

Abundance and Productivity of Birds Over an Elevational Gradient¹

Kathryn L. Purcell²

Abstract

This study is investigating the abundance and productivity of birds breeding in four forest types over an elevational gradient in conifer forests of the southern Sierra Nevada of California to identify the most productive habitats for each species, and to examine elevational shifts in abundance, especially as they relate to temperature and precipitation. Species richness and abundance decreased with increasing elevation, although higher elevations were important for cavity-nesting species. Abundance and nest success varied across years and forest types. Dark-eyed juncos (*Junco hyemalis*) were most abundant at the lowest and highest elevations and had their highest nest success in the lodgepole pine (*Pinus contorta*) forest type. Excluding the ponderosa pine (*Pinus ponderosa*) forest type, where they were rare, dusky flycatchers (*Empidonax oberholseri*) were least abundant in true fir sites but had their highest nest success and productivity there. Abundance vs. nest success and number of young fledged were both negatively correlated, suggesting that dusky flycatchers were unable to assess the probability of successfully nesting in a given habitat prior to settling. In accordance with expectations, 15 species exhibited downslope elevational shifts following severe winters in 1995 and 1998, and six species exhibited upslope shifts.

USDA Forest Service lands include many forest types, broadly distributed along elevational and latitudinal gradients. Specific management activities are often concentrated in certain elevational bands and forest types, and wildlife species are affected according to their distribution and response. Identification of species' requirements for survival and reproduction and knowledge of their responses to forest management practices are crucial to maintaining biodiversity.

To manage for a species, we need to know what limits its abundance and distribution, whether it is primarily interactions between species, abiotic factors such as temperature and precipitation, or factors relating to historical and evolutionary constraints. Individuals of a species do not survive independently of individuals of other species. Predation, competition, and parasitism are often cited as potential factors regulating the organization of bird communities (Hairston and others 1960, Hudson and Dobson 1991, MacArthur 1958, Price 1986). Interspecific competition for resources has received much attention in this regard, especially in birds, although the importance of competition has been challenged (for review see Wiens 1989). Disproportionate predation on prey species may favor differences in relative abundance of coexisting species. Nest predation is recognized as a major cause of reproductive failure in birds (Ricklefs 1969), and it may be an important selective force affecting the distribution of species across habitats (Martin 1988a).

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² Research Wildlife Biologist, Pacific Southwest Research Station, USDA Forest Service, 2081 E. Sierra Ave., Fresno, CA 93710.

Weather can also be an important factor influencing bird abundance in temperate montane forests (Hejl and Beedy 1986, Hejl and others 1988, Raphael and White 1984). The response of a particular species may be mediated by migration status or nest type, with neotropical migrants and cavity nesters generally less negatively impacted by harsh winters (Bock and Lynch 1970). Weather conditions can exert an influence on both the upper and lower elevational limits of species, with some species moving upslope in years with light precipitation and downslope in years with heavy precipitation (DeSante 1990). Extreme weather conditions can also exert a strong influence on bird abundance, and the resulting changes in abundance do not necessarily reflect habitat choice (Hejl and Beedy 1986, Hejl and others 1988). To include the range of variability encountered, long-term studies are required to examine the effects of yearly variations in weather on bird abundance and productivity (Verner and Purcell 1999).

Monitoring programs based solely on census data may detect population problems only long after they have occurred. Healthy populations are those in which reproduction is sufficient to maintain population size. Unhealthy populations can be maintained only by immigration from healthy populations, causing some population problems to go undetected for years. Presence of a species may not reflect a population's health because data on species abundance may not be a reliable indicator of the value of a habitat (Purcell and Verner 1998, Van Horne 1983). Identification of productive or source habitats is crucial when managing for species persistence. When bird abundance and productivity shift in response to weather conditions, source habitats may shift as well and an understanding of these relations and the ability to predict this response is also needed. Relations between bird abundance and productivity can help elucidate the mechanisms by which birds select breeding habitat, whether those choices are adaptive, and, if not, what the mechanism for settling on breeding territories might be.

Long-term studies, involving multiple species at large spatial scales are needed to assess the response of a bird community to silvicultural methods, with results being used to improve future planning (so-called adaptive management). Nongame birds are particularly appropriate for monitoring environmental health. Breeding productivity is more easily monitored for birds than for any other group of vertebrate taxa.

The objectives of this study were to assess the abundance and productivity of bird species in four forest types over an elevational gradient in the southern Sierra Nevada of California; to identify species' breeding habitat requirements, including identification of the most productive habitats for each species; to assess current population health of a wide range of species, including the identification of source and sink habitats; to examine relations between abundance and productivity across the four forest types; to develop models of habitat needs for healthy populations of coexisting species and to predict species' vulnerabilities to habitat change; and to examine elevational shifts in bird abundance, especially as they relate to the severity of the previous winter's weather, and to examine whether, in years of unusual weather conditions, variations in productivity are associated with these shifts. This paper reports preliminary results from the first 4 years of a planned 10-year study.

