

Preliminary Assessment of Species Richness and Avian Community Dynamics in the Madrean Sky Islands, Arizona

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Abstract—The Sky Island mountain ranges of southeastern Arizona contain a unique and rich avifaunal community, including many Neotropical migratory species whose northern breeding range extends to these mountains along with many species typical of similar habitats throughout western North America. Understanding ecological factors that influence species richness and biological diversity of both resident and migratory species is important for conservation of this unique bird assemblage. We used a 5-year data set to evaluate avian species distribution across montane habitat types within the Santa Rita, Santa Catalina, Huachuca, Chiricahua, and Pinaleno Mountains. Using point-count data from spring-summer breeding seasons, we describe avian diversity and community dynamics. We use a Bayesian hierarchical model to describe occupancy as a function of vegetative cover type and mountain range latitude, and detection probability as a function of species heterogeneity and sampling effort. By identifying important habitat correlates for avian species, these results can help guide management decisions to minimize loss of key habitats and guide restoration efforts in response to disturbance events in the Madrean Archipelago.

Introduction

The Sky Island mountain ranges of southeastern Arizona, USA, contain a unique and rich avifaunal community. Habitat diversity from mixing of Madrean and Cordilleran flora supports many species, including Neotropical migratory species whose northern breeding ranges extend to these mountains, and species typical of similar habitats throughout western North America. Many species of concern from the National Audubon Society/American Bird Conservancy Watchlist (2007) and U.S. Fish and Wildlife Service (2008) Birds of Conservation Concern (<http://www.fws.gov/birdhabitat/Grants/NMBCA/BirdList.shtm>) occur within this area. The Mexican Highlands Partners In Flight (PIF) Physiographic Area Plan (http://www.blm.gov/wildlife/pl_81sum.htm, Sonoran Joint Venture Technical Committee 2006) and Arizona PIF plan (Latta and others 1999) indicate conservation issues of water use, urban development, overgrazing, and recreation. Understanding ecological factors that influence species richness of both resident and migratory species is important for conservation of this unique bird assemblage, yet few studies describe bird habitat requirements in the Sky Islands (e.g., Balda 1967; Block and others 1992; Block and Severson 1992; Hall and Mannan 1999; Marshall 1957). Past studies indicate riparian areas support the most bird species (Balda 1967; Strong and Bock 1990), but upland habitats also contribute to species diversity (Marshall 1957).

In: Gottfried, Gerald J.; Ffolliott, Peter F.; Gebow, Brooke S.; Eskeew, Lane G.; Collins, Loa C., comps. 2013. Merging science and management in a rapidly changing world: Biodiversity and management of the Madrean Archipelago III; 2012 May 1-5; Tucson, AZ. Proceedings. RMRS-P-67. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

We studied occupancy and cover type associations of forest birds across montane vegetative cover types in the Santa Rita, Santa Catalina, Huachuca, Chiricahua, and Pinaleno Mountains of southeastern Arizona from 1991 to 1995 (Block and others 1992; Block and Severson 1992). We used occupancy models (MacKenzie and others 2006) to estimate species richness and community dynamics (local species extinction, local species colonization), while accounting for detection (e.g., Dorazio and others 2006). Imperfect detection of species is important to include in analyses, especially with rare or elusive species, or when trying to assess change over time. Estimates of species richness and community dynamics could be biased if species occupy an area but were never detected during a survey or multiple surveys. This could lead to biased study conclusions used to guide management actions. Our objectives were to (1) estimate species richness across mountain range and cover type; (2) relate species occurrence to forest cover types within these ranges; and (3) estimate probability of local species extinction and colonization.

Methods

Study Area

Our study area (elevation: 1,470–3,000 m) consisted of woodlands, pine-oak forests (*Pinus* spp. – *Quercus* spp.), pine forests, and mixed-conifer forests within the Santa Rita, Santa Catalina, Huachuca, Chiricahua, and Pinaleno Mountains, of the Coronado National Forest and Fort Huachuca (Department of Defense) in southeastern Arizona, USA (fig. 1). Major tree species included Arizona white (*Q. arizonica*), silverleaf (*Q. hypoleucoides*), Emory (*Q. emoryi*), Gambel (*Q. gambeli*), and netleaf (*Q. reticulata*) oaks; ponderosa (*P. ponderosa*), Apache (*P. engelmanni*), Chihuahuan (*P. leiophylla*), Mexican white (*P. strobiformis*), and border pinyon (*P. discolor*)

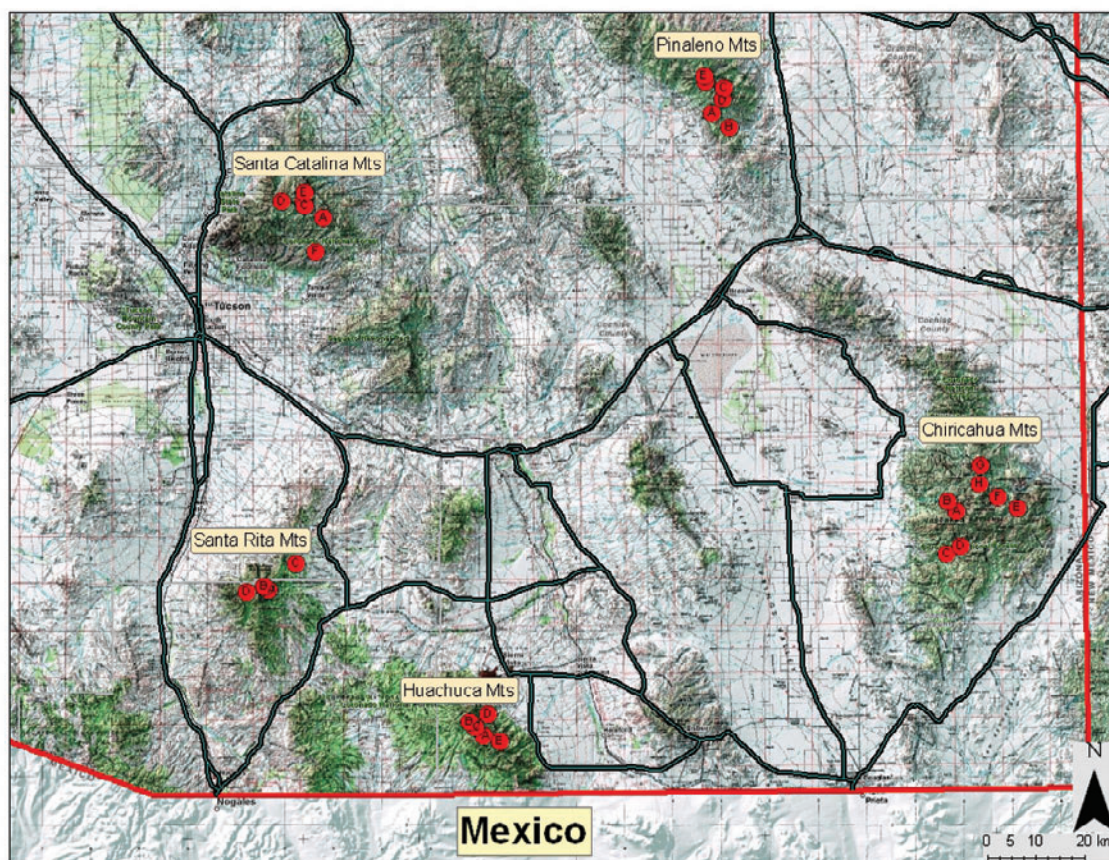


Figure 1—Study area from the Sky Island mountain ranges of Santa Catalina, Piñaleno, Santa Rita, Huachuca, and Chiricahua mountains of southeastern Arizona, USA from 1991 to 1995. Labeled dots within the mountain ranges indicate transect locations for avian point counts.

