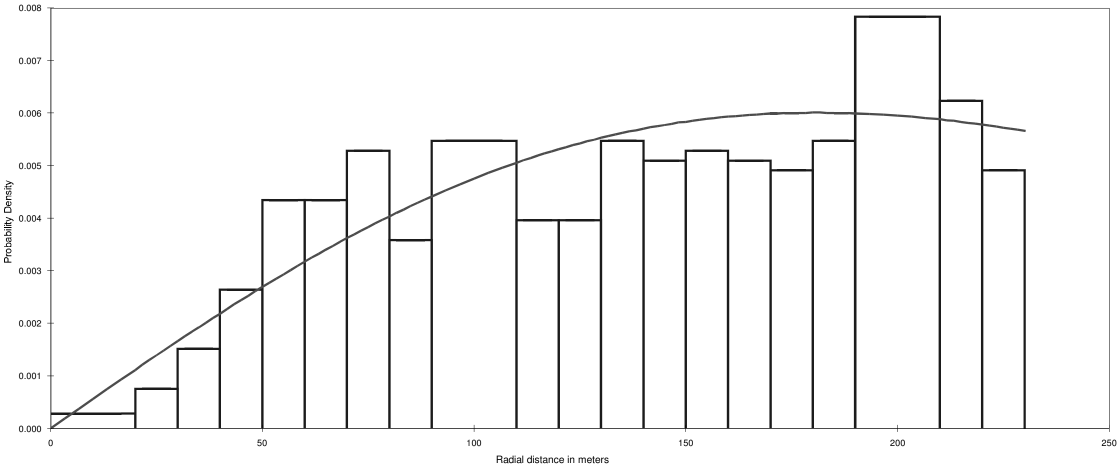


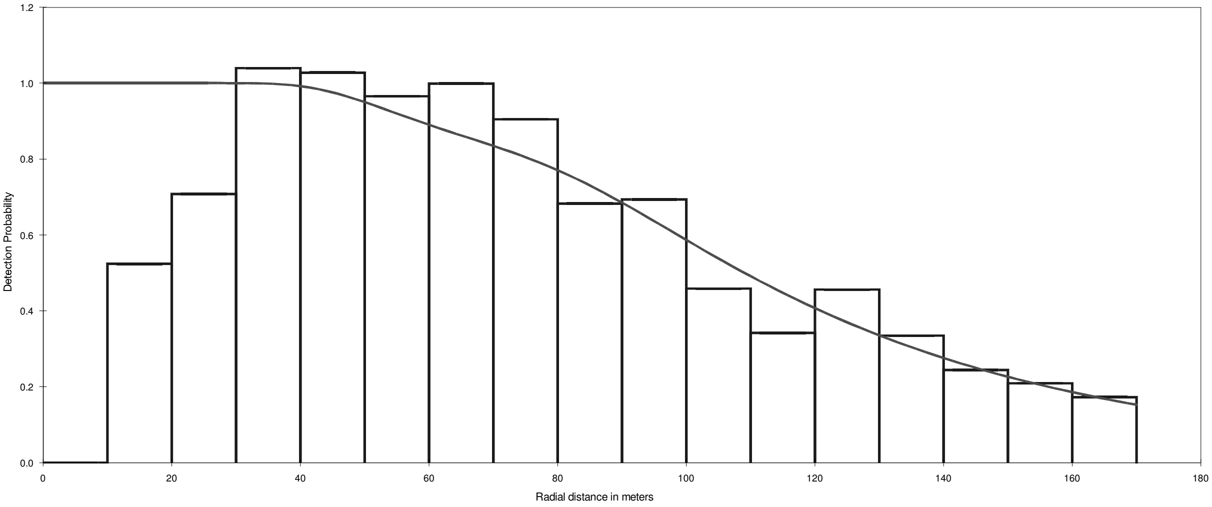
Figure C5. (Continued)

```
                        Estimate      %CV     df     95% Confidence Interval
                       ------------------------------------------------------
Stratum: 1. BR94
Half-normal/Cosine
                m       2.0000
                h(0)   0.55015E-04    9.60    35.86 0.45298E-04  0.66817E-04
                p      0.68721        9.60    35.86 0.56583      0.83463
                EDR     190.67        4.80    35.86  172.98       210.16
Stratum: 2. BR99
Half-normal/Cosine
                m       2.0000
                h(0)   0.55554E-04    9.17    43.83 0.46195E-04  0.66810E-04
                p      0.68055        9.17    43.83 0.56589      0.81842
                EDR     189.74        4.59    43.83  172.99       208.10
Stratum: 3. BRUN
Half-normal/Cosine
                m       2.0000
                h(0)   0.57834E-04    7.33    72.72 0.49979E-04  0.66925E-04
                p      0.65371        7.33    72.72 0.56492      0.75647
                EDR     185.96        3.67    72.72  172.86       200.06
Stratum: 4. BD88
Half-normal/Cosine
                m       2.0000
                h(0)   0.57057E-04   10.19    35.86 0.46431E-04  0.70115E-04
                p      0.66262       10.19    35.86 0.53922      0.81427
                EDR     187.22        5.09    35.86  168.86       207.59
Stratum: 5. BDUN
Half-normal/Cosine
                m       2.0000
                h(0)   0.56343E-04    7.72    59.77 0.48294E-04  0.65734E-04
                p      0.67102        7.72    59.77 0.57515      0.78285
                EDR     188.41        3.86    59.77  174.41       203.52
Stratum: 6. CP96
Half-normal/Cosine
                m       2.0000
                h(0)   0.54931E-04    5.12   129.51 0.49646E-04  0.60779E-04
                p      0.68826        5.12   129.51 0.62204      0.76153
                EDR     190.81        2.56   129.51  181.40       200.72
Stratum: 7. CPUN
Half-normal/Cosine
                m       2.0000
                h(0)   0.56383E-04    4.93   150.43 0.51150E-04  0.62151E-04
                p      0.67055        4.93   150.43 0.60831      0.73915
                EDR     188.34        2.47   150.43  179.38       197.74

Note: Detection function was modelled globally, and estimated separately in
      each straum, given the covariate values of the observations in the strata.
```

Figure C6. Select program DISTANCE model output for Green-tailed Towhee.

```
Effort        :    479.0000
 # samples     :   479
 Width         :    170.0000
 Left          :       0.0000000
 # observations:   716

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))

    s = A(1) * Exp(fcn(A(3)) + fcn(A(4)) + fcn(A(5)) + fcn(A(6)) + fcn(A(7)) +
fcn(A(8)))
    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the power parameter.
    Parameter A(3) is the coefficient of level N of factor covariate SING.
    Parameter A(4) is the coefficient of level AH of factor covariate INITIALS.
    Parameter A(5) is the coefficient of level AMH of factor covariate INITIALS.
    Parameter A(6) is the coefficient of level BZ of factor covariate INITIALS.
    Parameter A(7) is the coefficient of level JEB of factor covariate INITIALS.
    Parameter A(8) is the coefficient of level MD of factor covariate INITIALS.


              Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      105.3        1.189
    A( 2)      4.092        2.101
    A( 3)    -0.6408       0.7724E-01
    A( 4)    -0.1787       0.3181
    A( 5)     0.8295E-01   0.1080
    A( 6)    -0.6681E-01   0.7745E-01
    A( 7)     0.1006       0.7953E-01
    A( 8)     0.4344       0.9331E-01
    h(0)     0.14203E-03  0.50307E-05       3.54      0.13249E-03  0.15226E-03
    p        0.48724      0.17258E-01       3.54      0.45452      0.52232
    EDR       118.66       2.1015           1.77       114.61       122.86
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


        A( 1)   A( 2)   A( 3)   A( 4)   A( 5)   A( 6)   A( 7)   A( 8)
 A( 1)  1.000   0.073  -0.168  -0.137  -0.461  -0.660  -0.624  -0.518
 A( 2)  0.073   1.000   0.093   0.052   0.012   0.020  -0.007  -0.174
 A( 3) -0.168   0.093   1.000  -0.100  -0.043   0.043  -0.079  -0.230
 A( 4) -0.137   0.052  -0.100   1.000   0.083   0.105   0.113   0.103
 A( 5) -0.461   0.012  -0.043   0.083   1.000   0.317   0.314   0.272
 A( 6) -0.660   0.020   0.043   0.105   0.317   1.000   0.429   0.357
 A( 7) -0.624  -0.007  -0.079   0.113   0.314   0.429   1.000   0.377
 A( 8) -0.518  -0.174  -0.230   0.103   0.272   0.357   0.377   1.000
```

