Chapter 4

Songbird Status and Roles

Linnea S. Hall, Michael L. Morrison, and William M. Block

Introduction

This chapter reviews studies on songbird ecology conducted in Arizona, New Mexico, and Colorado; studies from outside this region are mentioned when they bear direct relevance to our primary region. The studies were conducted in sites where ponderosa pine occurred at least in equal coverage with other trees. We also include studies conducted in pine-oak (pine predominant) or oak-pine (oak predominant) woodlands of southeastern Arizona and Southwestern New Mexico. Our review begins with population studies, including research on distribution, abundance, and trends in population numbers. We then discuss the various roles of birds in the ponderosa pine forest. Next we cover the multifaceted topic of avian natural history and habitat preferences, including use of vegetation and special habitat features, nest predation, foraging habits, and migration habits. We also review the prioritization systems for identifying species of special research and management concern.

Population Status

Research Limitations

Long-term data sets such as Breeding Bird Surveys (Robbins et al. 1986; Peterjohn et al. 1995) and Christmas Bird Counts (Bock and Root 1981) usually allow for indices of relative abundance. Results of many research studies compare absolute or relative abundance of birds among different impacts (such as logging and fire) or conditions (such as varying tree density and season). But few data exist to estimate population parameters such as survival and reproduction. Few data are available to examine nonbreeding or migrating populations because most of the data are collected during the breeding season. Trend data are limited to Breeding Bird Surveys (BBS) and Christmas Bird Counts (CBC); we found no relevant Breeding Bird Census trend data (Marshall 1991). Breeding Bird Atlas data for the Southwest are too recent (collecting started in 1994) to provide trend information (T. Corman, Arizona Dept. of Game and Fish, personal communication).

Therefore, we review here the information on populations by summarizing relevant research results and by summarizing BBS data to examine population trends. Rigorous comparisons of population estimates from different research projects are difficult because of different data collection methods, different sampling intensities, different skill levels of observers, and different analytic techniques. Also, methods used to sample avian populations have inherent biases (compare Verner 1985, for a review of avian census methods). Thus, we limit our discussion of research results to brief descriptions of major studies and to generalizations based on the collective results of these studies.

Research Results

Szaro and Balda (1979) measured breeding bird populations within the Beaver Creek watershed of the Coconino National Forest, Arizona. Vegetation within their study area was dominated by ponderosa pine with Gambel oak and alligator juniper in the understory. They used spot mapping to index densities of individual species and selected guilds (as defined by Root 1967:335) on five plots representing different intensities of logging, from clearcut to control (that is, no logging). As might be expected, bird densities varied among plots and among years. Whether the variations in numbers represented effects of different cutting regimes, however, is difficult to assess; inferences about cause-effect relationships of logging will be covered in the following chapters and we will not duplicate that material here. However, bird populations were generally greatest on the "strip cut" and "silviculturally cut" plots and lowest on the clearcut plots; densities of birds on the control (unlogged) plot were intermediate to these extremes (table 1). Spotted towhees and rock wrens were the most abundant species on the clearcut plot; dark-eyed junco, Steller's jay, and white-breasted nuthatch were most abundant on the "severely thinned" plot; Grace's warbler, solitary vireo, dark-eyed junco, and chipping sparrow on the strip cut plot; dark-eyed junco, pygmy nuthatch, and Grace's warbler on the silviculturally cut plot; and white-breasted nuthatch, pygmy nuthatch, dark-eyed junco, and Grace's warbler on the control plot.

Siegel (1989) examined habitats and populations of breeding birds in old-growth ponderosa pine forests on the Kaibab Plateau, Arizona. He compared bird numbers among stands representing different densities of trees:

Table 1. Comparison of population estimates in ponderosa pine forests. See text for details of each study. Numbers provided are ranges of population estimates from study sites sampled in each study.

Species	Szaro & Balda[a]	Siegel[b]	Overturf[c]	Horton & Mannan[d]	Blake[e]			Haldeman et al[f]	
					Fall	Winter	Spring	Spring	Winter
Mourning dove	3.0–6.0	0.2–2.6	0.0–10.0		0.0–0.2			7	
Band-tailed pigeon			0.0–0.8				0.0–0.4		
Common poorwill		0.0–0.4			0.0–0.2				
Common nighthawk	0.0–3.0	0.0–0.4	0.0–10.0						
Br-tailed hurnrningbird	3.0–15.0	4.4–22.1	0.0–15.0				0.0–0.5	3	
Lewis' woodpecker					0.0–2.0	0.0–1.4			
Yellow-bellied sapsucker						0.0–0.2			0.1
Acorn woodpecker	0.0–3.0	0.0–0.4	0.0–5.0	1.1–4.0	0.0–1.2	0.0–0.2	0.0–0.2		
Hairy woodpecker	1.5–6.0	2.8–5.8	2.0–12.0	0.7–1.0	0.0–7.3	0.0–1.2	0.0–2.4	5	1.3
Three-toed woodpecker		0.0–2.3	0.0–5.0						0.04
Northern flicker	1.5–3.8	2.5–8.1	2.0–10.0	1.7–2.6	0.0–0.6		**0.0–0.8**	**9**	0.9
Williamson's sapsucker		0.6–6.1							
Cassin's kingbird							0.0–0.2		
Ash-throated flycatcher							0.0–0.2		
Say's phoebe	0.0–3.0								
Western wood pewee	1.5–9.0	0.2–8.2	0.0–15.0		0.0–1.0			4	
Olive-sided flycatcher		0.4–0.8	0.0–5.0				0.0–0.2		
Cordilleran flycatcher	3.0–6.8	0.0–0.4	0.0–3.0	39.2–67.0			0.0–0.2	7	
White-throated swift	0.0–0.4	0.0–0.4							
Violet–green swallow	3.0–9.0	0.4–20.1	0.0–50.0	17.6–37.4			0.0–10.3	30	
American crow									0.1
Common raven		**0.0–1.0**							
West. scrub jay					0.0–0.2				
Steller's jay	3.0–9.0	1.1–1.8	0.0–10.0		0.0–0.5	0.0–2.0	0.0–0.2	8	0.1
Clark's nutcracker		0.0–0.3							0.04
Mountain chickadee	1.5–9.0	0.4–8.7	0.0–30.0	5.6–12.2	0.0–0.9	0.0–0.4		20	3.4
Plain titmouse						0.0–0.2			
White-breasted nuthatch	3.0–15.0	1.6–3.3	0.0–13.0	2.9–7.0	0.0–4.9	0.0–0.4	0.0–0.8	7	4.1
Red-breasted nuthatch	0.2								
Pygmy nuthatch	1.5–18.0	7.7–16.0	0.0–53.0	14.2–26.2	0.0–0.6		0.0–2.6	26	10.3
Brown creeper		3.4–12.2	0.0–17.0	5.8–9.8			0.0–0.8	8	
House wren	2.3–3.0	0.0–4.4	0.0–54.0	15.0–96.8	0.0–0.2		0.0–1.5		
Canyon wren	0.0–0.2								
Rock wren	3.8–8.3	4.9–16.8	0.0–9.0				0.0–1.0		
Ruby-crowned kinglet					0.0–8.0	0.0–7.1	0.0–0.5		
Loggerhead shrike							0.0–0.2		
American robin	1.0–7.5	2.3–4.2	0.0–17.0		0.0–2.7		0.0–0.2	20	1.1
Townsend's solitaire		0.4–2.6							
Hermit thrush	0.8–2.3	1.9–4.6	0.0–3.0		0.0–0.2			8	
Western bluebird	3.0–15.0	5.8–14.1	5.0–30.0	6.1–12.4	0.0–6.5	0.0–17.4	0.0–5.8	15	3.4
Mountain bluebird	0.0–1.0		0.0–5.0						
Cedar waxwing						0.0–0.2			
Solitary vireo	**1.5–12.0**	**9.1–18.1**	**0.0–0.7**			0.0–0.2	5		
Warbling vireo		1.7–27.6							
Yellow-rumped warbler	**3.0–15.0**	23.4–47.0	**0.0–13.0**		**0.2–2.8**	**0.0–1.6**	**8**		
Townsend's warbler							**0.0–1.8**		
Black-throated gray warbler					0.0–0.2		0.0–0.2		
Red-faced warbler	1.5–4.5								
Grace's warbler	**3.8–19.5**	**29.7–50.2**	**0.0–7.0**				0.0–0.4	5	
Virginia warbler		0.4–0.8					0.0–0.5		
Brown–headed cowbird		**0.4–0.8**	**0.0–7.0**				0.0–0.5		

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Table 1. (continued)

Species	Szaro & Balda[a]	Siegel[b]	Overturf[c]	Horton & Mannan[d]	Blake[e]			Haldeman et al[f]	
					Fall	Winter	Spring	Spring	Winter
Western tanager	1.5–6.7	6.2–10.3	0.0–5.0						
Hepatic tanager	0.0-3.0						0.0-0.2		
White-crowned sparrow					0.0–59.4				
Lark sparrow			0.0–39.0						
Fox sparrow					0.0–0.2				
Chipping sparrow	1.5–1 2.0	0.6–4.3		0.0-29.0	0.0-0.2		0.0-8.8		
Spotted towhee	5.5–7.3				0.0-0.2		0.0-3.6		
Dark-eyed junco	1.5–22.5	23.8–43.3	5.0–32.0		0.2–44.6	0.0–65.4		23	2.3
Black–headed grosbeak	1.5–4.5	0.0–1.4						1	
Evening grosbeak									0.2
Cassin's finch		1.8–8.2			0.0–2.1	0.0–8.2	0.0–0.4		0.2
Red crossbill	2.0–17.1								
Lesser goldfinch					0.0–1.3				
Pine siskin		0.0–2.6	0.0–37.0				0.5–8.0	9	
Brewer's blackbird								3	

[a] Szaro and Balda (1979); units are number of pair/40 ha.
[b] Siegel (1989); units are number of birds140 ha.
[c] Overturf (1979); units are number of pair/40 ha.
[d] Horton and Mannan (1988); units are number of birds140 ha.
[e] Blake (1982); units represent an index of occurrence based on numbers and distribution of a species with a sampling site.
[f] Haldeman et al. 1973.

open, medium, and dense. Species richness showed little difference among stands, although dense stands had more individuals, particularly warbling vireos, violet-green swallows, western wood pewees, and Williamson's sapsuckers. He also found that Grace's warbler, yellow-rumped warbler, and dark-eyed junco were the three most abundant species in all stands, collectively accounting for >40 percent of all birds detected.