pinus; alligator-bark juniper (*Juniperus deppeana*); white fir (*Abies concolor*); and Douglas-fir (*Pseudotsuga menziesii*) (Iniguez and others 2005).

Field Sampling

Count points ($n = 344$) were located along transects consisting of 12 points spaced at 300 m intervals, with the exception of one transect that had only 8 points. Transects ($n = 29$) were established using a systematic-random sampling design (Cochran 1977), and occurred in proportion to occurrence of vegetation types in the landscape. Using the variable-radius point count method (Reynolds and others 1980), we sampled birds at each point three times during each breeding season (Apr-July) from 1991 to 1995. Counts (5 min/point) began within 30 min of sunrise and completed no later than 4 hr after sunrise. Observers remained still for 1-2 min after reaching a point, then recorded species, age, and sex of birds detected.

We sampled diameter at breast height (DBH) of all trees and snags in four 0.1-ha circular plots located within 100 m of each point count station. We used these data to estimate a weighted percent basal area average (WBA) of live and dead trees for each point count plot. We used cluster analysis with WBA (Iniguez and others 2005) to classify plots into 7 broad vegetative types for covariates in our occupancy models: deciduous forest, mixed-conifer forest, pine-oak forest, broadleaf evergreen woodland, conifer woodland, conifer riparian, and ponderosa pine.

Analytical Analyses

Our sampling design was a robust design (Pollock 1982), in which sampling occurred on up to three secondary periods (visits) during each primary period (years). Occupancy states of species can change with local extinction and colonization between primary periods, but not during secondary periods. We condensed data across points within each mountain $\times$ cover type combination to increase species detections per combination and reduce model complexity. Using these occupancy states with latent variable z_{ihmt} for occupancy of species i , cover type h , mountain m at time t , we calculated derived parameters, including species richness (N), species colonization (γ) and species extinction (ϵ). We calculated the average number of species in each mountain range and cover type over all 5 years:

$$N_{hm} = \frac{\sum_{t=1}^5 \sum_{i=1}^M z_{ihmt}}{5}.$$

We also calculated the average over all 5 years for local species colonization (γ), probability that a species selected at random from the community was not present in the community at time $t-1$, and local species extinction (ϵ), or probability that a species selected at random from the community was present at time $t-1$ but not at time t (Williams and others 2002):

$$\gamma(mh) = \frac{\sum_{t=1}^5 \left[\frac{\sum_{i=1}^M (z_{imht}) \times (1 - z_{imh,t-1})}{\sum_{i=1}^M z_{imh,t-1}} \right]}{5}$$

$$\varepsilon(mh) = \frac{\sum_{t=1}^5 \left[\frac{\sum_{i=1}^M (1 - z_{imht}) \times (z_{imh,t-1})}{\sum_{i=1}^M z_{imh,t-1}} \right]}{5}$$

We used a data matrix y , where element y_{imht} was a binary indicator of species detection. When $y_{imht} = 1$, species i ($i = 1, \dots, N$) was detected in mountain range m ($m = 1, \dots, 5$) in cover type h ($h = 1, \dots, 7$) of year t ($t = 1, \dots, 5$). We used the sum of binary species detection indicators for each species $\times$ mountain range $\times$ cover type $\times$ year combination over all three secondary periods during that combination ($y_{imht} = \{0, 1, 2, 3\}$). We used species and effort (eff) to model species detection and expected detection probability to increase with effort and to vary among species. We used latitude (lat) and cover type (hab) to model probability of occupancy of species. Since we condensed points by cover type and mountain range, we were unable to use elevation as an explanatory variable; however, there is a weak relationship between cover type and elevation (table 1). We expected that species occupancy patterns would vary among cover types, and species richness would decrease with increasing latitude due to loss of species with Mexican and Central American distributions. For numerical reasons, we used normalized covariates for effort and latitude. We defined effort as

number of points in each mountain range $\times$ cover type combination (table 1). Each sampling unit ($n = 35$) consists of points classified by cover type within each mountain range. We used the mean latitude from UTM coordinates of each mountain range as a covariate (Chiricahuas = 3533798, Huachucas = 3474145, Pinalenos = 3618746, Santa Catalinas = 3589560, Santa Ritas = 3509745).

Since we were interested in the whole avian community, quantification of both observed species and species we did not detect, but may have been present, were of interest. Bayesian hierarchical models with unknown species richness (Royle and Dorazio 2008: 384–387) that rely on data augmentation (e.g., Dorazio and others 2006) allow us to make inference on the entire community. We used a fixed supercommunity size M , so the posterior distribution of Ω , probability a species from the supercommunity was available for sampling during primary sampling periods, was centered well below its upper limit (e.g., $\Omega \leq 0.5$). We augmented the species observation matrix y with $(M - n_{obs})$ rows of zeros for all mountain range $\times$ cover type $\times$ primary period sampling sessions. We modeled probability of latent variable w_i of species i being available for sampling during all primary sampling periods given Ω as a Bernoulli trial:

$$[w_i | \Omega] \sim \text{Bern}(\Omega).$$

To model community change, we assumed a Markovian process described the current occupancy state of each species, whereby probability of occupancy at time t was partially dependent on probability of occupancy at time $t-1$. We modeled probability of Bernoulli latent variable z_{imht} for occupancy given probability of occupancy ψ_{imht} and w_i as:

$$[z_{imht} | \psi_{imht}, w_i] \sim \text{Bern}(\psi_{imht} \times w_i),$$

where occupancy probability ψ_{imht} is a function of covariates and the previous occupancy state:

Table 1—Number of avian sample points and elevation range across seven cover types within five mountain ranges in the Sky Islands, Arizona, USA 1991–1995. Normalized values of sampling effort were used as a covariate for estimating detection probability in our Bayesian hierarchical model. Elevation ranges (m) for each mountain range $\times$ cover type combination are indicated within parentheses below the number of sample points.