Figure C6. (continued)



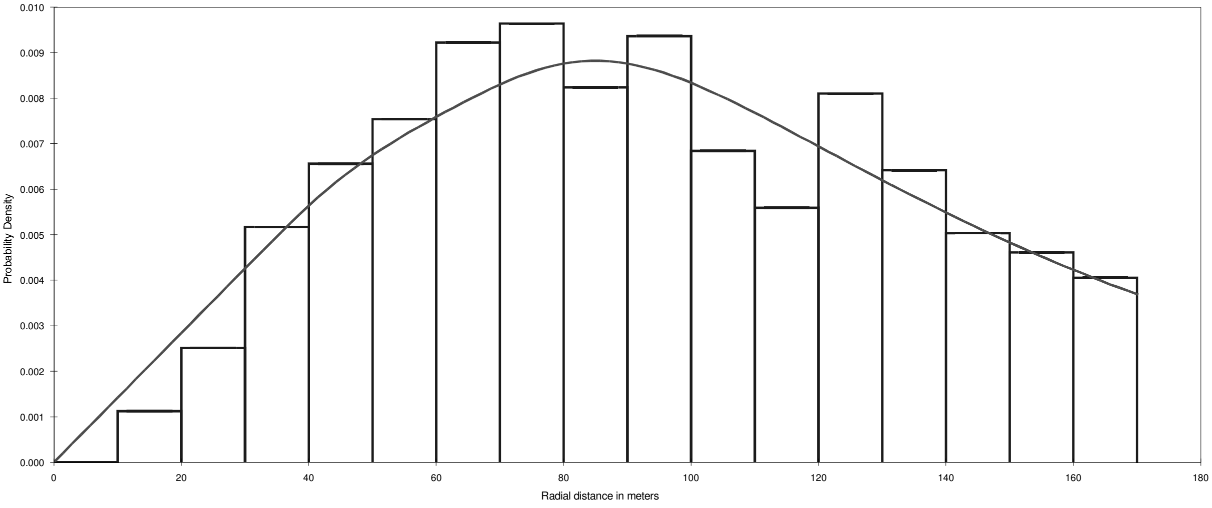


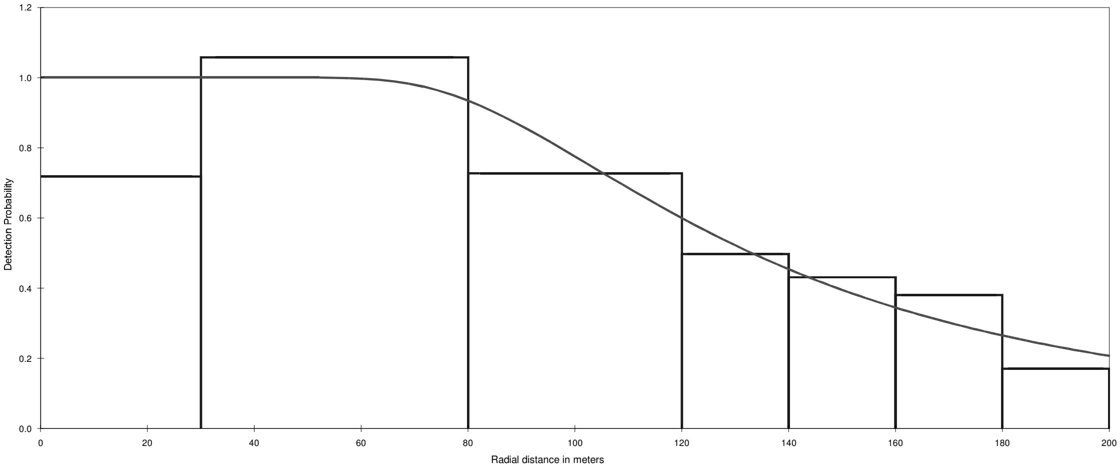
Figure C6. (Continued)

```
                  Estimate      %CV     df     95% Confidence Interval
                     ------------------------------------------------------
Stratum: 1. BR94
Hazard/Polynomial
                m       8.0000
                h(0)   0.13097E-03    7.87   124.59 0.11211E-03  0.15302E-03
                p      0.52838        7.87   124.59 0.45227      0.61731
                EDR     123.57        3.94   124.59  114.32       133.58
Stratum: 2. BR99
Hazard/Polynomial
                m       8.0000
                h(0)   0.14390E-03   14.41    40.54 0.10772E-03  0.19222E-03
                p      0.48093       14.41    40.54 0.36003      0.64244
                EDR     117.89        7.20    40.54  101.95       136.33
Stratum: 3. BRUN
Hazard/Polynomial
                m       8.0000
                h(0)   0.14323E-03    6.06   229.41 0.12711E-03  0.16139E-03
                p      0.48317        6.06   229.41 0.42881      0.54443
                EDR     118.17        3.03   229.41  111.32       125.44
Stratum: 4. BD88
Hazard/Polynomial
                m       8.0000
                h(0)   0.14965E-03   15.95    44.50 0.10874E-03  0.20597E-03
                p      0.46242       15.95    44.50 0.33599      0.63643
                EDR     115.60        7.98    44.50  98.466       135.72
Stratum: 5. BDUN
Hazard/Polynomial
                m       8.0000
                h(0)   0.14502E-03    7.82   156.23 0.12428E-03  0.16922E-03
                p      0.47720        7.82   156.23 0.40896      0.55682
                EDR     117.44        3.91   156.23  108.71       126.87
Stratum: 6. CP96
Hazard/Polynomial
                m       8.0000
                h(0)   0.14899E-03   18.55    24.72 0.10199E-03  0.21765E-03
                p      0.46450       18.55    24.72 0.31797      0.67856
                EDR     115.86        9.27    24.72  95.745       140.21
Stratum: 7. CPUN
Hazard/Polynomial
                m       8.0000
                h(0)   0.14260E-03   10.15    88.01 0.11662E-03  0.17438E-03
                p      0.48529       10.15    88.01 0.39686      0.59344
                EDR     118.43        5.07    88.01  107.07       130.98

Note: Detection function was modelled globally, and estimated separately in
      each straum, given the covariate values of the observations in the strata.
```