Methods

Eighteen study sites in four forest types were selected on the King's River Ranger District of the Sierra National Forest in 1994 (fig. 1). Sites at the lowest elevations are in ponderosa pine (*Pinus ponderosa*) stands (elevation 1,024-1,372 m), followed by mixed-conifer stands (elevation 1,707-2,012 m), and true fir stands (elevation 2,170-2,347 m), with lodgepole pine (*Pinus contorta*) stands at the highest

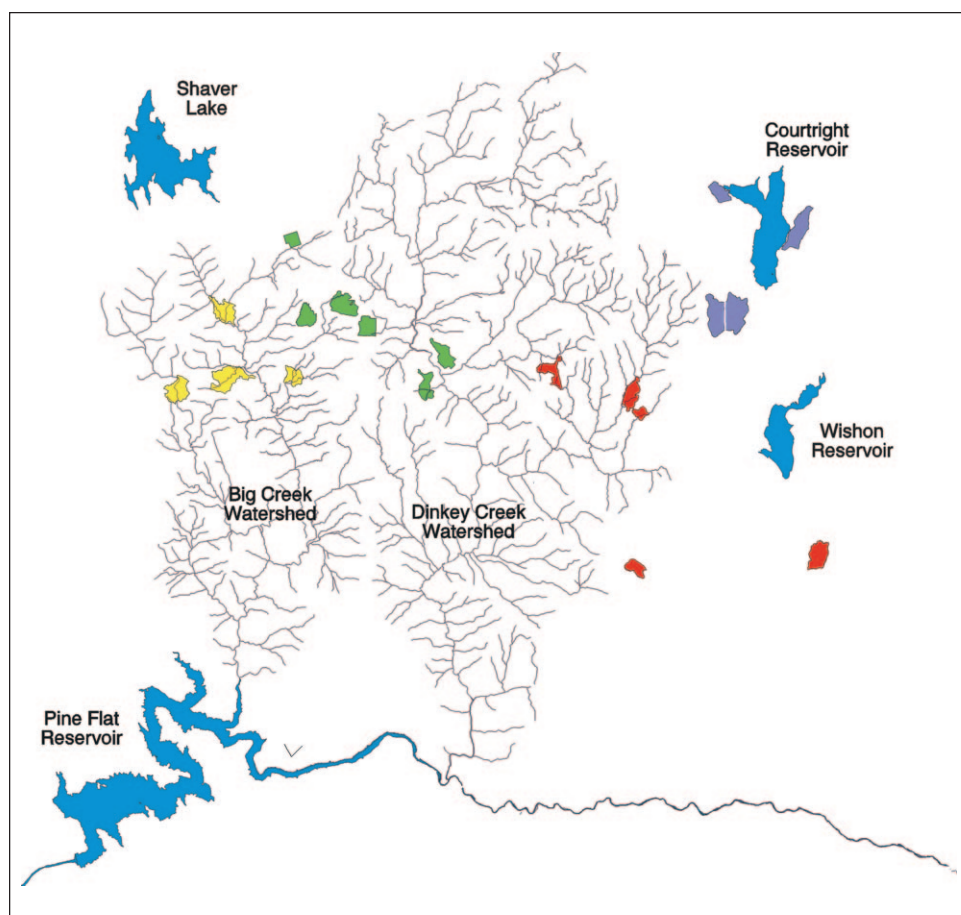


Figure 1—Locations of study sites in the Sierra National Forest, California: yellow = ponderosa pine (elevations 1,041–1,372 m); green = mixed conifer (elevations 1,701–2,012 m); red = true fir (elevations 2,170–2,347 m); and purple = lodgepole pine (elevations 2,469–2,774 m).

elevations (2,469–2,774 m). Each forest type has four replicates, except mixed conifer, which has six replicates. Of the six mixed-conifer sites, three lie in each watershed of the Kings River Sustainable Forest Ecosystems Project area. All sites are protected from major disturbance for 10 years, including timber harvest, road construction, and major fuel breaks, after which they will be incorporated into the adaptive landscape treatment appropriate to their watershed. All sites consist of at least 60 ha of mature forest with relatively high canopy cover. A 40-ha gridded plot has been established in each of the 60-ha sites to allow censusing and to facilitate mapping and relocation of nests.

From 1995 to 1998, field crews censused birds on 8 (1995) or 16 (1996–1998) plots each year, using a timed transect method. Transects were 1000 m long and observers walked at a rate of 50 m per 3 min. Observers recorded all birds seen or heard <50 and >50 m from the transect line. Censuses were trained during a 2-week period at the beginning of the field season, with additional training as they moved into higher forest types and encountered new species; each observer's hearing was tested yearly. Each transect was counted six times during the breeding season, with two visits by each of three observers. The order of census visits and starting points of observers were randomly selected, with the constraint that visits were evenly divided between the two starting points. Censuses began at 07:00 PDT in all forest types except ponderosa pine, where they began at 07:30 PDT to accommodate the shorter day lengths earlier in the season. All censuses were completed within 1.5 hr. In 1996 through 1998, field crews recorded the percent cover and depth of snow in a 1-m-radius circle around the census markers on each plot following each census.