Mountain Range	Forest and woodland habitat types						
	Deciduous forest	Mixed-conifer forest	Pine-oak forest	Broadleaf evergreen woodland	Conifer woodland	Conifer Riparian	Ponderosa pine
Chiricahua	1 (2340)	12 (2207–2621)	24 (1780–2304)	17 (1692–2280)	25 (1591–2377)	4 (1890–2012)	9 (2283–2530)
Huachuca	1 (2446)	9 (2012–2438)	9 (1964–2278)	17 (1585–2134)	23 (1626–2568)	0 -	1 (2301)
Pinaleno	4 (1951–2749)	28 (2012–2926)	4 (2195–2414)	13 (1500–2118)	11 (1469–1987)	0 -	12 (2048–2554)
Santa Catalina	1 (2091)	25 (1957–2707)	11 (2018–2475)	13 (1487–2088)	6 (1561–1905)	0 -	16 (2048–2487)
Santa Rita	0 -	6 (2262–2396)	6 (1768–2219)	29 (1667–2341)	7 (1707–2274)	0 -	0 -

$$\text{logit}(\psi_{ihmt}) = \begin{cases} a_{i0} + a_{i1(0)} \times z_{ihm0} + a_{i2} \times \text{lat}_m + a_{i3h}, & t = 1 \\ a_{i0} + a_{i1} \times z_{ihm,t-1} + a_{i2} \times \text{lat}_m + a_{i3h}, & t > 1. \end{cases}$$

Values $a_{i1(0)}$ and a_{i1} describe local probability of survival for species i . These terms describe species-specific normal random effects: a_{i0} (intercept), a_{i3h} (cover type), and a_{i2} (latitude).

We modeled probability of observation of species i , y_{ihmt} , given the number of secondary periods J , probability of detection p_{ihm} and latent variable z_{ihmt} , using a binomial distribution with J trials and probability of success $p_{ihm} \times z_{ihmt}$:

$$[y_{ihmt} | J, p_{ihm}, z_{ihmt}] \sim \text{Bin}(J, p_{ihm} \times z_{ihmt}).$$

We used species and sampling effort (eff) as covariates to model probability of detection p :

$$\text{logit}(p_{ihm}) = b_{i0} + b_1 \times eff_{hm}.$$

We modeled heterogeneity among species using a covariance term between species intercepts of occurrence (a_{i0}) and detection probability (b_{i0}) (Royle and Dorazio 2008: p. 391), which allows us to make inference on occupancy and detection probability of species we never detected.

We used Bayesian hierarchical models (Gelman and others 2004) in R2WinBUGS (Sturtz and others 2005), an R (R Development Core Team 2011) package that interfaces with WinBUGS (Lunn and others 2000) to obtain parameter estimates. We used independent non-informative priors for parameters (uniform: $\Omega, a_{i1(0)}$; Bernoulli: z_{ihm0} ; Normal: $a_{i0}, a_{i1}, a_{i2}, a_{i3h}, b_{i0}, b_1$; e.g., $b_{i0} \sim N(\mu_{b_0}, \sigma_{b_0}^2)$). We ran four parallel chains (length 35,000 *it*, burn-in period 20,000 *it*, thinning 10 *it*) to obtain median parameter estimates and 95% Bayesian Credible Intervals (BCI). Convergence was reached ($\hat{R} = 1.0$ -1.1 [Brooks and Gelman 1998]). We assessed goodness-of-fit (GOF) using the squared loss and deviance test statistics for Bayesian p -values (Gelman and others 2004: p. 162).

Results

Over all mountain ranges, cover types, and years, we detected 158 bird species (table 2). Number of species observed (n_{obs}) was comparable ($n_{obs,1991} = 119, n_{obs,1992} = 117, n_{obs,1993} = 107, n_{obs,1994} = 120, n_{obs,1995} = 110$) across years. There was evidence of overdispersion (Bayesian p -value squared loss = 1.0, Bayesian p -value deviance = 0.66). The probability of a species being a supercommunity member (median $\Omega = 0.506$, 95% BCI: 0.408-0.68) indicates that our data augmentation step was appropriate. Detection probabilities varied by species (logit scale hyperprior medians: $\hat{\mu}_{b_0} = 0.078, \hat{\sigma}_{b_0}^2 = 0.797$)

and increased with increased sampling effort (median $\hat{b}_1 = 0.671$, 95% BCI: 0.627-0.714).

Average species richness was different for each mountain range and cover type, although 95% BCIs overlapped (fig. 2). For all mountain ranges, species richness was greatest in broadleaf evergreen woodland and conifer woodland cover types and least in deciduous forest. Species richness decreased as latitude increased in mixed-conifer, pine-oak woodland, broadleaf evergreen woodland and conifer riparian cover types. Deciduous forest, conifer woodland, and ponderosa pine cover types had no association with species richness and latitude. Average local extinction and colonization were similar for all cover types and mountain ranges (fig. 3), except for Pinaleno Mountain ponderosa pine ($\hat{\mathcal{E}} : 0.205 [0.156, 0.256]; \hat{\mathcal{Y}} : 0.383 [0.282, 0.549]$). Species turnover, or the process of local extinction and replacement of species

through local colonization, was greatest within deciduous forest for most mountain ranges and smallest within pine-oak forest, broadleaf evergreen woodland, and conifer woodland cover types.

Fourteen species had positive slopes with latitude and 18 species had negative slopes associated with latitude (95% BCIs for these species did not cross zero; fig. 4). Some species had positive median cover type slopes, although the 95% BCIs overlapped zero, for deciduous forest ($n = 3$), mixed-conifer forest ($n = 35$), pine-oak forest ($n = 25$), broadleaf evergreen woodland ($n = 57$), conifer woodland ($n = 64$), conifer riparian ($n = 6$) and ponderosa pine ($n = 17$) (table 2).

Discussion

We identified associations between forest cover type and avian species: broadleaf evergreen woodland and conifer woodland contributed the most species. Deciduous forest cover type, which occurred at higher elevations in these mountain ranges, had the greatest species turnover, but fewest species. As expected, species richness increased with decreased latitudes in four of the seven cover types. Many species that occur in southerly latitudes have Mexican and Central American distributions (e.g., elegant trogon, eared trogon, thick-billed parrot [scientific names given in table 2]). Southernmost Arizona mountain ranges encompass the northern part of these species ranges. These relationships in mixed-conifer, pine-oak woodland, broadleaf evergreen woodland and conifer riparian cover types may have implications for avian range shifts with climate change. Most climate models predict warmer and drier future conditions in the southwestern United States (Seager and others 2007), thus species whose ranges are more southern may move northward with warming climates, particularly if changes create expanded habitat availabilities. Lower elevation cover types may shift upwards and higher elevation cover types may shrink or disappear, leading to decline or loss of species with strong habitat associations.