Figure C7. Select program DISTANCE model output for Spotted Towhee.

```
Effort        :    479.0000
 # samples     :   479
 Width         :    200.0000
 Left          :       0.0000000
 # observations:    33

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/A(1))**-A(2))


             Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      116.1        38.44
    A( 2)      2.688        1.753
    h(0)     0.93748E-04  0.29276E-04      31.23      0.50323E-04  0.17465E-03
    p        0.53334      0.16656          31.23      0.28629      0.99358
    EDR       146.06       22.806          15.61       106.43       200.45
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


        A( 1)   A( 2)
 A( 1)  1.000   0.776
 A( 2)  0.776   1.000
```

Figure C7. (Continued)



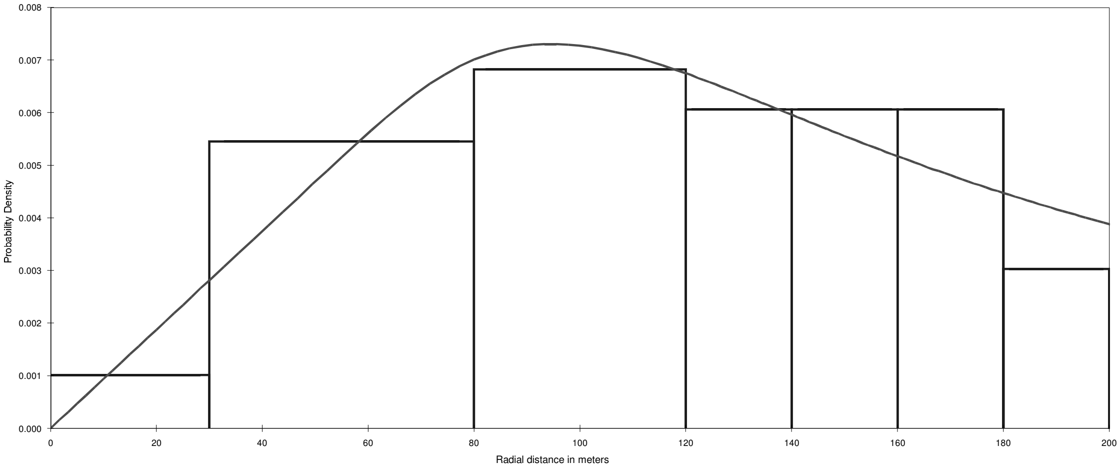
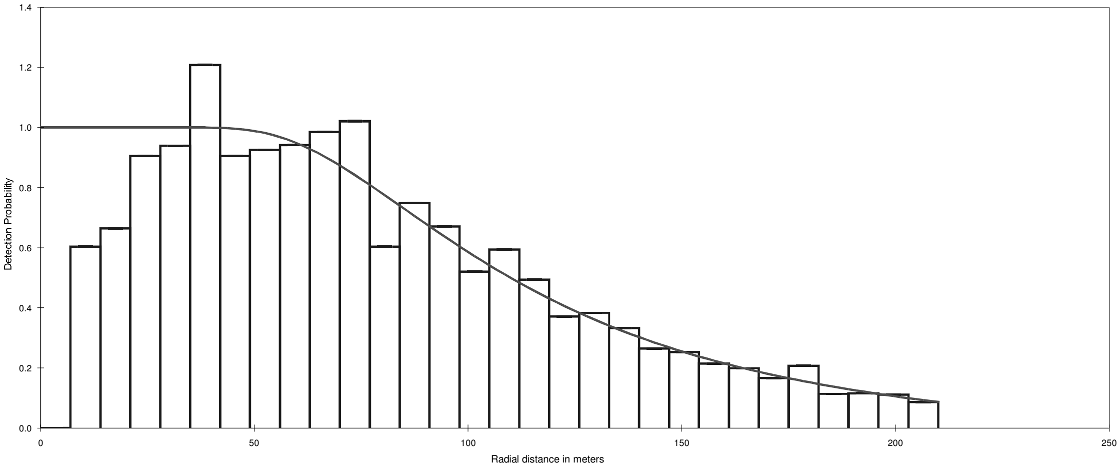


Figure C8. Select program DISTANCE model output for Vesper Sparrow

```
Effort        :    479.0000
 # samples     :   479
 Width         :    210.0000
 Left          :       0.0000000
 # observations:  1123

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))
    Simple polynomial adjustments of order(s) :  4

    s = A(1) * Exp(fcn(A(3)) + fcn(A(4)) + fcn(A(5)) + fcn(A(6)) + fcn(A(7)) +
fcn(A(8)))
    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the power parameter.
    Parameter A(3) is the coefficient of covariate TIME.
    Parameter A(4) is the coefficient of level AH of factor covariate INITIALS.
    Parameter A(5) is the coefficient of level AMH of factor covariate INITIALS.
    Parameter A(6) is the coefficient of level BZ of factor covariate INITIALS.
    Parameter A(7) is the coefficient of level JEB of factor covariate INITIALS.
    Parameter A(8) is the coefficient of level MD of factor covariate INITIALS.
    Parameter A(9) is the coefficient of the adjustment term of order  4.


              Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      189.8        10.71
    A( 2)      2.784        1.224
    A( 3)    -0.1056E-02   0.4208E-03
    A( 4)    -0.7626E-01   0.2746
    A( 5)     0.3514       0.1247
    A( 6)    -0.5114E-01   0.1155
    A( 7)    -0.1451       0.1019
    A( 8)     0.2317       0.1047
    A( 9)    -0.2960       0.1539
    h(0)     0.12042E-03  0.30302E-05       2.52      0.11462E-03  0.12652E-03
    p        0.37660      0.94761E-02       2.52      0.35846      0.39565
    EDR       128.87       1.6214           1.26       125.73       132.09
  ---------  -----------  -----------  --------------  ----------------------
```

Figure C8. (Continued)