Overturf (1979) indexed populations using a spot mapping method to examine the effects of fire on ponderosa pine birds in northern Arizona. Populations were sampled from three to nine years post fire, with the exception of one control area where fire had not occurred recently (table 1). The control area was the Gus Pearson Natural Area, Ft. Valley Experimental Forest. Generally, burned areas supported fewer numbers of birds and fewer species than the unburned area. Species found on the control but not found on the burned areas included violet-green swallow, mountain chickadee, hermit thrush, yellow-rumped warbler, Grace's warbler, and pine siskin. Burned areas, however, tended to have more species that nested or foraged on the ground than were found on the control site. Species that appeared to exhibit positive numerical responses to fire included the chipping sparrow, lark sparrow, dark-eyed junco, green-tailed towhee, western bluebird, northern flicker, and house wren. Overturf attributed this difference to burned sites possessing a more well developed herbaceous understory than that in the control plot.

In one of the few studies to examine populations of nonbreeding birds, Blake (1982) found pronounced seasonal differences between fall, winter, and spring in bird species composition and bird abundances in ponderosa pine forests of the Prescott National Forest, Arizona (table 1). He also noted spatial differences that corresponded to differences in fire and logging histories. Generally, burned areas contained more individuals, but they were distributed among fewer species than unburned sites. Species restricted to burned areas included common poorwill, western wood-pewee, scrub jay, house wren, hermit thrush, and lesser goldfinch during the fall; and Cassin's kingbird, rock wren, American robin, solitary vireo, Grace's warbler, hepatic tanager, and black-headed grosbeak during the spring. Species restricted to unburned areas included band-tailed pigeon, acorn woodpecker, Lewis' woodpecker, Steller's jay, pygmy nuthatch, canyon wren, American robin, ruby-crowned kinglet, black-throated gray warbler, spotted towhee, chipping sparrow, and fox sparrow during the fall; yellow-bellied sapsucker, Lewis' woodpecker, Steller's jay, plain titmouse, pygmy nuthatch, ruby-crowned kinglet, and cedar waxwing during the winter; and band-tailed pigeon, acorn woodpecker, ash-throated flycatcher, Steller's jay, pygmy nuthatch,

brown creeper, Bewick's wren, ruby-crowned kinglet, loggerhead shrike, Virginia's warbler, black-throated gray warbler, Townsend's warbler, and spotted towhee during the spring.

Haldeman et al. (1973) reported breeding season and wintering populations of birds from a ponderosa pine forest northwest of Flagstaff, Arizona (table 1). Their single study area was the 13-ha Gus Pearson Natural Area that they characterized as undisturbed. They recorded 18 species during winter counts and 69 species during breeding counts. Because they used different methods to calculate relative abundance for each season, comparisons between seasons are difficult. However, of the resident species (that is, those present year round), the pygmy nuthatch was the most common species during both seasons. Other common wintering birds were the mountain chickadee, white-breasted nuthatch, western bluebird, and dark-eyed junco. Besides the pygmy nuthatch, other common breeding birds included the violet-green swallow, dark-eyed junco, mountain chickadee, American robin, and western bluebird.

Horton and Mannan (1988) sampled populations of cavity-nesting birds in the Santa Catalina Mountains, southeastern Arizona, as part of a study to evaluate the effects of prescribed fire. The violet-green swallow and northern flicker exhibited population declines following the fire, whereas the mountain chickadee population appeared to increase. Horton and Mannan (1988) speculated that the population shifts were possibly attributable to changes in prey abundance and shifts in habitat use following fire.

Bennetts (1991) investigated the relationship of breeding birds and dwarf mistletoe in Colorado ponderosa pine forests. He found positive correlations between mistletoe and total bird abundance and number of species, as well as with abundances of eight foraging guilds. He also found strong positive correlations of mistletoe with snag numbers and the abundance of cavity nesting birds.

General Comparisons Among Studies

As noted previously, differences in how studies were conducted preclude rigorous comparisons. However, some generalizations are possible. Species richness (number of species) during the breeding season ranged from 23 (Haldeman et al. 1973) to 47 (Siegel 1989). Fewer species were detected during winter (14 to 16, Blake 1982 and Haldeman et al. 1973) or fall (27, Blake 1982) than during the breeding season. The range in species richness during the breeding season could have resulted from temporal or geographic differences, or variations in methodologies or skill levels of observers.

Across the studies, there was a mixture of responses to heavy alteration of forest vegetation. In regard to fire, abundances of birds either increased (Blake 1982) or decreased (Overturf 1979), whereas species composition was lower on burned sites in both studies. In clearcuts studied by Szaro and Balda (1979), bird numbers decreased, but in open stands studied by Siegel (1989), species richnesses were similar among open and "closed" stands. These differences indicate that treatments can elicit variable responses from bird species, probably because of variations in geographic location, and because of the historic (prior) conditions of the areas.

Population Trends

BBS data provide one of only a few sources of long-term population data from which trends may be inferred. However, without going into details here, it must be noted that many problems have been identified with BBS data and analyses (Peterjohn et al. 1995, Thomas and Martin 1996). These problems include observer bias and biases associated with sampling design. Furthermore, a lot of discussion has been devoted to identifying the correct way to analyze BBS data (Thomas and Martin 1996).

Regardless of these potential limitations, Miller (1992) evaluated population trends of ponderosa pine birds using BBS data. BBS routes were selected from Colorado ($n = 5$), Utah ($n = 5$), Arizona ($n = 5$), and New Mexico ($n = 6$) that sampled managed ponderosa pine forests. Whether or not these managed pine forests were a representative sample of pine forest of the southwest is unknown, but population trends in unmanaged pine forests (for example, old-growth forest, wilderness lands) may have differed from those in managed forests. To ensure that standardized methods were used, analyses were done by the U.S. Fish and Wildlife Service, Patuxent Research Center.

Miller examined trends of individual species and groups of species as defined by nesting strategy (for example, primary-cavity, secondary-cavity, or cup nesters), nesting habitat (woodland or coniferous forest), or residency status (resident, short-distant migrant, neotropical migrant). Analyses were done at the state level for New Mexico (because this was the only state with adequate samples); New Mexico and Arizona combined; Colorado and Utah combined; and all four states combined. For New Mexico, Miller found declining populations of 77 percent of all birds examined (46 of 61), and from 50 to 100 percent of the species within any of the groups that he evaluated (table 2). Fewer population declines were noted when census routes from states were pooled (table 2). Of particular interest was that about two-thirds (50) of the species found in New Mexico and Arizona (75 total bird species) exhibited significant population declines (table 2), and many of these were birds that nested in open cups and species that tended to be year-round residents. Miller identified 50 species that exhibited declines and 25 that exhibited population increases (table 3).

The Christmas Bird Count program, sponsored by the National Audubon Society, provides information on the abundance of birds wintering in various locations in North America. There are, however, only two count locations

Table 2. Proportion of bird species declining 1968 to 1990 along managed ponderosa pine breeding bird survey routes, for species with ≥5 routes counted, and an average of 20.5 birds per route (modified from Miller 1992).

Guild	New Mexico	New Mexico & Arizona	Colorado & Utah	All four states
Woodland nesting	11 of 13 (85%)	9 of 16 (56%)	5 of 11 (45%)	6 of 19 (32%)
Coniferous nesting	8 of 8 (100%)	6 of 11 (55%)	5 of 7 (71%)	4 of 14 (29%)
Primary cavity nesting	1 of 2 (50%)	2 of 3 (67%)	1 of 2 (50%)	1 of 4 (25%)
Secondary cavity nesting	9 of 12 (75%)	7 of 14 (50%)	3 of 6 (50%)	8 of 15 (53%)
Open cup nesting	23 of 26 (88%)	20 of 31 (65%)	10 of 18 (56%)	26 of 41 (63%)
Permanent resident	11 of 11 (100%)	10 of 12 (83%)	3 of 5 (60%)	10 of 14 (71%)
Short distance migrant	15 of 25 (60%)	16 of 33 (48%)	10 of 22 (45%)	20 of 39 (51%)
Neotropical migrant	10 of 13 (77%)	9 of 15 (60%)	4 of 11 (36%)	12 of 22 (55%)
All birds	46 of 61 (77%)	50 of 76 (66%)	21 of 45 (47%)	54 of 97 (57%)

that have been regularly surveyed in Southwestern ponderosa pine forest: one centered near Flagstaff, Arizona, which has been surveyed since 1968, and another centered near Mormon Lake, Arizona, which has been surveyed since 1982. CBC data have been shown to produce reliable indications of trends in bird abundance when a count has been conducted for a sufficient period of time (that is, about 20 years), and when a sufficient count effort has been expended each year (Bock and Root 1981). Although the Flagstaff count meets these requirements, trend analyses should not be based on only one or a few counting locations (Bock and Root 1981). Therefore, we have not included analyses of CBC data in this report.