Our results suggest not all species present were detected during sampling and detection probability increased with increased sampling effort. This highlights the importance of sample design and accounting for detection probabilities within occupancy models (MacKenzie and others 2006). Detection probabilities are critical in studies that assess changes over time or responses to disturbance events, because detection probability may change over time or with habitat changes. Several species in our study had low detectability, which is known to cause bias in occupancy estimates (MacKenzie and others 2006: p. 107) and can lead to inflated estimates of species richness.

Our preliminary analyses suggest that cover type may not be the best explanatory variable for the probability of occupancy due to some evidence of overdispersion. Other factors like elevation, microhabitat structure, slope and aspect, mountain range area, and distance to other mountains may have more explanatory power, which warrants future exploration. Future analyses will focus on estimating relative abundances (sensu Royle and Nichols 2003), detailed habitat relationships of individual avian species, especially species of conservation concern, and evaluation of resident and migratory species for their relative contributions to species richness and community dynamics. This information will be valuable to managers charged with conserving this unique avifauna, and aid in assessing potential impacts of changing climates.

Our study also provides a baseline for future studies in this Global Important Bird Area (Audubon Society). The Sky Islands have been impacted by several large-scale, habitat altering disturbance events in recent years (e.g., the 2011 Horseshoe Two fire burned 90,307 ha

within the Chiricahua Mountains) and these large-scale disturbance events may become more frequent as climate in the southwestern United States becomes warmer and drier (McKenzie and others 2004). Consequent changes in habitat structure could influence avian

community dynamics in these ranges. We know little about effects of fire and other disturbances on Neotropical migratory birds in this region (Ganey and others 1996; Kirkpatrick and others 2006), thus, future monitoring aimed at evaluating effects of fire events and climate shifts on avian species in the region are paramount.

Table 2—Avian species with positive posterior medians associated with cover types within the five Sky Island mountain ranges in southeastern Arizona, USA from 1991 to 1995. The number '1' indicates a positive posterior median for the specific habitat type. Some species did not have any positive associations and some species were associated with more than one cover type.

Common species name	Scientific name	Dec. for.	Mix.- conf. for.	Pine- oak for.	Brd. Evgr. wd.	Conf. wd.	Conf. ripa.	Pond. pine
Mallard	<i>Anas platyrhynchos</i>	0	0	0	0	1	0	0
Gambel's quail	<i>Callipepla gambelii</i>	0	0	0	1	1	0	0
Scaled quail	<i>Callipepla squamata</i>	0	0	0	0	0	0	0
Montezuma quail	<i>Cyrtonyx montezumae</i>	0	0	0	1	1	0	0
Wild turkey	<i>Meleagris gallopavo</i>	0	0	0	0	0	0	0
Turkey vulture	<i>Cathartes aura</i>	0	0	0	1	1	0	0
Cooper's hawk	<i>Accipiter cooperii</i>	0	0	0	0	0	0	0
Northern goshawk	<i>Accipiter gentilis</i>	0	1	0	0	0	0	1
Sharp-shinned hawk	<i>Accipiter striatus</i>	0	0	0	0	1	0	0
Gray hawk	<i>Buteo nitidus</i>	0	0	0	0	0	0	0
Zone-tailed hawk	<i>Buteo albonotatus</i>	0	0	0	0	0	0	1
Red-tailed hawk	<i>Buteo jamaicensis</i>	0	0	0	1	0	0	0
Common black-hawk	<i>Buteogallus anthracinus</i>	0	0	0	0	0	0	1
Golden eagle	<i>Aquila chrysaetos</i>	0	0	0	0	0	0	0
Prairie falcon	<i>Falco mexicanus</i>	0	0	0	0	1	0	0
American kestrel	<i>Falco sparverius</i>	0	0	0	0	0	0	0
Band-tailed pigeon	<i>Patagioenas fasciata</i>	0	0	1	0	0	0	0
Rock dove	<i>Columba livia</i>	0	0	0	0	0	0	1
White-winged dove	<i>Zenaida asiatica</i>	0	0	0	1	1	0	0
Mourning dove	<i>Zenaida macroura</i>	0	0	0	1	1	0	0
Thick-billed parrot	<i>Rhynchopsitta pachyrhyncha</i>	0	1	0	0	0	0	0
Greater roadrunner	<i>Geococcyx californianus</i>	0	0	0	1	1	0	0
Great horned owl	<i>Bubo virginianus</i>	0	0	0	0	0	0	0
Northern pygmy-owl	<i>Glaucidium gnoma</i>	0	0	1	0	0	0	0
Flammulated owl	<i>Otus flammeolus</i>	0	1	0	0	0	0	0
Whiskered screech-owl	<i>Megascops trichopsis</i>	0	0	1	0	0	0	0
Spotted owl	<i>Strix occidentalis</i>	0	1	0	0	0	0	0
Lesser nighthawk	<i>Chordeiles acutipennis</i>	0	0	0	0	1	0	0
Eastern whip-poor-will	<i>Caprimulgus vociferus</i>	0	0	0	1	0	0	1
White-throated swift	<i>Aeronautes saxatalis</i>	0	1	0	0	0	1	0
Black-chinned hummingbird	<i>Archilochus alexandri</i>	0	0	1	1	1	0	0
Anna's hummingbird	<i>Calypte anna</i>	0	0	0	1	0	0	0
Costa's hummingbird	<i>Calypte costae</i>	0	0	0	0	0	0	0
Broad-billed hummingbird	<i>Cynanthus latirostris</i>	0	0	0	0	1	1	0
Magnificent hummingbird	<i>Eugenes fulgens</i>	0	1	0	0	0	0	0

(continued)