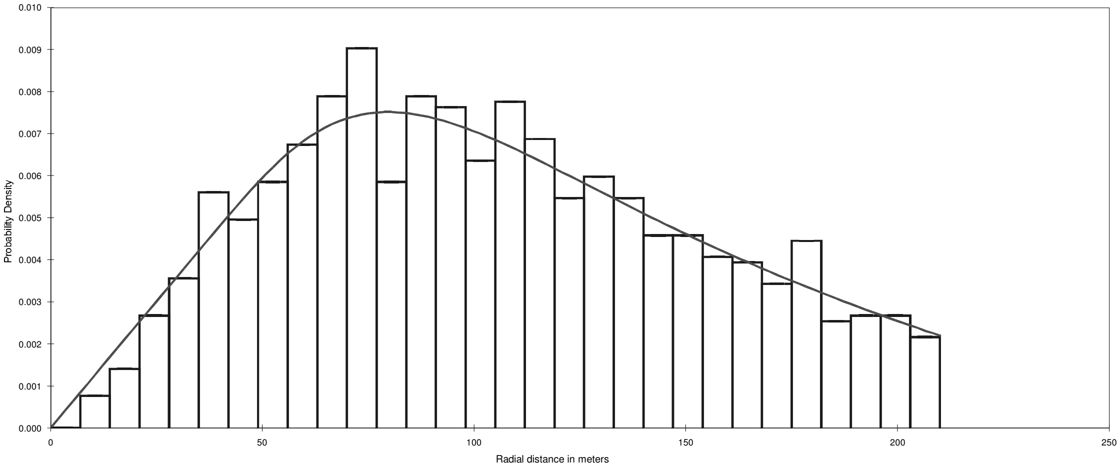


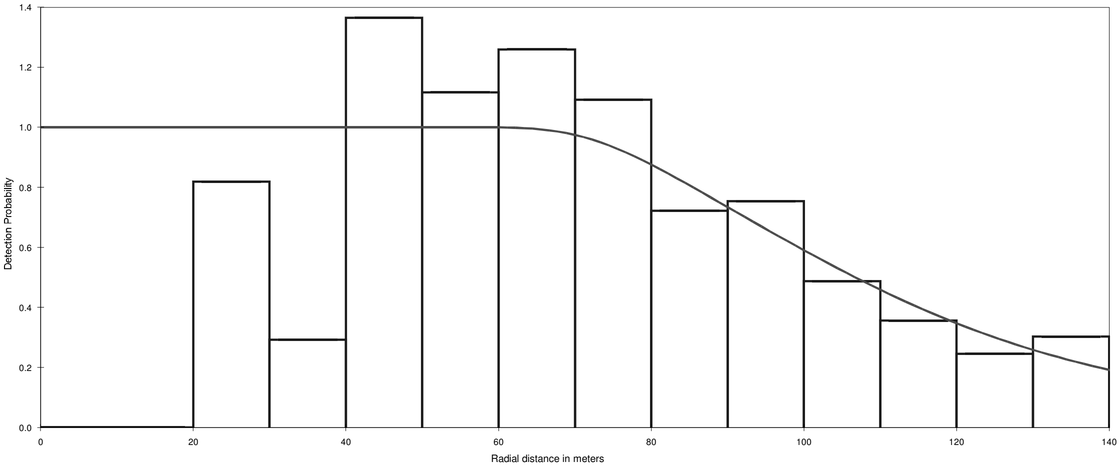
Figure C8. (Continued)

```
                       Estimate      %CV     df     95% Confidence Interval
                       ------------------------------------------------------
Stratum: 1. BR94
Hazard/Polynomial
                m       9.0000
                h(0)   0.11818E-03    5.51   227.16 0.10604E-03  0.13171E-03
                p      0.38376        5.51   227.16 0.34433      0.42770
                EDR     130.09        2.75   227.16  123.22       137.34
Stratum: 2. BR99
Hazard/Polynomial
                m       9.0000
                h(0)   0.11826E-03    5.15   262.88 0.10685E-03  0.13089E-03
                p      0.38349        5.15   262.88 0.34650      0.42442
                EDR     130.05        2.58   262.88  123.61       136.81
Stratum: 3. BRUN
Hazard/Polynomial
                m       9.0000
                h(0)   0.12932E-03    8.43   101.18 0.10943E-03  0.15282E-03
                p      0.35070        8.43   101.18 0.29676      0.41444
                EDR     124.36        4.22   101.18  114.39       135.21
Stratum: 4. BD88
Hazard/Polynomial
                m       9.0000
                h(0)   0.11693E-03   11.46    53.57 0.93000E-04  0.14703E-03
                p      0.38784       11.46    53.57 0.30846      0.48765
                EDR     130.78        5.73    53.57  116.60       146.69
Stratum: 5. BDUN
Hazard/Polynomial
                m       9.0000
                h(0)   0.11738E-03    6.70   154.75 0.10284E-03  0.13397E-03
                p      0.38637        6.70   154.75 0.33851      0.44100
                EDR     130.53        3.35   154.75  122.18       139.46
Stratum: 6. CP96
Hazard/Polynomial
                m       9.0000
                h(0)   0.12018E-03    5.79   210.30 0.10722E-03  0.13469E-03
                p      0.37737        5.79   210.30 0.33670      0.42296
                EDR     129.00        2.90   210.30  121.85       136.58
Stratum: 7. CPUN
Hazard/Polynomial
                m       9.0000
                h(0)   0.12897E-03    8.44   104.16 0.10912E-03  0.15242E-03
                p      0.35166        8.44   104.16 0.29754      0.41561
                EDR     124.53        4.22   104.16  114.54       135.40

Note: Detection function was modelled globally, and estimated separately in
      each straum, given the covariate values of the observations in the strata.
```

Figure C9. Select program DISTANCE model output for Sage Sparrow.

```
Effort        :    479.0000
# samples     :   479
Width         :    140.0000
Left          :       0.0000000
# observations:    60

Model
   Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))

   s = A(1) * Exp(fcn(A(3)))
   Parameter A(1) is the intercept of the scale parameter s.
   Parameter A(2) is the power parameter.
   Parameter A(3) is the coefficient of level 2007 of factor covariate YEAR.


             Point        Standard    Percent Coef.        95 Percent
 Parameter   Estimate       Error      of Variation     Confidence Interval
 ---------  -----------  -----------  --------------  ----------------------
   A( 1)      120.3        3.951
   A( 2)      4.953        8.733
   A( 3)    -0.3036       0.1879
   h(0)     0.16295E-03  0.14126E-04       8.67      0.13702E-03  0.19377E-03
   p        0.62623      0.54290E-01       8.67      0.52660      0.74471
   EDR       110.79       4.8023           4.33       101.58       120.83
 ---------  -----------  -----------  --------------  ----------------------


Sampling Correlation of Estimated Parameters


        A( 1)   A( 2)   A( 3)
A( 1)  1.000  -0.131  -0.843
A( 2) -0.131   1.000   0.155
A( 3) -0.843   0.155   1.000
```

Figure C9. (Continued)



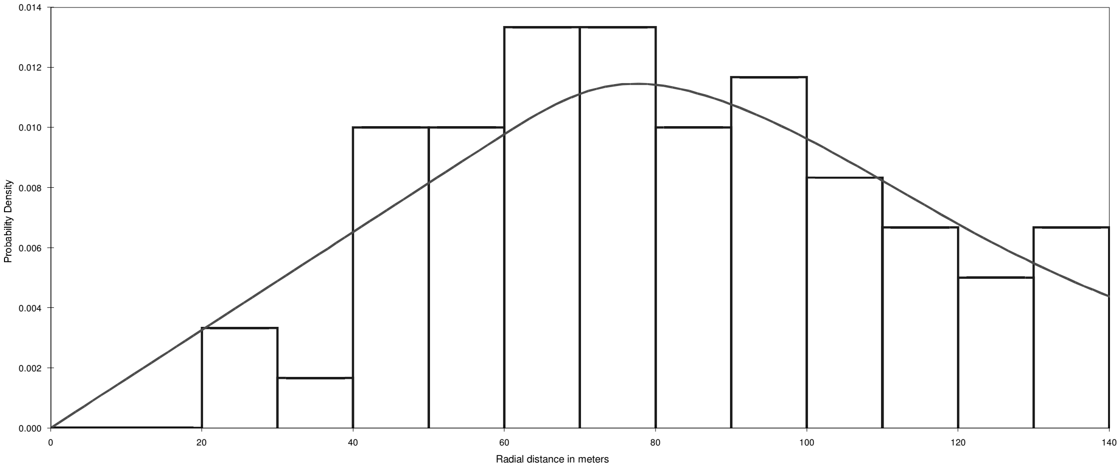
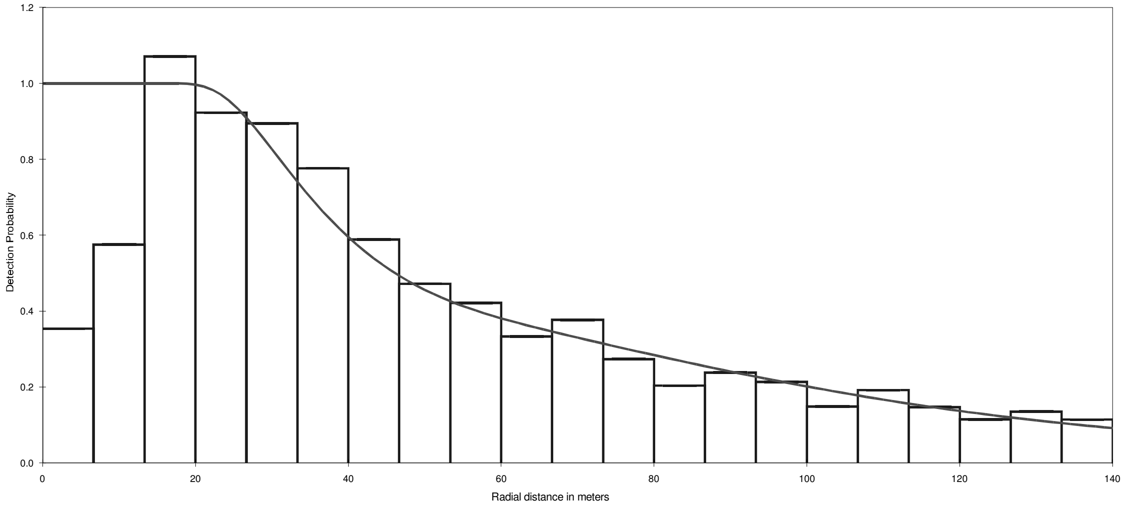