Several authors have recently documented range and population shifts for particular Southwestern bird species. For example, Johnson (1994) suggested northward expansion of the ranges of Grace's warbler, painted redstart, hepatic tanager, and summer tanager in response to "natural" climate change over the past century. Based on an extensive literature review, DeSante and George (1994) concluded that willow flycatcher, buff-breasted flycatcher, western bluebird, Bell's vireo, summer tanager, and song sparrow populations were decreasing across the west, whereas berryline hummingbird, violet-crowned hummingbird, black phoebe, European starling, red-faced warbler, and brown-headed cowbird populations were increasing. Whether or not these range shifts and population trends apply to Southwestern ponderosa pine forest is unclear, however, because the western region reviewed by DeSante and George encompasses many different vegetation types.

Brawn and Balda (1988a) reviewed the population status of Southwestern ponderosa pine birds and suggested that broad-tailed hummingbird, acorn woodpecker, three-toed woodpecker, purple martin, violet-green swallow, mountain chickadee, white-breasted nuthatch, pygmy nuthatch, brown creeper, western bluebird, mountain bluebird, American robin, red-faced warbler, chipping sparrow, and lark sparrow populations would also be likely to decline over time in response to past and present land-use activities. Many of these species are ones that nest in cavities or rely on a well-developed herbaceous understory. We can presume that the synergistic and cumulative effects of natural vegetation change, livestock grazing, logging, fuelwood harvest, and fire suppression will underlie many of the predicted population declines (discussed in detail in Finch et al., this volume).

Carothers et al. (1973a) briefly summarized the status of selected species in northern Arizona. They noted that the Lewis' woodpecker had become a fairly common permanent resident, and the evening grosbeak a locally common permanent resident in ponderosa pine forest around Flagstaff. In contrast, they noted a decline in numbers of red-breasted nuthatches in ponderosa pine. They also noted that the exotic European starling had changed in status from a rare winter visitor or transient to a common winter resident and an uncommon summer resident in the Flagstaff area.

Table 3. Increasing and decreasing bird species on managed ponderosa pine Breeding Bird Survey routes in Arizona and New Mexico, for species with ≥5 routes and 20.5 birds per route (modifled from Miller 1992). These lists include both songbirds and non-songbirds.

Decreasing	Increasing
Mallard	Turkey vulture
Killdeer	Red-tailed hawk
Band-tailed pigeon	American kestrel
Mourning dove	Northern flicker
Hairy woodpecker	Cassin's kingbird
Acorn woodpecker	Cordilleran flycatcher
Common nighthawk	Steller's jay
Broad-tailed hummingbird	European starling
Western Kingbird	Brown-headed cowbird
Ash-throated flycatcher	Vesper sparrow
Say's phoebe	Spotted towhee
Western wood-pewee	Green-tailed towhee
Gray flycatcher	Blue grosbeak
Horned lark	Western tanager
Western scrub jay	Hepatic tanager
Common raven	Purple martin
American crow	Barn swallow
Clark's nutcracker	Rough-winged swallow
Pinyon jay	Bewick's wren
Red-winged blackbird	House wren
Eastern meadowlark	Red-breasted nuthatch
Western meadowlark	Townsend's solitaire
Brewer's blackbird	Hermit thrush
House finch	American robin
Red crossbill	Western bluebird
Lesser goldfinch	
Pine siskin	
Lark sparrow	
Chipping sparrow	
Canyon towhee	
Black-headed grosbeak	
Cliff swallow	
Violet-green swallow	
Loggerhead shrike	
Warbling vireo	
Solitary vireo	
Virginia's warbler	
Yellow-rumped warbler	
Grace's warbler	
Black-throated gray warbler	
House sparrow	
Northern mockingbird	
Rock wren	
White-breasted nuthatch	
Pygmy nuthatch	
Plain titmouse	
Mountain chickadee	
Common bushtit	
Ruby-crowned kinglet	
Mountain bluebird	

Ecological Roles

Seed Dissemination

Mistletoe

Hudler et al. (1979) studied the role of birds in the spread of dwarf mistletoe (*Arceuthobium* spp.) in a Colorado ponderosa pine forest. Long-distance seed transmission (that is, farther than possible by normal seed discharge) occurred infrequently; successful infection occurred once every four years on average. Mountain chickadees and pygmy nuthatches were the primary vectors of the parasite. Laboratory studies showed that seeds seldom remained viable when ingested by birds. Rather, successful movement of the seeds occurred when they became attached to bird feathers and later transferred to foliage.

Bennetts (1991) and Bennetts and Hawksworth (1991) studied the indirect effects of dwarf mistletoe on birds in a Colorado ponderosa pine forest. The total number of birds and the total number of bird species detected increased with increasing levels of mistletoe infestation; this pattern was consistent across most foraging assemblages of birds. In addition, the number of snags and the abundance of cavity-nesting birds increased with increasing levels of mistletoe. The authors suggested that dwarf mistletoe should not be viewed solely as a forest pest (because of its often negative influence on commercial timber volume), but rather in the context of an ecological disturbance process and its influence on wildlife communities. That is, mistletoe is a disturbance process that changes the structure and function of ponderosa pine and other host communities. In their review of the literature, they also found that the witches' brooms caused by the mistletoe are an important nesting and roosting substrate for many species of birds and squirrels, and that some species use mistletoe as a food source. Mistletoe has been shown to serve as a nesting substrate by Forsman et al. (1984), Bull and Henjum (1990), Bull et al. (1989); as a roosting substrate by Martinka (1972); and as a food source for birds and other animals by Taylor (1935), Broadbooks (1958), Urness (1969), Farentinos (1972), Craighead et al. (1973), Currie et al. (1977), Hall (1981), and Severson (1986).

Pine Seeds

Balda and his coworkers (for example, Balda and Bateman 1971; Balda 1973, Bateman and Balda 1973) conducted a long-term, intensive study of the ecology and behavior of the pinyon jay in a northern Arizona ponderosa pine forest. Pinyon jays are year-round residents and obtain part of their winter food from pine seeds that they cached during the fall. This caching behavior helps spread pine seeds and thus plays a major role in the population dynamics of these trees. Clark's nutcrackers are also a

seed-predator and a very important seed-disperser for wingless seeds (for example, *Pinus edulis*) (Tomback and Linhart 1990). Nutcrackers have been found to affect forest regeneration and to possibly extend the range of pinyon pines (reviewed in Christensen et al. 1991). They also forage on ponderosa pine seeds, when they are available, and may therefore play a part in the dynamics of ponderosa pine forests. Another ponderosa pine seed-predator is the red crossbill. The crossbill is nomadic, following sporadic, scattered pine seed crops (Gill 1995:290). In the Rocky Mountains, crossbills will nest in January and February if pine seeds are abundant (Gill 1995:275).

Indicators of Forest Conditions

Szaro and Balda (1982) discussed the selection and subsequent monitoring of birds as indicators of environmental change, using their data from a ponderosa pine forest of northern Arizona as an example. They noted that many different definitions have been applied to the term "indicator" for use in environmental management, including: 1) endangered and threatened plants and animals; 2) species commonly hunted, fished, or trapped; 3) species with specialized habitat needs; and 4) plants or animals selected because changes in their populations are thought to indicate the effects of natural- or human-induced changes on the collective species of a major biological community. The use of birds as indicators is controversial (for example, see Morrison et al. 1992), primarily because indicator species may be affected differently from other species by habitat changes. Nevertheless, the concept is important here because there are diverse opinions on the subject, and because in certain situations (for example, chemically polluted environments) birds can indicate habitat conditions (Morrison 1986).

Szaro and Balda (1982) found that species such as the hermit thrush, red-faced warbler, Cordilleran flycatcher, and pygmy nuthatch, which are found in old-growth ponderosa pine forest and only lightly disturbed areas, are replaced in moderately to heavily cut areas by species such as the western wood-pewee, yellow-rumped warbler, and rock wren. Therefore, those species that are most sensitive to habitat perturbations may potentially make the best indicator species. Some species that are too rare to be useful as indicators of the general community—such as Virginia's warbler, brown creeper, and hepatic tanager—may be useful indicators of special habitat needs because they breed in ponderosa pine. Szaro and Balda concluded that the two species that best indicated the overall "health" of the bird community were the pygmy nuthatch and violet-green swallow. They based this finding on the fact that, when they found high densities of pygmy nuthatches and violet-green swallows, they also found high densities of most of the other ponderosa pine forest bird species (see Szaro and Balda 1982, table 1).

"Habitat specialists" as indicator species are discussed in Rich and Mehlhop (this volume).