Table 2—Continued

Common species name	Scientific name	Dec. for.	Mix.- conf. for.	Pine- oak for.	Brd. Evgr. wd.	Conf. wd.	Conf. ripa.	Pond. pine
Blue-throated hummingbird	<i>Lampornis clemenciae</i>	0	0	0	0	0	1	0
Broad-tailed hummingbird	<i>Selasphorus platycercus</i>	0	1	0	0	0	0	0
Rufous hummingbird	<i>Selasphorus rufus</i>	0	0	0	0	0	0	0
Eared quetzal	<i>Euptilotis neoxenus</i>	0	0	0	0	0	0	0
Elegant trogon	<i>Trogon elegans</i>	0	0	1	0	0	1	0
Northern flicker	<i>Colaptes auratus</i>	0	0	0	0	0	0	0
Acorn woodpecker	<i>Melanerpes formicivorus</i>	0	0	1	1	1	0	0
Gila woodpecker	<i>Melanerpes uropygialis</i>	0	0	0	1	0	0	0
Ladder-backed woodpecker	<i>Picoides scalaris</i>	0	0	0	1	1	0	0
Strickland's woodpecker	<i>Picoides stricklandii</i>	0	0	0	1	1	0	0
Hairy woodpecker	<i>Picoides villosus</i>	0	1	1	0	0	0	1
Red-naped sapsucker	<i>Sphyrapicus nuchalis</i>	0	1	0	0	0	0	0
Northern beardless-tyrannulet	<i>Camptostoma imberbe</i>	0	0	0	1	1	0	0
Black phoebe	<i>Sayornis nigricans</i>	0	0	0	0	1	0	0
Say's phoebe	<i>Sayornis saya</i>	0	0	0	1	0	0	0
Olive-sided flycatcher	<i>Contopus cooperi</i>	0	0	0	0	0	0	0
Greater pewee	<i>Contopus pertinax</i>	0	1	1	0	0	0	1
Western wood-pewee	<i>Contopus sordidulus</i>	0	0	1	0	0	0	0
Pacific-slope flycatcher	<i>Empidonax difficilis</i>	0	1	0	0	0	0	0
Buff-breasted flycatcher	<i>Empidonax fulvifrons</i>	0	1	0	0	0	0	0
Hammond's flycatcher	<i>Empidonax hammondi</i>	0	1	0	0	0	0	0
Dusky flycatcher	<i>Empidonax oberholseri</i>	0	0	0	0	1	0	0
Cordilleran flycatcher	<i>Empidonax occidentalis</i>	0	1	0	0	0	0	0
Gray flycatcher	<i>Empidonax wrightii</i>	0	0	0	1	0	0	0
Dusky-capped flycatcher	<i>Myiarchus tuberculifer</i>	0	0	0	0	1	0	0
Ash-throated flycatcher	<i>Myiarchus cinerascens</i>	0	0	0	1	1	0	0
Brown-crested flycatcher	<i>Myiarchus tyrannulus</i>	0	0	0	0	1	0	0
Sulphur-bellied flycatcher	<i>Myiodynastes luteiventris</i>	0	0	1	0	0	0	0
Thick-billed kingbird	<i>Tyrannus crassirostris</i>	0	0	0	0	1	0	0
Western kingbird	<i>Tyrannus verticalis</i>	0	0	0	0	0	0	0
Cassin's kingbird	<i>Tyrannus vociferans</i>	0	0	0	1	1	0	0
Rose-throated becard	<i>Pachyramphus aglaiae</i>	0	0	0	1	0	0	0
Loggerhead shrike	<i>Lanius ludovicianus</i>	0	0	0	1	0	0	0
Bell's vireo	<i>Vireo bellii</i>	0	0	0	0	1	0	0
Warbling vireo	<i>Vireo gilvus</i>	0	1	1	0	0	0	0
Hutton's vireo	<i>Vireo huttoni</i>	0	0	1	1	0	0	0
Plumbeous vireo	<i>Vireo plumbeus</i>	0	0	1	0	0	0	0
Gray vireo	<i>Vireo vicinior</i>	0	0	0	0	1	0	0
Western scrub-jay	<i>Aphelocoma californica</i>	0	0	0	1	1	0	0
Stellar's jay	<i>Cyanocitta stelleri</i>	0	0	1	0	0	0	0
Gray jay	<i>Perisoreus canadensis</i>	0	0	1	1	1	0	0
Common raven	<i>Corvus corax</i>	0	0	0	1	0	0	0
Chihuahan raven	<i>Corvus cryptoleucus</i>	0	0	0	0	0	0	0
Tree swallow	<i>Tachycineta bicolor</i>	0	1	0	0	0	0	0

(continued)

Table 2—Continued

Common species name	Scientific name	Dec. for.	Mix.- conf. for.	Pine- oak for.	Brd. Evgr. wd.	Conf. wd.	Conf. ripa.	Pond. pine
Violet-green swallow	<i>Tachycineta thalassina</i>	0	1	0	0	0	0	0
Mountain chickadee	<i>Poecile gambeli</i>	0	0	0	0	0	0	0
Mexican chickadee	<i>Poecile sclateri</i>	0	0	0	0	0	0	0
Juniper titmouse	<i>Baeolophus ridgwayi</i>	0	0	0	1	1	0	0
Bridled titmouse	<i>Baeolophus wollweberi</i>	0	0	0	1	1	0	0
Verdin	<i>Auriparus flaviceps</i>	0	0	0	0	1	0	0
Bushtit	<i>Psaltiriparus minimus</i>	0	0	0	1	1	0	0
Red-breasted nuthatch	<i>Sitta canadensis</i>	0	1	0	0	0	0	0
White-breasted nuthatch	<i>Sitta carolinensis</i>	0	0	0	0	0	0	0
Pygmy nuthatch	<i>Sitta pygmaea</i>	0	1	0	0	0	0	1
Brown creeper	<i>Certhia americana</i>	0	1	1	0	0	0	1
Canyon wren	<i>Catherpes mexicanus</i>	0	0	0	1	1	1	0
Rock wren	<i>Salpinctes obsoletus</i>	0	0	0	1	1	0	0
Bewick's wren	<i>Thryomanes bewickii</i>	0	0	0	1	1	0	0
House wren	<i>Troglodytes aedon</i>	0	1	0	0	0	0	0
Winter wren	<i>Troglodytes hiemalis</i>	0	0	0	0	0	0	1
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>	0	0	0	1	1	0	0
Black-tailed gnatcatcher	<i>Poliophtila melanura</i>	0	0	0	1	0	0	0
Ruby-crowned kinglet	<i>Regulus calendula</i>	0	0	0	1	1	0	0
Golden-crowned kinglet	<i>Regulus satrapa</i>	0	1	0	0	0	0	0
Mountain bluebird	<i>Sialia currucoides</i>	0	0	0	0	0	0	1
Western bluebird	<i>Sialia mexicana</i>	0	0	0	0	0	0	0
Eastern bluebird	<i>Sialia sialis</i>	0	1	0	0	0	0	0
Townsend's solitaire	<i>Myadestes townsendi</i>	0	0	0	0	0	0	1
Hermit thrush	<i>Catharus guttatus</i>	0	1	1	0	0	0	0
Swainson's thrush	<i>Catharus ustulatus</i>	0	1	0	0	0	0	0
American robin	<i>Turdus migratorius</i>	0	0	1	0	0	0	0
Northern mockingbird	<i>Mimus polyglottos</i>	0	0	0	1	1	0	0
Bendire's thrasher	<i>Toxostoma bendirei</i>	0	0	0	0	0	0	0
Crissal thrasher	<i>Toxostoma crissale</i>	0	0	0	1	1	0	0
Curve-billed thrasher	<i>Toxostoma curvirostre</i>	0	0	0	1	1	0	0
Cedar waxwing	<i>Bombycilla cedrorum</i>	0	0	0	1	1	0	0
Phainopepla	<i>Phainopepla nitens</i>	0	0	0	1	0	1	0
Olive warbler	<i>Peucedramus taeniatus</i>	0	1	0	0	0	0	1
Red-faced warbler	<i>Cardellina rubrifrons</i>	0	1	1	0	0	0	0
Yellow-rumped warbler	<i>Setophaga coronata</i>	0	1	1	0	0	0	0
Grace's warbler	<i>Setophaga graciae</i>	0	1	1	0	0	0	0
Black-throated gray warbler	<i>Setophaga nigrescens</i>	0	0	1	1	1	0	0
Hermit warbler	<i>Setophaga occidentalis</i>	0	1	0	0	0	0	0
Townsend's warbler	<i>Setophaga townsendi</i>	0	0	0	1	0	0	1
Painted redstart	<i>Myioborus picta</i>	0	0	1	0	0	0	0
MacGillivray's warbler	<i>Geothlypsis tolmiei</i>	1	0	0	0	0	0	0
Orange-crowned warbler	<i>Oreothlypsis celata</i>	1	1	0	0	0	0	0
Lucy's warbler	<i>Oreothlypsis luciae</i>	0	0	0	0	1	0	0