Figure C10. Select program DISTANCE model output for Brewer's Sparrow

```
Effort        :    479.0000
 # samples     :   479
 Width         :    140.0000
 Left          :       0.0000000
 # observations:  2732

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))

    s = A(1) * Exp(fcn(A(3)) + fcn(A(4)) + fcn(A(5)) + fcn(A(6)) + fcn(A(7)) +
fcn(A(8)))
    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the power parameter.
    Parameter A(3) is the coefficient of level N of factor covariate SING.
    Parameter A(4) is the coefficient of level AH of factor covariate INITIALS.
    Parameter A(5) is the coefficient of level AMH of factor covariate INITIALS.
    Parameter A(6) is the coefficient of level BZ of factor covariate INITIALS.
    Parameter A(7) is the coefficient of level JEB of factor covariate INITIALS.
    Parameter A(8) is the coefficient of level MD of factor covariate INITIALS.


              Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error     of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      93.43       0.7050
    A( 2)      3.602       0.9581
    A( 3)     -1.052       0.3469E-01
    A( 4)     0.1141       0.1359
    A( 5)     0.2305       0.5771E-01
    A( 6)     0.2108E-01   0.5796E-01
    A( 7)    -0.6787E-01   0.4367E-01
    A( 8)     0.3659       0.5106E-01
    h(0)     0.37232E-03  0.93262E-05       2.50      0.35448E-03  0.39106E-03
    p        0.27406      0.68649E-02       2.50      0.26093      0.28786
    EDR       73.292      0.91793           1.25       71.514       75.114
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


        A( 1)   A( 2)   A( 3)   A( 4)   A( 5)   A( 6)   A( 7)   A( 8)
 A( 1)  1.000   0.047  -0.424  -0.211  -0.492  -0.520  -0.666  -0.532
 A( 2)  0.047   1.000   0.142  -0.004  -0.023   0.008   0.028  -0.164
 A( 3) -0.424   0.142   1.000   0.016   0.023   0.099   0.080  -0.065
 A( 4) -0.211  -0.004   0.016   1.000   0.121   0.122   0.161   0.137
 A( 5) -0.492  -0.023   0.023   0.121   1.000   0.286   0.377   0.324
 A( 6) -0.520   0.008   0.099   0.122   0.286   1.000   0.382   0.315
 A( 7) -0.666   0.028   0.080   0.161   0.377   0.382   1.000   0.417
 A( 8) -0.532  -0.164  -0.065   0.137   0.324   0.315   0.417   1.000
```

Figure C10. (Continued)



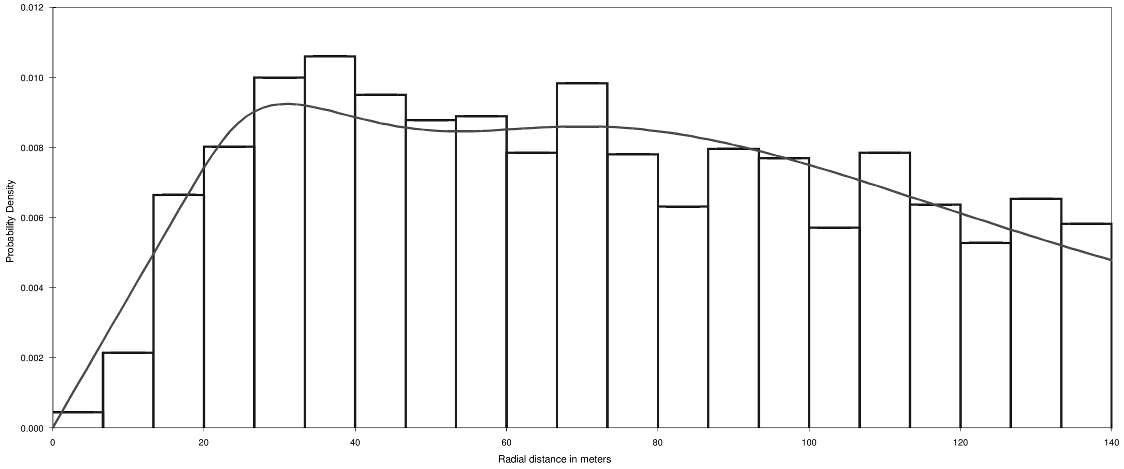


Figure C10. (Continued)

```
                        Estimate      %CV     df     95% Confidence Interval
                       ------------------------------------------------------
Stratum: 88_2007
Hazard/Polynomial
                m       8.0000
                h(0)   0.43740E-03   10.33   154.55 0.35685E-03  0.53613E-03
                p      0.23329       10.33   154.55 0.19033      0.28595
                EDR     67.620        5.17   154.55  61.065       74.879
Stratum: 88_2008
Hazard/Polynomial
                m       8.0000
                h(0)   0.34304E-03   13.28    87.74 0.26374E-03  0.44617E-03
                p      0.29746       13.28    87.74 0.22870      0.38690
                EDR     76.356        6.64    87.74  66.923       87.119
Stratum: 94_2007
Hazard/Polynomial
                m       8.0000
                h(0)   0.40730E-03    8.25   236.31 0.34627E-03  0.47909E-03
                p      0.25053        8.25   236.31 0.21299      0.29468
                EDR     70.074        4.13   236.31  64.604       76.007
Stratum: 94_2008
Hazard/Polynomial
                m       8.0000
                h(0)   0.30566E-03    9.95   170.50 0.25128E-03  0.37179E-03
                p      0.33384        9.95   170.50 0.27446      0.40608
                EDR     80.891        4.97   170.50  73.331       89.230
Stratum: 96_2007
Hazard/Polynomial
                m       8.0000
                h(0)   0.42773E-03    7.56   288.15 0.36868E-03  0.49623E-03
                p      0.23857        7.56   288.15 0.20563      0.27678
                EDR     68.380        3.78   288.15  63.480       73.659
Stratum: 96_2008
Hazard/Polynomial
                m       8.0000
                h(0)   0.26847E-03    9.47   190.44 0.22284E-03  0.32345E-03
                p      0.38008        9.47   190.44 0.31547      0.45792
                EDR     86.311        4.73   190.44  78.621       94.752
Stratum: 99_2007
Hazard/Polynomial
                m       8.0000
                h(0)   0.44900E-03    9.74   169.50 0.37060E-03  0.54397E-03
                p      0.22726        9.74   169.50 0.18759      0.27534
                EDR     66.741        4.87   169.50  60.625       73.474
Stratum: 99_2008
Hazard/Polynomial
                m       8.0000
                h(0)   0.25181E-03   10.97   133.61 0.20281E-03  0.31264E-03
                p      0.40524       10.97   133.61 0.32639      0.50313
                EDR     89.121        5.49   133.61  79.963       99.329
Stratum: BD_2007
Hazard/Polynomial
                m       8.0000
                h(0)   0.45750E-03    7.69   266.22 0.39331E-03  0.53217E-03
                p      0.22304        7.69   266.22 0.19175      0.25944
                EDR     66.118        3.84   266.22  61.299       71.315
```