Roost and Nest Cavity Formation

Scott (1978) summarized the frequent use of cavities in dead or partially dead trees in ponderosa pine forest and mixed pine woodlands in Arizona and New Mexico by the American kestrel, 7 species of owls, the elegant trogon, 11 species of woodpeckers, 2 flycatchers, 3 swallows, 5 chickadees and titmice, 3 nuthatches, the brown creeper, 4 wrens, and 3 bluebirds. Similarly, Ffolliott (1983) summarized the scant literature on cavity-nesting animals in Southwestern ponderosa pine forests and found that at least 49 species of birds, 10 species of mammals, and numerous species of insects and herpetofauna used tree cavities in these forests. In addition, he noted that 63 percent of the birds and 75 percent of the mammals that are snag-dependent in Southwestern forests are insectivorous. This diet preference is important because birds and mammals have been credited with insect control that helps maintain ecosystem functioning.

An important interaction exists in ponderosa pine forests involving the location and suitability of potential nest trees, the type and number of primary cavity excavating species (especially woodpeckers), and the number and distribution of secondary cavity nesting species. Although secondary cavity nesting species will use non-bird excavated holes (for example, holes resulting from disease or broken branches) for nesting, their frequent use of bird-excavated holes indicates a likely preference for such cavities or a limitation of alternative nest sites.

Brawn and Balda (1988b; see also Brawn 1985, Brawn and Balda 1983) tested the common assumption that nest sites limit the breeding density of secondary cavity nesters in an Arizona ponderosa pine forest. They found this assumption to be only partially correct. They found that secondary cavity nesters, as a group, can indeed be limited by nest sites. But only three of the six species they studied significantly increased in density when provided with artificial nest boxes; these were the violet-green swallow, pygmy nuthatch (which can also be a primary cavity-nesting species), and western bluebird. Numbers of house wrens, mountain chickadees, and white-breasted nuthatches did not differ. They concluded that a given population appears to be limited by nest sites if it is sufficiently common during the breeding season and dependent upon snags as a source of nest sites. Within species that are nest site limited, availability of food or foraging substrates and territoriality may determine an upper limit to breeding densities if nest sites are in ample supply. Thus, a dynamic exists between nest sites, food availability, and intra- and interspecific competition for nest sites.

A study of secondary cavity nesters in northern Arizona by Cunningham et al. (1980) found pronounced in-

terspecific variation in the use of snags for nest sites; certain species were reliant on snags, whereas others rarely used snags. For example, nearly all violet-green swallows and pygmy nuthatches nested in snags, whereas white-breasted nuthatches were not so dependent upon snags. Cunningham et al. also found that mountain chickadees, white-breasted nuthatches, and house wrens were relatively uncommon regardless of the availability of snags and foraging substrate. It is the common species that seem to increase the most after provision of nest boxes. Brawn and Balda (1988b) speculated that this was because relatively rare populations do not contain enough non-breeding individuals (that is, floaters) to be able to take advantage of the increase in nesting sites. Common species thus can be nest-site limited, whereas rare species are being suppressed by other factors. Brawn et al. (1987) also found that, during the breeding season, interspecific competition for food among secondary cavity nesters appeared to be unimportant in ponderosa pine bird communities. The factors holding down numbers of rare species are still generally unknown.

There is apparently an interaction between the species of snag retained after treatments and the response of birds to total snag density. Scott (1979) found that populations of some species of cavity-nesting birds can be reduced significantly by removal of conifer snags even when some aspen snags are left. Other hardwoods, such as oak, provide nesting sites for some species of birds within the ponderosa pine type. Some birds such as swallows, however, may not make the change from ponderosa pine snags to the smaller hardwood snags.

Hay and Guntert (1983) examined the seasonal requirements for snags by pygmy nuthatches in northern Arizona ponderosa pine forest. They found that trees with nest cavities were shorter and consequently had a small diameter at breast height (dbh) compared to those used for roosting during other seasons. Greater cavity height of the fall and spring roosts compared to summer roosts was related to more absorption of spring-fall radiation by the former. In contrast, nest cavities appeared to be positioned to obtain moderate insolation and shielding from the wind. Hay and Guntert stated that cavity selection is interrelated with the overall biology of the species, and management should emphasize snag and/or cavity quality, rather than the absolute quantity of snags available. They also concluded that additional baseline research into the seasonal quality of cavities and snags needed for cavity-dependent species in ponderosa pine forests was needed.

Horton and Mannan (1988) studied the interrelationship between fire and snag dynamics in southeastern Arizona ponderosa pine and mixed pine-oak forest. Natural fires burned every 2 to 12 years in Southwestern ponderosa pine before suppression by humans beginning in the late 19th century (for more details, see Moir et al. and Finch et al., this volume). These fires were usually light surface fires that produced generally open, park-like conditions. Modern forest management uses broadcast understory fires to reduce accumulations of woody debris left by logging or natural processes to reduce the risk of catastrophic crown fires. These fires also impact snag dynamics by consuming existing snags and creating others by killing trees. Horton and Mannan found that a single application of moderately intense surface fire resulted in a net decrease of 33 percent of snags preferred for nesting. However, no species of cavity-nesting bird disappeared in the first breeding season following the fires, and only the northern flicker and violet-green swallow declined in abundance. They concluded that these changes were not due to a shortage of snags. Their study, however, was conducted for only one year following fire treatment.

Snag Management

According to Scott (1978), little information existed on management guidelines for cavity nesting birds in Southwestern ponderosa pine forests prior to the late 1970s. Before that time, snags were removed during forest harvest because of potential fire and safety hazards, and many thought they had poor aesthetic value and were indicative of an unhealthy forest. Using his own research and that of Balda (1975), Scott (1978) concluded that, on average, at least 2.5 large (243 cm dbh) snags per acre should be retained in ponderosa pine forests. In addition, all naturally occurring snags should be left during timber harvest. Specifically, he found that 1) snags usually did not become suitable for nesting until 6 years after the trees died; 2) snags that retained more than 40 percent of their bark were used more frequently and contained more holes than those with less bark; 3) snags in higher dbh classes (243 cm) were used significantly more than smaller snags and the larger snags also contained more holes; 4) snags on northern and southern aspects were used at about the same frequency, but those on northern exposures averaged more holes per snag; and 5) snags over 23 m tall were used at a significantly higher rate than shorter snags, but comprised only 16 percent of the available snags.

Balda (1975) found that 4.2 snags/ha were necessary in ponderosa pine forests to achieve average densities and natural species diversity of secondary cavity nesters. He also stated that 6.7 snags/ha were necessary to maintain maximum densities and natural species diversity of these birds.

Ffolliott (1983) examined the implementation of USDA Forest Service snag guidelines on study areas across the ponderosa pine belt of northern Arizona, examining both present conditions and simulated (modeled) conditions at the end of a 20-year period. Snags were defined as standing dead trees at least 30 cm dbh and 3.1 m in height; no differentiation was made between hard and soft snags. His analyses showed that none of his study areas that had been subjected to various silvicultural treatments met any

of the suggested polices for snag retention (USDA Forest Service 1977). From his analysis, only virgin forest would meet a retention policy of 2.5 to 5.0 snags/ha through natural mortality.

Rosenstock (1996) found that snags >46 cm dbh and >10 m tall were frequently used for nesting in ponderosa pine forest. Cunningham et al. (1980) found a preference for snags >58 cm dbh and >20 m tall on the Beaver Creek Watershed in northern Arizona. Paine and Martin (1995, as cited in Rosenstock 1996) found that 84 percent of ponderosa snags used for nesting on their Mogollon Rim study sites were >30 cm dbh and >10 m tall. Horton and Mannan (1988) found a preference for snags >51 cm dbh.

This review indicates that little research has been conducted on snag requirements in ponderosa pine forests. Studies that have been conducted demonstrate that at least 5 large snags/ha may be necessary to maintain populations of cavity-nesting species. However, it also appears that these guidelines are not being attained on at least some of the forested lands.

Predator-Prey Relationships/Pest Control

As reviewed by Holmes (1990), numerous bird species respond both functionally and numerically to increasing prey densities. While birds seem unable to prevent population epidemics of their prey, they do appear to have a substantial impact when prey populations are at endemic levels. From his review of the literature, Holmes concluded that birds could delay the onset of an insect outbreak. For example, modeling of spruce budworm populations suggested that predation by birds may be a significant factor in maintaining endemic population levels of this species.

As reviewed by Dahlsten et al. (1990) for western mixed-conifer forests (which include ponderosa pine as a major component), many species of forest birds concentrate their foraging activities on insect species considered to be forest pests. In addition, Koplin (1969) demonstrated a functional response of woodpeckers to insect outbreaks. Insectivorous birds may also increase the fitness of the plants on which they forage for arthropod prey. For example, Marquis and Whelan (1994) examined the effect of insectivorous birds on white oak (Quercus alba) growth in a deciduous forest in Missouri. Through experimental manipulations they demonstrated that the presence of birds enhanced the growth of juvenile oaks via bird consumption of leaf-chewing insects (primarily Lepidopteran larvae). They suggested that forest management practices that promote the conservation of insectivorous bird species will help maintain forest productivity. The extension of this to ponderosa pine forests (with or without an oak component) is obvious. Marquis and Whelan further suggest that although insecticide spraying and handpicking insects off trees can reduce their numbers, these are not necessarily feasible alternatives for controlling arthropod numbers in forests.

Insect consumption of cones and seeds can negatively impact vertebrate use of such resources. Christensen and Whitham (1993) found that stem- and cone-boring insects, birds (Clark's nutcrackers, pinyon jays, and [western] scrub jays), and mammals competed for pinyon pine seeds. And insect herbivores indirectly affected resource use by the vertebrates through a 57 percent average reduction in crop sizes. Thus, the foraging of birds on insects plays several important roles and is a significant factor to consider in the management of ponderosa pine forests. There is a paucity of information on this subject, however, so this is an important area for research.