(continued)

Table 2—Continued

Common species name	Scientific name	Dec. for.	Mix.- conf. for.	Pine- oak for.	Brd. Evgr. wd.	Conf. wd.	Conf. ripa.	Pond. pine
Nashville warbler	<i>Oreothlypis ruficapilla</i>	0	0	0	0	1	0	0
Virginia's warbler	<i>Oreothlypis virginiae</i>	0	0	1	0	0	0	0
Wilson's warbler	<i>Cardellina pusilla</i>	0	0	0	1	0	0	0
Abert's towhee	<i>Melospiza aberti</i>	0	0	0	0	1	0	0
Green-tailed towhee	<i>Pipilo chlorurus</i>	0	0	0	1	1	0	0
Canyon towhee	<i>Melospiza fusca</i>	0	0	0	1	1	0	0
Spotted towhee	<i>Pipilo maculatus</i>	0	0	0	0	0	0	0
Rufous-crowned sparrow	<i>Aimophila ruficeps</i>	0	0	0	1	1	0	0
Black-throated sparrow	<i>Amphispiza bilineata</i>	0	0	0	1	1	0	0
Lark sparrow	<i>Chondestes grammacus</i>	0	0	0	0	0	0	0
Black-chinned sparrow	<i>Spizella atrogularis</i>	0	0	0	1	1	0	0
Chipping sparrow	<i>Spizella passerina</i>	0	0	0	1	1	0	0
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	0	0	0	0	1	0	0
Dark-eyed junco	<i>Junco hyemalis</i>	0	0	0	1	1	0	0
Yellow-eyed junco	<i>Junco phaeonotus</i>	0	1	1	0	0	0	0
Hepatic tanager	<i>Piranga flava</i>	0	0	0	1	1	0	0
Western tanager	<i>Piranga ludoviciana</i>	0	0	0	0	0	0	0
Summer tanager	<i>Piranga rubra</i>	0	0	0	0	1	0	0
Northern cardinal	<i>Cardinalis cardinalis</i>	0	0	0	1	1	0	0
Pyrrhuloxia	<i>Cardinalis sinuatus</i>	0	0	0	0	1	0	0
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	0	0	0	0	0	0	0
Blue grosbeak	<i>Passerina caerulea</i>	0	0	0	1	0	0	0
Lazuli bunting	<i>Passerina amoena</i>	0	0	0	0	1	0	0
Eastern meadowlark	<i>Sturnella magna</i>	0	0	0	0	0	0	0
Western meadowlark	<i>Sturnella neglecta</i>	0	0	0	0	1	0	0
Brown-headed cowbird	<i>Molothrus ater</i>	0	0	0	1	1	0	0
Hooded oriole	<i>Icterus cucullatus</i>	0	0	0	0	1	0	0
Bullock's oriole	<i>Icterus bullockii</i>	0	0	0	1	1	0	0
Scott's oriole	<i>Icterus parisorum</i>	0	0	0	1	1	0	0
Pine siskin	<i>Spinus pinus</i>	0	1	0	0	0	0	1
Lesser goldfinch	<i>Spinus psaltria</i>	0	0	0	1	1	0	0
Cassin's finch	<i>Carpodacus cassinii</i>	0	1	0	0	0	0	0
House finch	<i>Carpodacus mexicanus</i>	0	0	0	1	1	0	0
Evening grosbeak	<i>Coccothraustes vespertinus</i>	1	1	0	0	0	0	0
Red crossbill	<i>Loxia curvirostra</i>	0	0	0	0	0	0	1

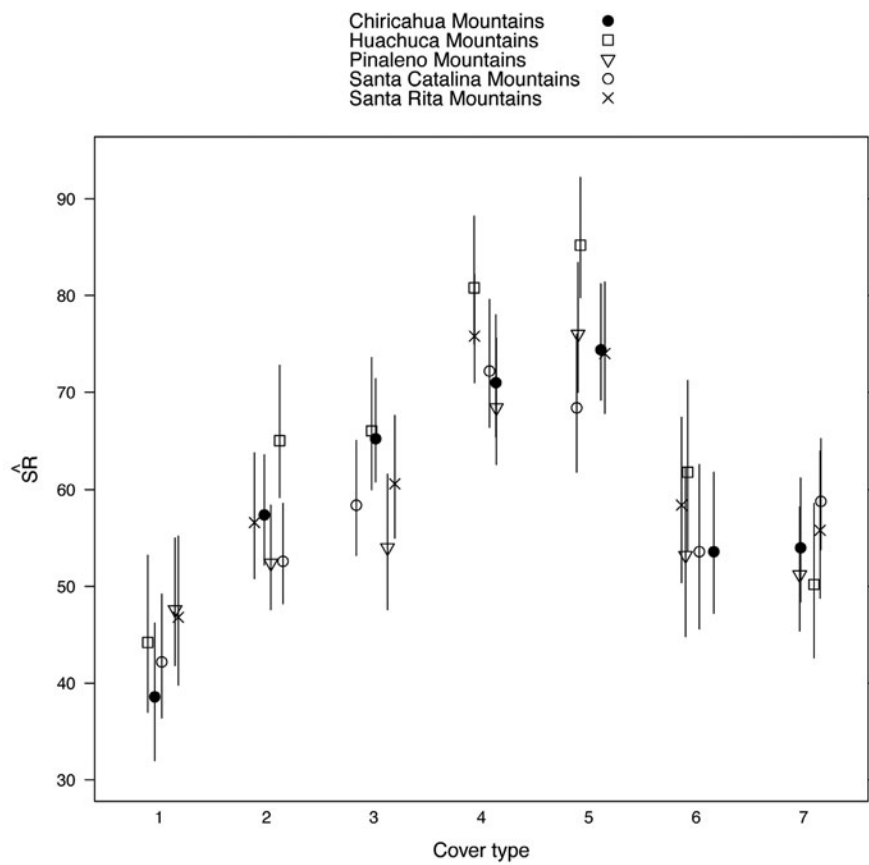


Figure 2—Median posterior estimates of average species richness (SR) and 95% Bayesian credible intervals over all years from 1991 to 1995 for the five Sky Island mountain ranges of southeastern Arizona, USA. Estimates are separated by cover type (1 = deciduous forest, 2 = mixed-conifer forest, 3 = pine-oak forest, 4 = broadleaf evergreen woodland, 5 = conifer woodland, 6 = conifer riparian, 7 = ponderosa pine).