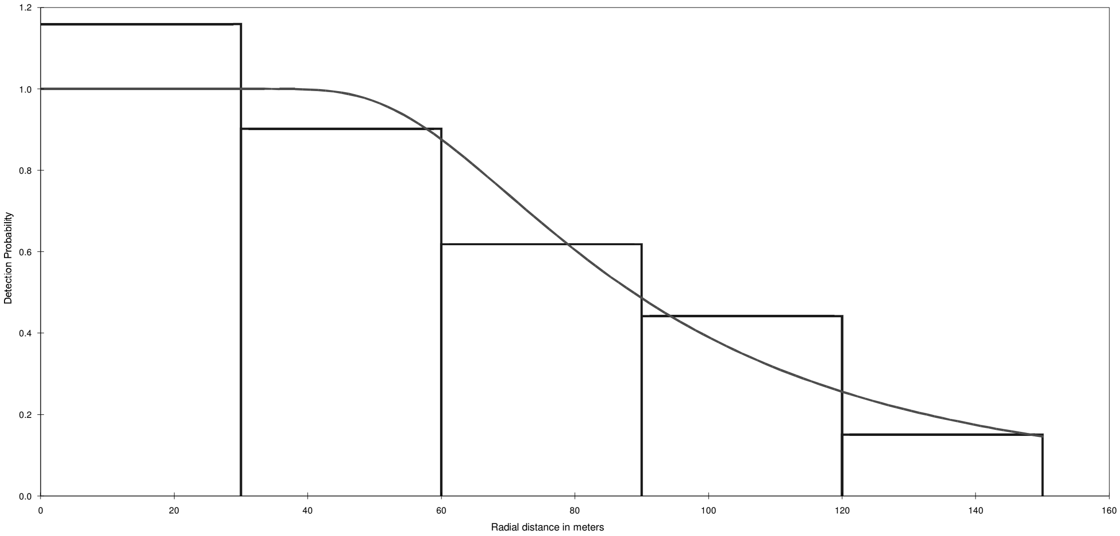
Figure C10. (Continued)

```
Stratum: BD_2008
Hazard/Polynomial
                m       8.0000
                h(0)   0.23335E-03    8.85   192.43 0.19603E-03  0.27778E-03
                p      0.43728        8.85   192.43 0.36734      0.52054
                EDR     92.578        4.43   192.43  84.841       101.02
Stratum: BR_2007
Hazard/Polynomial
                m       8.0000
                h(0)   0.45533E-03    8.64   222.35 0.38419E-03  0.53963E-03
                p      0.22411        8.64   222.35 0.18909      0.26560
                EDR     66.276        4.32   222.35  60.872       72.159
Stratum: BR_2008
Hazard/Polynomial
                m       8.0000
                h(0)   0.26649E-03   10.11   163.52 0.21836E-03  0.32523E-03
                p      0.38290       10.11   163.52 0.31375      0.46730
                EDR     86.631        5.06   163.52  78.404       95.721
Stratum: CP_2007
Hazard/Polynomial
                m       8.0000
                h(0)   0.44588E-03    7.52   287.16 0.38465E-03  0.51685E-03
                p      0.22885        7.52   287.16 0.19743      0.26528
                EDR     66.974        3.76   287.16  62.201       72.114
Stratum: CP_2008
Hazard/Polynomial
                m       8.0000
                h(0)   0.27530E-03   10.02   161.53 0.22600E-03  0.33535E-03
                p      0.37065       10.02   161.53 0.30428      0.45151
                EDR     85.234        5.01   161.53  77.212       94.089

Note: Detection function was modelled globally, and estimated separately in
      each straum, given the covariate values of the observations in the strata.
```

Figure C11. Select program DISTANCE model output for Brown-headed Cowbird

```
Effort        :    479.0000
 # samples     :   479
 Width         :    150.0000
 Left          :       0.0000000
 # observations:    59

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/A(1))**-A(2))


              Point         Standard    Percent Coef.        95 Percent
  Parameter   Estimate        Error     of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      77.88        18.67
    A( 2)      2.817        1.162
    h(0)     0.19493E-03  0.45893E-04      23.54      0.12243E-03  0.31036E-03
    p        0.45600      0.10736          23.54      0.28640      0.72602
    EDR       101.29       11.923          11.77       80.085       128.11
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


         A( 1)   A( 2)
 A( 1)  1.000   0.803
 A( 2)  0.803   1.000
```

Figure C11. (Continued)



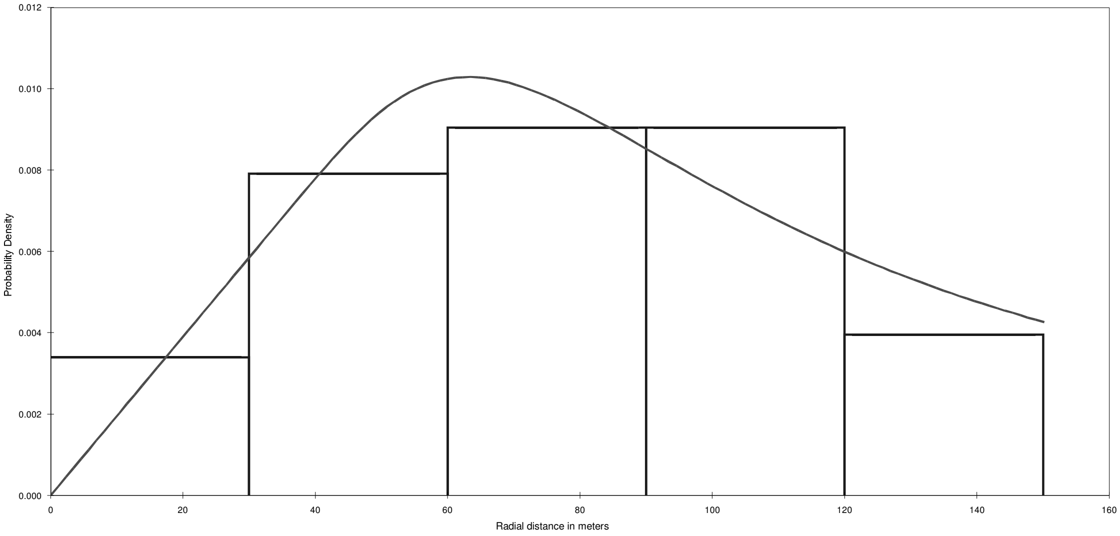
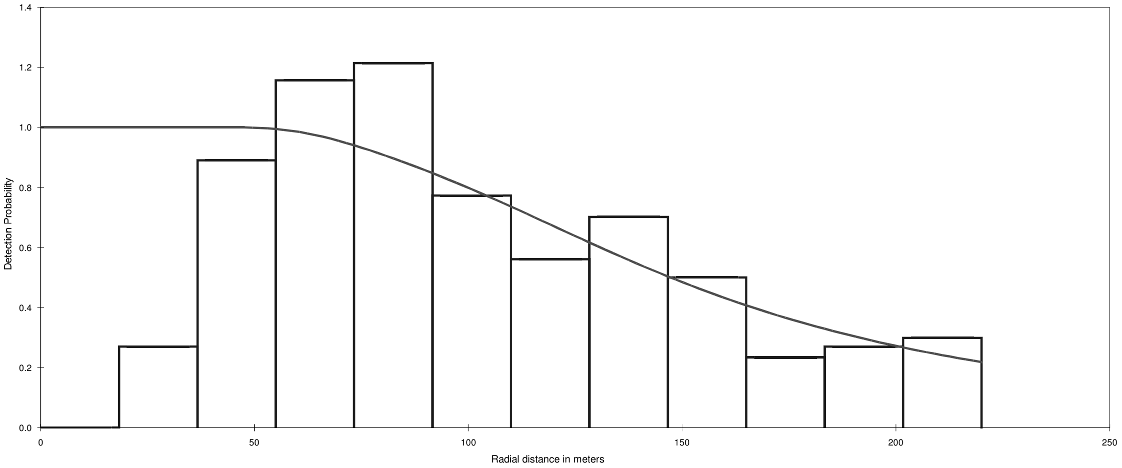