Habitat Use

General Habitat Use

Balda (1967,1969) studied the use of foliage by breeding birds in ponderosa pine and oak-juniper forests of the Chiricahua Mountains, Arizona. He found that certain species (such as the pygmy nuthatch) were closely associated with ponderosa pine of many heights, whereas other species (such as the chipping sparrow) were found in specific height layers regardless of the tree species involved. Other species such as Grace's warbler were restricted to particular heights in pines. The models for pines strongly suggested that foliage volume may be an important factor in limiting the densities of the pygmy nuthatch and Grace's warbler, even though the former species is a cavity nester. Balda (1970) also described the bird community present in oak and oak-juniper-pine woodlands.

Marshall (1957) summarized surveys he conducted in pine-oak woodlands during the summers of the early 1950s from the Pinaleno and Santa Catalina mountains in Arizona, south into central Sonora and to the Sierra Madre Occidental of northwestern Chihuahua, Mexico. Ponderosa pine entered his pine-oak woodlands only occasionally. The related Apache pine was more frequently encountered on his sites, along with chihuahua pine (*P.* leiophylla). Marshall provided descriptions of the overall relationship between the distribution of birds and plants in the region and summarized his observations in annotated species notes. Of particular interest are his observations of pine (and pine-oak) forest birds of current special concern, including the thick-billed parrot, buff-breasted flycatcher, elegant trogon, spotted owl, and Montezuma quail, because he details the population status and describes the habitat affinities of these species.

Carothers et al. (1973a) edited a volume that summarized the status and general habitat preferences of birds in the San Francisco and White mountains of Arizona, concentrating on breeding birds. A paper by Haldeman et al. (1973) included a brief section on wintering birds, where 18 species were observed during the winter in ponderosa pine forest, and 69 species were observed during summer, of which 23 were known to nest. They consid-

ered the following species to be exclusive users of the ponderosa pine forest during their study in this region: solitary vireo, western bluebird, and Brewer's blackbird. The pygmy nuthatch, violet-green swallow, American robin, white-breasted nuthatch, and Grace's warbler were considered to be "characteristic" of ponderosa pine forest (that is, found to be two to three times as abundant than in a comparison area).

Franzreb published a series of papers (1978, 1983, 1984) that detailed results of her study of birds in a mixed Douglas-fir, ponderosa pine, and Southwestern white pine forest in the White Mountains, Arizona. In this mixed-conifer forest, she found that ponderosa pine and Southwestern white pine were used less frequently than expected based on total foliage volume, whereas use exceeded availability for Douglas-fir, white fir, and Engelmann spruce. She also showed, however, that certain species, especially the Grace's warbler, relied upon pines for foraging. Franzreb's 1978 and 1983 papers also discussed the influence of logging on bird abundance and foraging behavior. Her 1984 paper detailed the foraging behaviors of the ruby-crowned and golden-crowned kinglets. Both species strongly preferred spruce and Douglas-fir and avoided pines for foraging.

Salomonson and Balda (1977) examined the winter behavior of the Townsend's solitaire in a pinyon-juniper-ponderosa pine ecotone in northern Arizona. Territory size, and ultimately survival, were related to the abundance of juniper berries. Laudenslayer and Balda (1976; also Laudenslayer 1973) studied the breeding birds of a pinyon-juniper-ponderosa pine ecotone in northern Arizona. They concentrated on five bird species and described their densities, foliage preferences, and foraging habitats. The mountain chickadee and solitary vireo preferred ponderosa pine; the bushtit and plain titmouse preferred pinyon-juniper; and chipping sparrows were found throughout the ecotone.

Overturf (1979) compared the breeding bird communities on burned and unburned sites in ponderosa pine of northern Arizona. The burned sites showed a decreased number of bird species and bird abundance, which were related to the decrease in habitat heterogeneity and loss of the canopy and shrub-sapling vegetation layer. In addition, burning caused a shift in bird species composition from foliage users to ground-using birds because burning caused an increase in herbaceous plants. Overturf concluded that burning in this "pyroclimatic monoculture" would be an effective management strategy because it simulated natural fires and increased the overall habitat heterogeneity in the forest (for more details, see Finch et al., this volume).

Szaro and Balda (1979, 1986) and Szaro et al. (1990) found that significant temporal variations occurred in habitat use and foraging behavior of ponderosa pine birds in northern Arizona. Szaro and Balda (1986) showed that bird density and species richness were influenced by both weather and timber harvest. The effects of weather on birds varied depending on the type of timber harvest conducted, although the harvest type was of primary importance in determining community structure. The impact of harvest was clearly more pronounced after the mildest winter and tended to be minimized after the severest winter. They concluded that studies must be conducted during a variety of weather conditions (over many years) to determine the trend of bird responses in different forest types (including different harvest types). Similarly, Szaro et al. (1990) showed that weather and harvest type significantly influenced foraging behaviors of ponderosa pine birds over a three-year period. They urged that studies be conducted that identified the proximate mechanisms that caused this variation in foraging behavior. They suggested that such causes would include resource availability, weather conditions, predation, and plant phenology.

Szaro and Balda (1982) summarized the habitat preferences of ponderosa pine forest species based on their study of various seral stages (see also Szaro and Balda 1986; Szaro et al. 1990; and as summarized above). The disturbance regime they used to simulate seral stages ranged from uncut, mature forest to severely thinned forest (see table 4). Six species (of 25 total species, or 24 percent) showed no distinct habitat preferences: the northern flicker, hairy woodpecker, Steller's jay, common nighthawk, mourning dove, and white-breasted nuthatch. Six species (24 percent) preferred undisturbed or only lightly thinned mature forest: the red-fared warbler, hermit thrush, Cordilleran flycatcher, pygmy nuthatch, violet-green swallow, and black-headed grosbeak. Similarly, two additional species (8 percent; dark-eyed junco and mountain chickadee) preferred undisturbed to moderately disturbed (cut) forest, and another four species (16 percent) preferred lightly to moderately disturbed areas (Grace's warbler, yellow-rumped warbler, western tanager, western bluebird). Thus, up to 18 species (72 percent) seemed to prefer mature forest with some disturbance (includes those species showing no distinct preferences). An additional six species (24 percent) preferred lightly to heavily disturbed (chipping sparrow and solitary vireo), moderately to heavily disturbed (western wood-pewee, American robin, and broad-tailed hummingbird), or heavily disturbed (rock wren) areas. Finally, the acorn woodpecker was confined to oak groves. The authors concluded that the hermit thrush, red-faced warbler, Cordilleran flycatcher, and pygmy nuthatch showed strong preference for undisturbed to only slightly disturbed forest.

Stallcup (1968) studied habitat segregation of foraging nuthatches and woodpeckers in a Colorado ponderosa pine forest and described the density and composition of this group of birds throughout the year. Birds studied were the white-breasted, red-breasted, and pygmy nuthatches, hairy woodpecker, northern (red-shafted) flicker, and

Table 4. Habitat preferences of birds in selected ponderosa pine stands in northern Arizona (from Szaro and Balda 1982). The disturbance regime ranged from (in increasing intensity of disturbance): untreated mature forest, silviculturally cut, irregular strip cut, to severely thinned cut.

Preference Species
None
Northern flicker
Hairy woodpecker
Steller's jay
Common nighthawk
Mourning dove
White-breasted nuthatch
Nondisturbed or lightly disturbed areas
Red-faced warbler
Hermit thrush
Cordilleran flycatcher
Pygmy nuthatch
Violet-green swallow
Black-headed grosbeak
Nondisturbed to moderately disturbed areas
Dark-eyed junco
Mountain chickadee
Moderately to heavily disturbed areas
Western wood pewee
American robin
Broad-tailed hummingbird
Heavily disturbed areas
Rock wren
Lightly or moderately disturbed areas
Grace's warbler
Yellow-rumped warbler
Western tanager
Western bluebird
Lightly to heavily disturbed areas
Chipping sparrow
Solitary vireo
Oak groves
Acorn woodpecker

Williamson's sapsucker. Red-naped sapsuckers, downy woodpeckers, and northern three-toed woodpeckers were present but rare. The absence of the red-breasted nuthatch during breeding may have resulted from a shortage of nest sites, or more likely, a lack of foraging space because of competition from other species. Stallcup suggested that food shortages might be responsible for segregating bird species.

Apparently the most recent study available on the general habitat affinities of ponderosa pine birds was conducted by Rosenstock (1996). He noted that previous studies on the effects of forest treatments on birds in Southwestern ponderosa pine (for example, Szaro and Balda 1979) examined treatments that are no longer in common use (for example, clear-cuttings, strip cuttings). As such, he examined the abundance of birds across a wider gradient of pine and pine-oak seral stages than had previously been conducted. In summary, he found 43 species in pine-oak, and 38 in pine. Two rather uncommon species (Clark's nutcracker and evening grosbeak) were found only in pine, whereas seven species were unique to pine-oak (dusky flycatcher, downy woodpecker, lesser goldfinch, rock wren, spotted towhee, Virginia's warbler, and, warbling vireo), and all but the Virginia's warbler were rare or uncommon. Four common species—acorn woodpecker, black-headed grosbeak, house wren, and red-faced warbler—were found primarily in pine-oak. Densities of violet-green swallows and western wood pewees were higher in pine patches, whereas American robins, hermit thrushes, and white-breasted nuthatches were more abundant at pine-oak sites. By vegetative structural stage (VSS; see Moir et al., this volume, for definitions of VSSs), neotropical migrant abundances and species richness were similar across VSS classes at pine-oak sites but were highest at VSS class 4 and 6 in pine. Residents and short-distance migrants had similar abundances and species richness in all VSS classes in pine-oak. At pine sites, however, abundance of these groups of species was lower in VSS class *3* stands but similar in all other classes; class 6 had a higher species richness than the other classes. Cavity nesting species had similar abundances and richnesses across all pine-oak classes, and across all pine classes except class 6, which had considerably higher values.