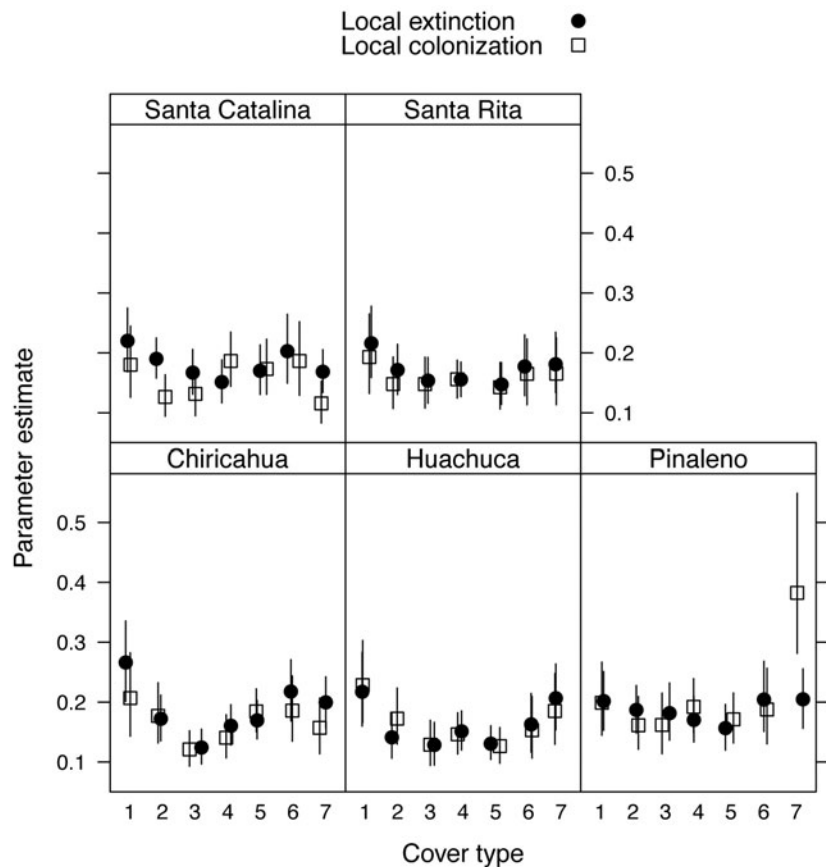


Figure 3—Median posterior estimates of local extinction and local colonization and 95% Bayesian credible intervals over all years from 1991 to 1995 for the five Sky Island mountain ranges of southeastern Arizona, USA. Estimates are separated by cover type (1 = deciduous forest, 2 = mixed-conifer forest, 3 = pine-oak forest, 4 = broadleaf evergreen woodland, 5 = conifer woodland, 6 = conifer riparian, 7 = ponderosa pine).