Figure C12. Select program DISTANCE model output for Western Meadowlark

```
Effort        :    479.0000
 # samples     :   479
 Width         :    220.0000
 Left          :       0.0000000
 # observations:   188

 Model
    Hazard Rate key, k(y) = 1 - Exp(-(y/s)**-A(2))

    s = A(1) * Exp(fcn(A(3)))
    Parameter A(1) is the intercept of the scale parameter s.
    Parameter A(2) is the power parameter.
    Parameter A(3) is the coefficient of level N of factor covariate SING.


             Point        Standard    Percent Coef.        95 Percent
  Parameter   Estimate       Error      of Variation     Confidence Interval
  ---------  -----------  -----------  --------------  ----------------------
    A( 1)      153.3        3.174
    A( 2)      2.780        2.901
    A( 3)    -0.5070       0.1949
    h(0)     0.78211E-04  0.45453E-05       5.81      0.69746E-04  0.87704E-04
    p        0.52834      0.30705E-01       5.81      0.47115      0.59247
    EDR       159.91       4.6466           2.91       151.00       169.34
  ---------  -----------  -----------  --------------  ----------------------


 Sampling Correlation of Estimated Parameters


        A( 1)   A( 2)   A( 3)
 A( 1)  1.000   0.204  -0.490
 A( 2)  0.204   1.000   0.109
 A( 3) -0.490   0.109   1.000
```

Figure C12. (Continued)



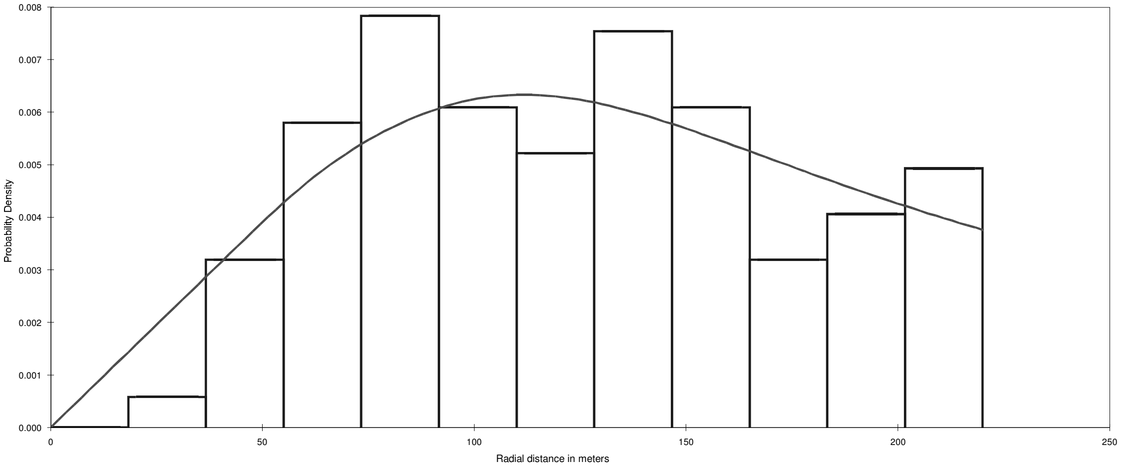


Figure C12. (Continued)

```
                         Estimate      %CV     df     95% Confidence Interval
                        ------------------------------------------------------
Stratum: 1. BR94
Hazard/Polynomial
                m        3.0000
                h(0)    0.90687E-04   21.86    14.76 0.57187E-04  0.14381E-03
                p       0.45566       21.86    14.76 0.28734      0.72259
                EDR      148.51       10.93    14.76  117.69       187.39
Stratum: 2. BR99
Hazard/Polynomial
                m        3.0000
                h(0)    0.70085E-04   12.42    33.46 0.54498E-04  0.90129E-04
                p       0.58961       12.42    33.46 0.45848      0.75824
                EDR      168.93        6.21    33.46  148.91       191.64
Stratum: 3. BRUN
Hazard/Polynomial
                m        3.0000
                h(0)    0.81303E-04   22.58    12.79 0.50179E-04  0.13173E-03
                p       0.50825       22.58    12.79 0.31369      0.82350
                EDR      156.84       11.29    12.79  122.94       200.09
Stratum: 4. BD88
Hazard/Polynomial
                m        3.0000
                h(0)    0.82816E-04   47.41     2.95 0.19497E-04  0.35177E-03
                p       0.49896       47.41     2.95 0.11747      1.0000
                EDR      155.40       23.71     2.95  73.330       329.33
Stratum: 5. BDUN
Hazard/Polynomial
                m        3.0000
                h(0)    0.80326E-04    9.10    77.74 0.67035E-04  0.96252E-04
                p       0.51443        9.10    77.74 0.42931      0.61643
                EDR      157.79        4.55    77.74  144.13       172.75
Stratum: 6. CP96
Hazard/Polynomial
                m        3.0000
                h(0)    0.75972E-04   16.29    22.63 0.54340E-04  0.10622E-03
                p       0.54391       16.29    22.63 0.38904      0.76044
                EDR      162.25        8.15    22.63  137.11       192.01
Stratum: 7. CPUN
Hazard/Polynomial
                m        3.0000
                h(0)    0.74384E-04   16.77    20.66 0.52592E-04  0.10520E-03
                p       0.55553       16.77    20.66 0.39278      0.78571
                EDR      163.97        8.38    20.66  137.75       195.19

Note: Detection function was modelled globally, and estimated separately in
      each straum, given the covariate values of the observations in the strata.
```

Table C1. Bird density models ranked by ΔAIC. Key functions are either hazard rate (Haz) or half normal (HN). The number that follows the key function in parenthesis indicates the number of adjustment terms, which are cosine for half normal models and simple polynomial for hazard rate models. EDR = Estimated detection radius.