Although Rosenstock noted that previous studies in Southwestern ponderosa pine were conducted before the importance of spatial variables on bird communities was widely acknowledged, he was not able to determine the influence of patch size and other spatial attributes on the bird community he studied.

Nesting Habitat

Martin (1988) studied the ability of nest predation to explain patterns of covariation in species numbers with area and habitat in mixed ponderosa pine forest and maple-dominated stands in central Arizona. Variation in numbers of species among drainages was positively correlated with variation in the density of foraging and nesting substrates. His results were consistent with a prediction that birds select nest sites based in part on the availability of sites that minimized their risk of nest predation, and that these sites increase in number with density of foliage at nest height. His results were also consistent with a hypothesis that availability of suitable nest sites is one of the bases for the relationship between species numbers and foliage density for foliage-nesting species. In a related study, Martin and Roper (1988) detailed their findings for the hermit thrush. They found that hermit thrushes had low nesting success (7 to 20 percent), due mostly to nest predation. The structure of vegetation around the nest influenced the predation rate and likely

the nest-site availability. Likewise, Li and Martin (1991) presented results from the same study region for cavity-nesting species. Although aspens accounted for only 12 percent of all trees present in the study area, dead aspen accounted for 88 percent of all nest sites. Li and Martin also identified specific aspen-conifer patches that were chosen for nesting and foraging. Nest cavity height influenced nesting success, with the lower nests showing the lowest success. The authors noted that populations of cavity nesters might decrease if aspen snags decreased in height and abundance; alternative conifer snags were rare because most large trees were harvested before they died.

Siegel (1989) examined the distribution and abundance of birds in virgin old growth and mature managed ponderosa pine forest in northern Arizona (table 1). The mature managed stands met the "minimum" USDA Forest Service standards for old-growth forest. Siegel reached the following conclusions. First, brown creepers used large (>20 inches dbh) snags, in denser stands of older trees, with large pieces of sloughing bark. Such conditions provided the necessary microsites for nest placement and also served as foraging sites. Second, hermit thrushes nested in the canopies of mature trees, in contrast to the much smaller trees this species uses in other parts of its range. Siegel felt that small pine were not used because they did not provide the necessary support branches for their nests nor the foliage necessary to conceal the nests. He also thought that placement of nests in the canopy served better to regulate nest temperatures. In addition, hermit thrushes also foraged in moist, cool sites. Third, a higher total density of birds was found in dense stands of pine compared to other stands and was apparently due to the greater abundance of aspen and the concomitant wetter conditions in these stands. The warbling vireo, violet-green swallow, western wood-pewee, Williamson's sapsucker, and three-toed woodpecker were more common in the dense stands because they used the groves of pine-aspen for nesting and foraging. Also, the mesic, dense stands may have supported higher bird abundances because of their greater total foliage volume, and concomitantly, higher densities of invertebrate prey. In contrast, species richness was only slightly higher in older and denser stands, indicating that this situation did not follow the standard positive relationship between foliage height diversity and bird species diversity.

Finally, Siegel (1988) concluded that the mesic conditions created in dense old growth likewise created conditions that were more characteristic of forests at higher elevations or latitudes (that is, Canadian and Hudsonian life zones). These conditions apparently provided the resources used by the brown creeper, hermit thrush, three-toed woodpecker, northern goshawk, and saw-whet owl in ponderosa pine. Warm and dry exposures in more open old-growth stands were either unsuitable or marginal locations for these species.

McEllin (1979) compared the demography, territorial spacing, and foraging behavior of white-breasted and pygmy nuthatches in Colorado ponderosa pine and mixed ponderosa pine-aspen stands. White-breasted nuthatches nested primarily in natural cavities in live pines, whereas pygmy nuthatches nested in pre-existing cavities in dead pines; cavity availability was higher for the latter species. Significant differences were shown for the foraging behaviors within sexes of each species and between species: differences in foraging heights, and foraging locations within trees (for example, limbs versus trunks). McEllin concluded that these species exploited different aspects of forest structure; that is, white-breasted nuthatches were more specialized in the vertical, horizontal, and tree structure dimensions, whereas pygmy nuthatches showed greater specialization in food items and prey acquisition behaviors. With regard to forest management, McEllin stated that careful analyses of these ecological relationships is a necessary requirement of any program. Artificial reproduction of favorable conditions for one species or one season might result in unfavorable conditions for another species or season. Detailed analyses of space utilization patterns within and between species under different forest conditions can provide ecological information that will be important in designing forest management strategies.

Brawn (1991) studied the reproduction and foraging of western bluebirds on two ponderosa pine sites in northern Arizona and found that breeding phenology and allocation of parental care were adjusted by bluebirds in response to local environmental conditions. Brawn also found that feeding rates of nestlings and fledging success were greater on the moderately logged site than on the heavily logged site.

Migrant Use of Ponderosa Pine

Very little information exists on use of stopover areas by migrant birds, including what vegetation types and habitats are most important to birds during migration, where these sites occur, and how their distribution and abundance are changing over time (Moore et al. 1995). Also, because more migrants pass through the eastern two-thirds of the United States, most of the literature on stopover sites concerns eastern migrants. Hence, there are few papers describing the specific use of Southwestern ponderosa pine forests as stopover sites. For example, Phillips et al. (1964) presented information on bird species in Arizona; and although in the species accounts they implied that several of the species migrated through ponderosa pine forests in the state, they did not state it explicitly (table 5). Hejl (1994, table 3), summarizing Brawn and Balda (1988a), also listed species that occur in Southwestern ponderosa pine forests but did not indicate those that were only migrating through the forests. On the other hand, Hutto (1985) found that stopover periods for transient (migrant) birds in fall and spring rarely exceeded

Table 5. Breeding (B), winterlng (W), and probable strictly migrant (M) birds in ponderosa pine forests (with oak or other plant species co-dominant) in Arizona and New Mexico, based on Phillips et al. (1964) and the New Mexico Partners in Flight list of sensitive bird species. Includes both Cordilleran (ponderosa pine) and Madrean (ponderosa and Apache) pine-oak forest types together. An asterisk (*) indicates a species for which there is some question about its use of ponderosa pine when it is in Arizona.

State Species		State Species	
Arizona	Rock wren* (B)	**New Mexico**	Red-tailed hawk (B,W)
Band-tailed pigeon (B)	American robin (B,W)	Virginia's warbler (B)	American kestrel (B,W)
Mourning dove (B)	Hermit thrush (B)	Olive-sided flycatcher (B)	American robin (B,W)
Whip-poor-will (B)	Eastern bluebird (B,W)	Grace's warbler (B)	
Vaux's swift* (M)	Western bluebird (B,W)	Band-tailed pigeon (B)	
White-throated swift (B)	Mountain bluebird (B,W)	Red-naped sapsucker (B,W)	
Black-chinned hummingbird (M)	Townsend's solitaire (B,M)	Willow flycatcher (B)	
Broad-tailed hummingbird (B)	Blue-gray gnatcatcher* (M)	Hammond's flycatcher (B)	
Rufous hummingbird* (M?)	Golden-crowned kinglet* (W)	Peregrine falcon (B)	
Allen's hummingbird* (M?)	Ruby-crowned kinglet* (M)	Williamson's sapsucker (B,W)	
Calliope hummingbird (M)	Olive warbler (B)	Dusky flycatcher (B)	
Rivoli's hummingbird (B)	Water pipit* (M)	Cordilleran flycatcher (B)	
Elegant trogon (B)	Cedar waxwing* (M)	Olive warbler (M)	
Northern flicker (B,W)	Loggerhead shrike (M)	Hepatic tanager (B)	
Acorn woodpecker (B,W)	Hutton's vireo (W)	Broad-tailed hummingbird (B)	
Lewis' woodpecker (B,M)	Solitary vireo (B,M)	Cassin's kingbird (B)	
Red-naped spasucker (W)	Warbling vireo (B,M)	Western bluebird (B,W)	
Yellow-breasted sapsucker (W)	Orange-crowned warbler (B)	Townsend's solitaire (B,W)	
Williamson's sapsucker* (B?,W,M)	Virginia's warbler (B)	Northern goshawk (B,W)	
Hairy woodpecker (B,W)	Yellow-rumped warbler (B,M)	Flammulated owl (B)	
Downy woodpecker (B,W)	Townsend's warbler (M)	Mountain bluebird (B,W)	
Three-toed woodpecker (B,W)	Hermit warbler (M)	Swainson's thrush (B)	
Cassin's kingbird (B)	Grace's warbler (B)	Wilson's warbler (B)	
Sulphur-bellied flycatcher (B)	Common yellow-throat* (M)	Cooper's hawk (B,W)	
Dusky-capped flycatcher (B)	Red-faced warbler (B)	White-throated swift (B)	
Black phoebe' (B,W?)	Wilson's warbler* (M)	Magnificent hummingbird (M)	
Buff-breasted flycatcher (B)	Painted redstart (B)	Greater pewee (M)	
Cordilleran flycatcher (B)	Red-winged blackbird (B,W)	Purple martin (B)	
Southwest willow flycatcher (B)	Brown-headed cowbird (B)	Golden-crowned kinglet (B,W)	
Greater pewee (B)	Bronzed cowbird (B	Hermit thrush (B,W)	
Olive-sided flycatcher (B,M)	Western tanager (B,M)	Veery (B)	
Western wood-pewee (B)	Hepatic tanager (B)	Warbling vireo (B)	
Violet-green swallow (B)	Black-headed grosbeak (B,M)	Orange-crowned warbler (B)	
Tree swallow* (B?)	Evening grosbeak (B,W)	Western tanager (B)	
Rough-winged swallow (B)	Red crossbill (B,W)	Black-headed grosbeak (B)	
Purple martin (B)	Cassin's finch (B,W)	Sharp-shinned hawk (B,W)	
Steller's jay (B,W)	House finch* (B,W)	Western wood-pewee (B)	
Western scrub jay* (M?)	Pine siskin (B)	Cassin's finch (B,W)	
Mexican jay (B,W)	Lesser goldfinch (B,W)	Ash-throated flycatcher (B)	
Common raven* (B,W)	Green-tailed towhee* (B)	Tree swallow (B,W)	
Pinyon jay (B,W)	Spotted towhee (B)	Violet-green swallow (B)	
Mexican chickadee (B,W)	Savannah sparrow* (W)	Ruby-crowned kinglet (B,W)	
Mountain chickadee (B,W)	Lark sparrow* (B)	Spotted towhee (B,W)	
White-breasted nuthatch (B,W)	Tree sparrow* (W)	Chipping sparrow (B)	
Red-breasted nuthatch (W)	Chipping sparrow (B,M,W)	Lincoln's sparrow (B)	
Pygmy nuthatch (B,W)	Dark-eyed junco (B,M,W)	Brown creeper (B,W)	
Brown creeper (B,W)	Yellow-eyed junco (B,W)	Yellow-rumped warbler (B,W)	
American dipper* (B,W)	White-crowned sparrow* (M)	Northern flicker (B,W)	
Winter wren (W)	Lincoln's sparrow* (B)	Dark-eyed junco (B,W)	
House wren (B)	Song sparrow* (B,W)	Pine siskin (B,W)	
Canyon wren* (B)		House wren (B)	