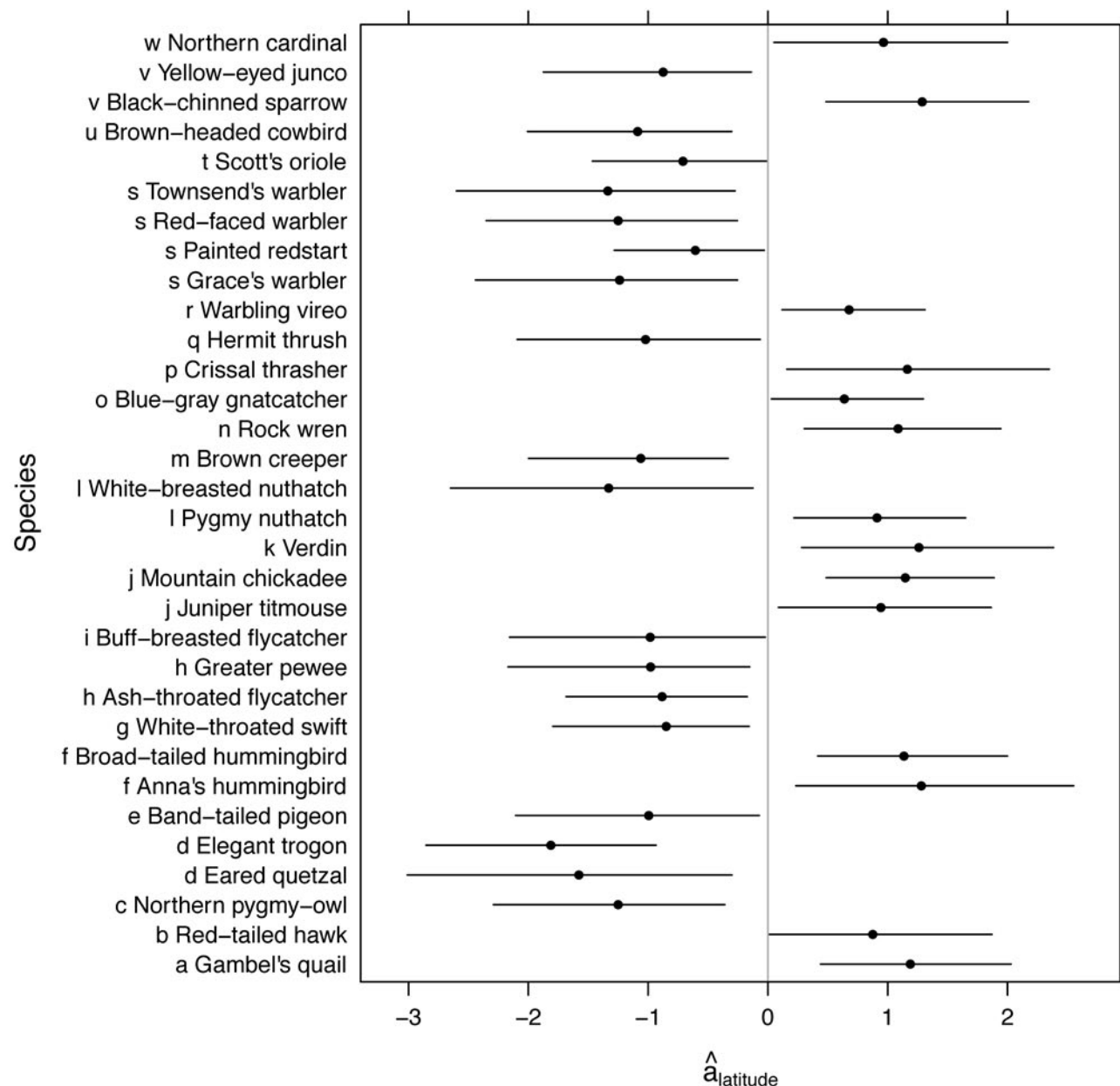


Figure 4—Significant median posterior estimates for the latitude slope parameter ($\hat{a}_{latitude}$) and 95% Bayesian credible intervals of individual avian species from a study conducted from 1991 to 1995 in five Sky Island mountain ranges of southeastern Arizona, USA. Positive associations indicate that the probability of occupancy for those species increases with increasing latitude, while negative associations indicate probability of occupancy decreases with increasing latitude. Scientific names for these species are given within Table 2. Species are ordered according to taxon or family group (letters indicate separate groups).

Acknowledgments

We thank field crews for collecting avian and vegetation data; The Coronado National Forest, The Nature Conservancy, Fort Huachuca, Santa Rita Experimental Station, and Audubon Research Ranch for logistics/technical assistance; National Fire Plan for funding (JSS); L. Hall, Q. Latif, and D. Turner for helpful comments during review.

References

- Balda, R.P. 1967. Ecological relationships of the breeding birds of the Chiricahua Mountains, Arizona. Ph.D. Dissertation, University of Illinois, Urbana.
- Block, W.M.; Ganey, J.L.; Severson, K.E.; and Morrison, M.L. 1992. Use of oaks by Neotropical migratory birds in the southwest. Pp. 65-70 in: Ffolliott, P.F.; Gottfried, G.J.; Bennett, D.A.; Hernandez, C.; Ortega-Rubio, A.; and Hamre, R.H., tech cord. Ecology and management of oak and associated woodlands: perspectives in the southwestern United States and northern Mexico. Gen. Tech. Rep. RM-218. U.S. Department of Agriculture, For-

- est Service, Rocky Mountain Forest and Range Experiment Station. Fort Collins, CO.
- Block, W.M.; and Ganey, J.L. 1992. Study Plan Number RM-4251-3-12: Habitat associations of Neotropical migrant birds in the insular mountains of southeastern Arizona. Rocky Mountain Research Station. Flagstaff, AZ.
- Block, W.M.; and Severson, K.E. 1992. Habitat associations of birds and herpetofauna in southeastern Arizona. Pp. 55-57 *in*: Chiricahua Mountains Research Symposium Proceedings; 1992 16-17 March; Chiricahua Mountains, AZ; Southwestern Parks and Monuments Association.
- Brooks, S.B.; and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434-455.
- Cochran, W.G. 1977. Sampling techniques, Third edition. Wiley, New York.
- Dorazio, R.M.; Royle, J.A.; Söderström, B.; and Glimskär, A. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842-854.
- Ganey, J.L.; Block, W.M.; and Boucher, P.F. 1996. Effects of fire on birds in Madrean forests and woodlands. Pp. 146-154 *in*: Ffolliott, P.F.; DeBano, L.F.; Baker, M.B.; [and others], tech coords. Gen. Tech. Rep. RM-GTR-289. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. Fort Collins, CO.
- Gelman, A.; Carlin, J.B.; Stern, H.S.; and Rubin, D.B. 2004. Bayesian data analysis, 2nd edition. Chapman and Hall/CRC, New York.
- Hall, L.S.; and Mannan, R.W. 1999. Multiscaled habitat selection by elegant trogons in southeastern Arizona. *Journal of Wildlife Management* 63:451-461.
- Iniguez, J.M.; Ganey, J.L.; Dougherty, P.J.; and Bailey, J.D. 2005. Using cluster analysis and a classification and regression tree model to identify cover types in the sky islands of southeastern Arizona. Pp.195-200 *in*: Gottfried, G.J.; Gebow, B.S.; Eskew, L.G.; and Edminster, C.B., comps. Connecting mountain islands and desert seas: biodiversity and management of the Madrean Archipelago II. Proc. RMRS-P-36. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, CO.
- Kirkpatrick, C.; Conway, C.J.; and Jones, P.B. 2006. Distribution and relative abundance of forest birds in relation to burn severity in southeastern Arizona. *Journal of Wildlife Management* 70:1005-1012.
- Latta, M.J.; Beardmore, C.J.; and Corman, T.E. 1999. Arizona Partners in Flight Bird Conservation Plan. Version 1.0. Nongame and Endangered Wildlife Program Technical Report 142. Arizona Game and Fish Department, Phoenix, AZ.
- Lunn, D.J.; Thomas, A.; Best, N.; and Spiegelhalter, D. 2000. WinBUGS – a Bayesian modeling framework: concepts, structure, and extensibility. *Statistics and Computing* 10:325-337.
- MacKenzie, D.I.; Nichols, J.D.; Royle, J.A.; Pollock, K.H.; Bailey, L.L.; and Hines, J.E. 2006. Occupancy estimation and modeling. Academic Press, New York.
- Marshall, J.T.Jr. 1957. Birds of the pine-oak woodland in southern Arizona and adjacent Mexico. *Pacific Coast Avifauna* 32.
- McKenzie, D.; Gedalof, Z.; Peterson, D.L.; and Mote, P. 2004. Climate change, wildfire, and conservation. *Conservation Biology* 18:890-902.
- Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:757-760.
- R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Reynolds, R.T.; Scott, J.M.; and Nussbaum, R.A. 1980. A variable circular plot method for estimating bird numbers. *Condor* 82:309-313.
- Royle, J.A.; and Nichols, J.D. 2003. Estimating abundance from repeated presence absence data or point counts. *Ecology* 84:777-790.
- Royle, J.A.; and Dorazio, R.M. 2008. Hierarchical modeling and inference in ecology. Academic Press, New York.
- Seager, R.; and others 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316:1181-1184.
- Strong, T.R.; and Bock, C.E. 1990. Bird species distribution patterns in riparian habitats in southeastern Arizona. *Condor* 866-885.
- Sturtz, S.; Ligges, U.; and Gelman, A. 2005. R2WinBUGS: A package for running WinBUGS from R. *Journal of Statistical Software* 12:1-16.
- Williams, B.K.; Nichols, J.D.; and Conroy, M.J. 2002. Estimation of community parameters. Pp. 555-573 *in* Analysis and management of animal populations. Academic Press, San Diego.