Species	Model	covariates	Key function	K	ΔAIC	EDR
Gray Flycatcher	global	Sing	Haz (0)	3	0.00	103
	global	Sing, observer	Haz (0)	8	2.79	104
	global	Sing, observer	HN (1)	8	2.96	124
	global	Strata, sing	Haz (0)	9	5.01	104
	global	Year	HN (1)	3	10.80	121
	Global	Time	HN (1)	3	10.82	121
	Global	-	Haz (1)	3	12.65	107
	Strata	-	HN	10	14.04	-
	Global	Strata	HN (0)	8	14.43	105
	Global	Time	Haz (0)	3	14.85	109
	Global	Observer	HN (0)	7	14.86	121
	Global	Strata, sing	HN (0)	8	15.22	90
	Global	Time, observer	HN (0)	8	16.12	121
	Global	Year	Haz (0)	3	16.26	110
	Global	Strata, observer	Haz (0)	13	19.53	105
	Global	Observer	Haz (0)	7	19.87	104
	Strata	-	Haz (0)	16	21.08	-
	Global	Time, observer	Haz (0)	8	21.10	105
	Global	Strata	HN (0)	7	21.54	91
	Global	Strata, observer	HN (0)	12	25.13	90
Horned Lark	Global	Sing, observer	Haz (0)	8	0.00	82
	Global	Sing	Haz (0)	3	14.26	83
	Strata	-	HN (1)	10	24.85	84
	Global	Time, observer	HN	8	34.75	112
	Global	Year	HN (1)	3	35.31	111
	Global	Sing, observer	HN (0)	7	35.84	71
	Global	Sing	HN (0)	2	46.37	72
	Global	Observer	Haz (0)	7	47.75	84
	Global	Time, observer	Haz (0)	8	47.79	83
	Global	-	Haz (0)	2	50.75	84
	Global	Year	Haz (1)	4	51.47	84
	Global	Time	Haz (0)	3	51.68	82
	Strata	-	HN (0-1)	12	52.73	-
	Global	-	HN (3)	4	55.66	82
	Global	Strata, sing	HN (0)	8	56.71	72
	Global	Strata, observer	Haz (0)	13	56.82	84

Table C1. (Continued)

Species	Model	covariates	Key function	K	ΔAIC	EDR
	Strata	-	Haz (0-1)	17	58.17	-
	Global	Strata	Haz (0)	8	60.48	84
	Global	Observer	HN (0)	6	74.48	73
	Global	Time	HN (0)	2	77.29	73
	Global	Strata, observer	HN (0)	12	85.19	73
	Global	Strata	HN (0)	7	86.34	73
Rock Wren	Global	-	Haz (0)	2	0.00	159
	Global	-	HN (0)	1	0.72	148
	Global	Time	HN(1)	3	1.96	158
	Global	Strata	Haz (0)	8	7.28	160
American Robin	Global	Strata	Haz (0)	8	0.00	121
	Global	-	HN (1)	2	1.46	122
	global	Time	Haz (0)	3	3.58	124
Sage Thrasher	Global	Time	HN (0)	2	0.00	189
	Global	-	HN (0)	1	4.88	191
	global	Year	Haz (1)	4	4.94	183
	Global	-	Haz (0)	2	5.08	180
	Global	Time	Haz (0)	3	6.60	182
	Global	Sing	Haz (0)	3	6.61	190
	Strata	-	HN (0-1)	8	10.24	-
	Global	Strata	HN (0)	7	12.08	190
	Global	strata	Haz (0)	8	12.67	187
	Strata	-	Haz (0-1)	16	18.46	-
Green-tailed Towhee	global	Sing, observer	Haz (0)	8	0.00	119
	Global	Sing, observer	HN (0)	7	19.52	107
	Global	Sing	Haz (0)	3	24.66	119
	Global	Sing, strata	Haz (0)	9	33.23	118
	Global	Sing, strata	HN (1)	9	45.16	134
	Global	Observer	Haz (0)	7	46.64	133
	Global	Sing	HN (0)	2	47.46	110
	Global	Observer, time	HN (1)	8	48.54	133
	Global	Observer	Haz (0)	7	51.78	122
	Global	Observer, time	Haz (0)	8	52.61	123
	Global	Strata, observer	Haz (0)	14	56.89	125
	Global	Strata, observer	HN (0)	12	62.09	110
	Global	-	Haz (0)	2	76.21	120

Table C1. (Continued)

Species	Model	covariates	Key function	K	ΔAIC	EDR
	Global	Year	Haz (0)	3	76.52	124
	Global	Time	Haz (0)	3	76.60	124
	Global	Year	HN (1)	3	77.04	131
	Global	Time	HN (1)	3	77.57	131
	global	-	HN (0)	1	80.53	113
	strata	-	Haz (0-1)	17	80.83	-
	Global	Strata	HN (1)	8	83.87	132
	Global	Strata	Haz (0)	8	83.90	124
	Strata	-	HN (0-1)	9	83.95	-
Spotted Towhee	Global	-	Haz (0)	2	0.00	146
	Global	Time	Haz (0)	3	2.10	154
	global	Year	Haz (0)	3	2.10	154
Vesper Sparrow	Global	Observer, time	Haz (1)	9	0.00	129
	Global	Observer	Haz (1)	8	5.15	129
	Global	Observer, strata	Haz (0)	13	6.63	132
	Global	Observer, time	HN (1)	8	10.50	128
	Global	Observer	HN (0)	6	12.20	122
	Global	Observer, strata	HN (1)	13	16.18	128
	Global	Time	Haz (0)	3	29.76	130
	Global	Year	Haz (0)	3	32.74	131
	Global	-	Haz (0)	2	35.68	133
	Strata	-	Haz (0-1)	16	35.71	-
	Strata	-	HN (0-1)	9	39.01	-
	Global	Time	HN (0)	2	39.19	123
	Global	Strata	Haz (0)	8	39.41	132
	Global	Year	HN (0)	2	41.07	123
	Global	Strata	HN (0)	7	43.38	123
Brewer’s Sparrow	global	Sing, observer	Haz (0)	8	0.00	73
	Global	Sing, strata	Haz (0)	9	124.06	72
	Global	Sing	Haz (1)	4	125.85	71
	Global	sing, observer	HN (0)	7	146.19	71
	Global	Sing, strata	HN (0)	8	225.55	73
	global	Sing	HN (0)	2	243.52	73
	Global	Observer	Haz (0)	8	889.39	79
	Global	Observer, time	Haz (0)	9	891.65	80
	Global	Observer, strata	Haz (0)	13	898.10	78
	Global	observer	HN (0)	7	909.47	71

Table C1. (Continued)

Species	Model	covariates	Key function	K	ΔAIC	EDR
	global	Observer, time	HN (0)	8	911.28	71
	Global	Observer, strata	HN (0)	13	911.34	71
	Global	Year	HN (1)	3	1002.6	71
	Global	Year	Haz (0)	4	1007.6	76
	Global	-	Haz (0)	2	1050.3	76
	global	Time	Haz (0)	4	1055.0	80
	strata	-	Haz (0-1)	19	1059.4	-
	Global	strata	Haz (1)	9	1060.0	80
	Global	-	HN (2)	3	1062.2	75
	Global	Strata	HN (1)	8	1072.0	71
	global	Time	HN (1)	3	1072.6	71
	strata	-	HN (1)	14	1079.6	-
Sage Sparrow	Global	Year	Haz (0)	3	0.00	111
	Global	-	Haz (0)	2	1.84	109
	Global	Time	Haz (0)	3	3.47	109
Brown-headed Cowbird	Global	-	Haz (0)	2	0.00	101
Western Meadowlark	Global	Sing	Haz (0)	3	0.00	160
	global	strata	Haz (0)	8	5.56	154
	Global	-	Haz (0)	2	6.01	164
	Global	Time	Haz (0)	3	7.33	162
	Global	Year	Haz (0)	3	7.68	163