four to six days in pine (mostly Apache; P. engelmanii) and other vegetation in the Chiricahua Mountains, Arizona; and Moore et al. (1995) demonstrated that riparian or riverine areas in the southwest are vital for Southwestern migrants, notably the woodland species.

In general, stopover sites are used for depositing and replenishing lipid stores, molting, and resting (Moore et al. 1995). Stopover sites are crucial to a migrant bird's survival, especially long-distance migrants. Migration, although it allows birds to avoid overwintering in harsh environments, also has large costs associated with it, including the high energetic demands of transport (especially when there are climatic stresses); the multiple adjustments necessary to exploit unfamiliar sites; the conflicting demands of predator avoidance and food acquisition at stopover sites; and competition with other migrants and resident species for resources (Morse 1989:205; Moore et al. 1995).

Various features may cue migrants into selecting stopover sites in ponderosa pine forests, such as the proximity to riparian corridors, the forest structure, or the feeding rates or numbers of other migrants at sites (Moore et al. 1995). In a study of spring migrants crossing the Gulf of Mexico, Moore et al. (1995) found that the birds clearly selected areas with greater structural diversity following the flight. The areas were comprised of forests with complex mixed-shrub layers and contained the greatest diversity and abundance of migrants. However, Morse (1989:96) summarized studies of habitat selection by migrating warblers and found that habitat selection is subject to immediate and major fitness payoffs, indicating that selection of stopover sites may be influenced by factors other than vegetative structure. Climate changes, for example, may affect the choice of stopover sites, and ultimately wintering sites. Terrill and Ohmart (1984) found that the wintering ranges of yellow-rumped warblers differed from year to year in Arizona and adjacent Mexico apparently because the birds were retreating farther south in years when the winters were severe.

The amount of habitat actually available to migrants along the migration route is probably inherently limited, however, because migrants cannot take the time to search extensively for the "best" stopover sites (Moore and Simons 1992). This is due to a bird's need to reach the breeding area before it is saturated with conspecifics, or to reach the wintering area before the onset of severe weather. Studies of warbler species have demonstrated that some species use stopover sites that resemble those used on the breeding grounds, whereas other species do not use similar sites (reviewed in Morse 1989, chapter 9). Furthermore, the distributions of migrant birds are often correlated with changes in food availabilities (Morse 1989; Martin and Karr 1990; Moore et al. 1995). Because migration is a period of exceptional energy demand, it probably exerts strong selective pressures on the maximization of foraging efficiency (Moore and Simm 1985). Hutto (1985) found that the distribution of most insectivorous migrant birds in the Chiricahua Mountains, Arizona, was correlated with the abundance of arthropods in those vegetation types. He concluded that birds forage where they can be most efficient, unless interspecific competitive interactions force them to modify their first choice.

Species of Special Concern in Ponderosa Pine Forests

In this section we summarize current information on species of special concern in Southwestern ponderosa pine forests. To identify such species, we consulted the 1995 Arizona Partners in Flight (AZPIF) and 1994 New Mexico Partners in Flight (NMPIF) lists of sensitive breeding and wintering terrestrial bird species in the states. For these lists, bird species were ranked according to scores derived from their local and global distributions and abundances; the severity of threats on their breeding and wintering grounds; and the "importance" of Arizona and New Mexico to their overall distributions.

AZPIF and NMPIF also summarized the primary vegetation associations used by each bird species. The lists were created based on species accounts in the literature (for example, Phillips et al. 1964), as well as unpublished data. We did not consult state wildlife agency publications on threatened and sensitive species (for example, Threatened Native Wildlife in Arizona, Arizona Department of Game and Fish, 1988; BISON-M database, New Mexico Department of Game and Fish, 1996) because Atwood (1994) demonstrated that these publications were often incomplete and erroneous. We caution that the AZPIF and NMPIF lists may also suffer from the same weaknesses, but at a minimum the lists have been reviewed by authorities who are familiar with the distribution of birds in each state.

Arizona

Species of special concern received ranks from 1 to 100. Of the approximately 240 species given ranks in Arizona, 100 of these use ponderosa pine for breeding, wintering, and/or migrating. Of these hundred, 11 species were given ranks 150 (table 6), indicating that they are very high priority species—ones of special concern in the state—either because of low local or global abundances; restricted global or Arizona breeding distributions; substantial potential for extirpation on the breeding or wintering grounds; and/or a high importance of Arizona to the total breeding distribution of the species. Of these species, the whip-poor-will, elegant trogon, buff-breasted flycatcher, and sul-

phur-bellied flycatcher are at the northern edge of their ranges in Arizona, with the majority of their numbers occurring in Mexico. Atwood (1994) suggested that the inclusion of these species based solely on their limited occurrence at the northern extension of their ranges may ultimately divert research and management attention that should be given to truly threatened species. Two species on the list, the southwest willow flycatcher and olive-sided flycatcher, have shown declines in the state (and elsewhere), probably due to habitat destruction, and for the willow flycatcher, cowbird parasitism (Robinson et al. 1995). The remaining species on the list were placed there because of perceived moderate to extensive threats on the breeding and/or wintering grounds, and/or localized and isolated breeding distributions.

Another 20 ponderosa pine species were given ranks between 51 and 100 (table 6), indicating that they are of moderate concern but not exposed to threats as severe as the species with scores ≤50. These species were mostly considered uncommon (in abundance) in Arizona and globally. They were also considered to have moderate threats on their breeding and/or wintering grounds.

The 69 remaining species had ranks >100, indicating that their populations may be stable.

New Mexico

Of the 156 total species given ranks in New Mexico, 52 of these use ponderosa pine for breeding, wintering, and/or migrating. Of these fifty-two, **31** species were given ranks >2.50 (table 6) by NMPIF, indicating that they either had experienced declines in abundances over the past 26 years; their trends were unknown; they had low local or global abundances; they had restricted global or New Mexico breeding distributions; there was substantial potential for extirpation on the breeding or wintering grounds; and/or New Mexico is important to the total breeding distribution of the species. Of the special concern species *oc*curring in ponderosa pine forests, only the peregrine falcon is currently listed as federally endangered or threatened. Another 12 species occurring in ponderosa pine were given ranks between 2.10 and 2.45 (table 6), indicating that their status is of moderate, rather than high, concern in the state.

Comparison of Lists

In both Arizona and New Mexico, the (southwest) willow flycatcher, olive-sided flycatcher, olive warbler, Virginia's warbler, and Grace's warbler were given high priority ranks. The NMPIF database listed six species of high concern that were considered of only moderate concern in Arizona: the band-tailed pigeon, Cordilleran flycatcher, greater pewee, Townsend's solitaire, orange-crowned warbler, and hepatic tanager. The NMPIF list also contained an additional 21 species of high concern, versus Arizona's six other species of high concern. For species of moderate concern, the AZPIF database listed an-

Table 6. Southwestern ponderosa pine forest birds in Arizona and New Mexico with ranks indicating that they are of high or moderate concern In each state. Criteria for rankings are given in the text.

Rank Species	Rank Species
Arizona	***New Mexico***
≤50	**>2.50**
Whip-poor-will	Virginia's warbler
Elegant trogon	Olive-sided flycatcher
Buff-breasted flycatcher	Grace's warbler
Southwest willow flycatcher	Band-tailed pigeon
Olive-sided flycatcher	Red-naped sapsucker
Olive warbler	Willow flycatcher
Solitary vireo	Hammond's flycatcher
Virginia's warbler	Peregrine falcon
Red-faced warbler	Williamson's sapsucker
Sulphur-bellied flycatcher	Dusky flycatcher
Grace's warbler	Cordilleran flycatcher
51–100	Olive warbler
Band-tailed pigeon	Hepatic tanager
Northern (glided) flicker	Broad-tailed hummingbird
Lewis' woodpecker	Cassin's kingbird
Red-naped sapsucker	Western bluebird
Yellow-breasted sapsucker	Townsend's solitaire
Williamson's sapsucker	Northern goshawk
Three-toed woodpecker	Flammulated owl
Cordilleran flycatcher	Mountain bluebird
Greater pewee	Swainson's thrush
Tree swallow	Wilson's warbler
Pygmy nuthatch	Cooper's hawk
Eastern bluebird	White-throated swift
Townsend's solitaire	Magnificent hummingbird
Loggerhead shrike	Greater pewee
Orange-crowned warbler	Purple martin
Painted redstart	Golden-crowned kinglet
Hepatic tanager	Hermit thrush
Lazuli bunting	Veery
Red crossbill	Warbling vireo
Green-tailed towhee	Orange-crowned warbler
	2.10–2.45
	Western tanager
	Black-headed grosbeak
	Sharp-shinned hawk
	Western wood-pewee
	Cassin's finch
	Ash-throated flycatcher
	Tree swallow
	Violet-green swallow
	Ruby-crowned kinglet
	Spotted towhee
	Chipping sparrow
	Lincoln's sparrow

other 14 beyond the six mentioned above, whereas New Mexico had only 12 total species listed (table 6).

Changes in Abundance

Hejl (1994), summarizing Brawn and Balda (1988a), proposed that 15 Southwestern ponderosa pine forest bird species have probably decreased in abundance from presettlement times to the present because of decreases in the prevalence of these forest conditions. Hejl based this on the birds' requirements for burned sites, old-growth forests, and/or snags. The species were the broad-tailed hummingbird (AZPIF ranking # 113; NMPIF ranking # 48), acorn woodpecker (AZPIF #129), three-toed woodpecker (AZPIF #52), purple martin (#116, #82), violet-green swallow (#172, #119), mountain chickadee (AZPIF #170), white-breasted nuthatch (AZPIF #206), pygmy nuthatch (AZPIF #68), brown creeper (#189, #138), western bluebird (#132, #51), mountain bluebird (#160, #66), American robin (#225, #156), red-faced warbler (#16, #17), chipping sparrow (#205, #129), and lark sparrow (#177, #93). For the most part, however, Hejl's projections do not coincide with the species of special concern on the AZPIF and NMPIF lists, and the purple martin, western bluebird, and American robin were shown by Miller (1992) to be increasing in Arizona and New Mexico. Hejl (1994) also proposed that nine other bird species have probably increased in abundance from presettlement times to the present because of fire suppression and increased amounts of second-growth forests. These species were the Cordilleran flycatcher (AZPIF #74, NMPIF #37), house wren (#224, #152), Townsend's solitaire (#98, #52), hermit thrush (#150, #85), solitary vireo (#45, #53), Virginia's warbler (#33, #11), yellow-rumped warbler (#217, #140), Grace's warbler (#49, #16), and western tanager (#145, #91). Miller (1992) found that numbers of solitary vireos, Virginia's warblers, and Grace's warblers have actually decreased in managed ponderosa pine forests. However, Johnson (1994) determined that Grace's warblers, painted redstarts, and hepatic tanagers have expanded their ranges northward in this century. On the AZPIF and NMPIF lists, these latter two species are considered fairly high priority ones for study because of their rarity and localization. In addition, the solitary vireo and Virginia's warbler are also ranked as species of special concern in Arizona and New Mexico, despite Hejl's indications that they should be responding positively to habitat changes in Southwestern forests.

As mentioned previously for the southwest willow flycatcher, a significant factor in the decline of some other bird species in the western United States is the increase in parasitism by brown-headed cowbirds. This species, along with two grackle species, has experienced the greatest rate of increase and largest expansion of any native bird species in the United States (Marzluff 1994). There are about 11 to 20 cowbirds per Breeding Bird Survey route in Arizona and 0 to 10 per route in New Mexico (Robinson et al. 1995). Because of their parasitic nature, cowbirds can breed in a wider range of vegetation types than probably any other North American passerine (Robinson et al. 1995). In the west, cowbirds occur regularly in coniferous forests but in fewer numbers than in other nearby areas such as meadows and riparian zones (for example, Rothstein et al. 1984).

Host species of cowbirds tend to be small-sized, open-cup-nesting birds with long incubation periods, including *Empidonax* flycatchers and phoebes, vireos, warblers, and sparrows such as the chipping sparrow. Hosts inhabiting forest edges and/or second-growth forests also tend to be more heavily parasitized. The largest declines in host numbers are seen in species with restricted geographic breeding ranges and with habitat that is fragmented, is threatened by direct destruction (such as that of the southwest willow flycatcher), and/or has been subject to fire suppression (reviewed in Robinson et al. 1995; see also Moir et al., this volume).

Despite concerns about increased parasitism by cowbirds in the western United States, parasitism has not been documented in several birds that would seem to be likely candidates. For example, Martin (1992, table 1) summarized reproductive data for neotropical migrant birds in Arizona and New Mexico. Black-headed grosbeaks in deciduous (oak) forests in New Mexico were not parasitized by cowbirds. Neither were warbling vireos, orange-crowned warblers, Virginia's warblers, yellow-rumped warblers, MacGillivray's warblers, red-faced warblers, western tanagers, and black-headed grosbeaks in mixed-conifer/deciduous forests in Arizona according to several recent studies. On the other hand, parasitism rates in other small flycatchers and warblers (such as western wood-pewees and painted redstarts in Arizona) can be quite high (L. Christoferson, unpubl. manuscript, University of Arizona). For example, Marvil and Cruz (1989) documented the fate of solitary vireo nests in ponderosa pine/Douglas-fir forests in Colorado. Approximately 49 percent of all vireo nests were parasitized with one to three brown-headed cowbird eggs during the breeding seasons of 1984–1986, leading to a significant decrease in the reproductive success of the nests.

Conclusions

We found specific information on the use of Southwestern ponderosa pine forests by approximately 50 bird species. However, of these species, only about 35 percent appear to restrict their vegetation use to primarily ponderosa pine, whereas about 65 percent are associated with other plant components (for example, aspen, oak, Douglas-fir,

fir, spruce, and pinyon-juniper) within ponderosa pine forests. This shows that most ponderosa pine bird species require features in addition to pine. It also implies that forest management must include consideration of these features if the retention of diverse bird communities is desired. Although many species are declining in abundance, few species are nearing extirpation. More effort could thus be expended on monitoring trends of species of special concern and on monitoring their demographies. The factors causing the apparent declines are still largely speculative and thus need to be investigated.

In regard to "disturbed" sites (either from fire or logging), bird species showed different responses, although most species appeared to tolerate (at least in terms of their abundances) light to moderate disturbance. With heavy alteration of the forest structure (for example, via fires, clearcutting, or strip-cutting), species composition varied in a predictable way, with more understory species using cleared forest stands. Nest predation apparently influenced the placement of nests to the extent that birds selected denser foliage. Nest success—as might be expected—varied among species and study areas, but bluebird nesting success decreased on heavily altered sites. Forest management must be site- and time-specific and management objectives must consider all of the different components that are used by the numerous species of ponderosa pine forests. Data also indicate a strong need for intensive studies of the reproductive success of ponderosa pine birds; without these data, any conclusions about the current status or current habitat requirements of the species are tenuous.

We know little specifically about the use of ponderosa pine forests by migrating birds. However, we can estimate that Southwestern pine forests are probably used as stopover sites by at least 25 migrant bird species in a given year. Research on migratory birds in other vegetation types suggests that forest structure, food availability, inter- and intraspecific competition for resources, and climate conditions all influence the use of these forests by migrant species. Therefore, we can probably assume that these same factors would influence the use of Southwestern ponderosa pine forests as stopover sites. And as such, the number of species that may depend on ponderosa pine forests for replenishment of lipids or as resting sites makes this vegetation type important to their survival. However, we need more research on how migratory birds use ponderosa pine forests. Most studies have also concentrated on breeding birds; more work needs to be conducted on non-breeding (wintering) birds. This information is critical for developing appropriate forest management plans because of the role that stopover sites can play in maintaining bird populations.

Natural expansions and increases in populations of some ponderosa pine forest species have been documented (DeSante and George 1994, Johnson 1994); however, a large percentage of species have declined, due probably to various causes. The many factors that may affect ponderosa pine songbird numbers (such as fire, logging, grazing, and climate change) and the variations in local site conditions make it difficult to predict exact trends in bird numbers. Again, the implications of this for management of ponderosa pine forests are that one treatment, or one management style, will not elicit the same population response from all bird species. Similarly, effects of past management practices may vary depending on location.

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