We searched for nests of all bird species and monitored nests every 3 to 4 days, following the methods of Martin and Geupel (1993). Open nests were checked directly, where possible, or with a mirror on a pole or a small video

Figure 2—Operational use of a fiberscope to check the contents of a white-headed woodpecker's cavity nest.



Figure 3—Climbing a large pine tree by using a stacked set of Swedish climbing ladders that are secured to the bole of the tree.



camera mounted on an extendable fiberglass pole. Cavity nests were checked with a fiberscope (Purcell 1997) (*fig. 2*). When nests were too high to reach from the ground and nest substrates were sturdy, field crews climbed to nests by using a variety of climbing techniques (*fig. 3*). Prior to field operations, field assistants received training in tree climbing techniques and were certified to national Forest Service standards.

Habitat measurements were taken at the nest site and at random sites on each plot each year. The variables recorded described the nest site and the habitat surrounding the nest. They included, but were not limited to: basal area

of trees and snags; number and species of trees and snags by size class; canopy cover; litter depth; slope; aspect; length, diameter, and decay class of logs; and percent cover of grasses, forbs, rock, soil, litter, logs, shrubs, and trees in the understory. Variables specific to the nest included nest height; species, height, and diameter of the nesting substrate; variables describing placement of open nests; and dimensions and orientation of cavity nests.

I estimated nest success and daily mortality rates based on Mayfield's methods (1961, 1975), with variances calculated following Hensler and Nichols (1981). Differences among daily mortality rates were tested using program Contrast (Hines and Sauer 1989), as described by Sauer and Williams (1989). I used two-way analysis of variance to test differences in abundance across years and forest types.

Results

From 1995 through 1998, crews detected a total of 92 bird species and monitored 1954 nests of 66 species. Thirty-five percent of the species recorded during censuses occurred in all four forest types. Eighteen percent, or 17 species, occurred in only one forest type; of these, 14 species only in the ponderosa pine forest type. Many of these 14 species are typical of drier, low-elevation habitats, such as ash-throated flycatcher (*Myiarchus cinerascens*), western scrub-jay (*Aphelocoma californica*), bushtit (*Psaltirparus minimus*), blue-gray gnatcatcher (*Poliophtila caerulea*), Hutton's vireo (*Vireo huttoni*), Bullock's oriole (*Icturus bullockii*), and Lawrence's goldfinch (*Carduelis lawrencei*).

Species richness declined with increasing elevation (fig. 4a), and abundance followed the same pattern (fig. 4b). Abundance of the cavity-nesting guild, however,

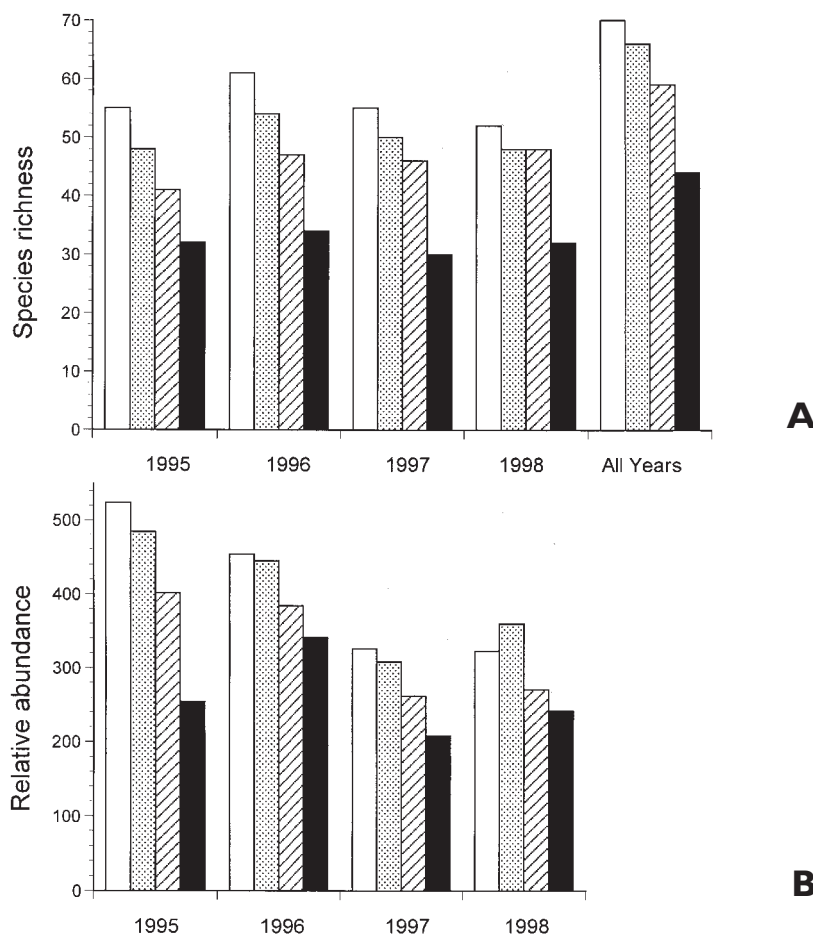
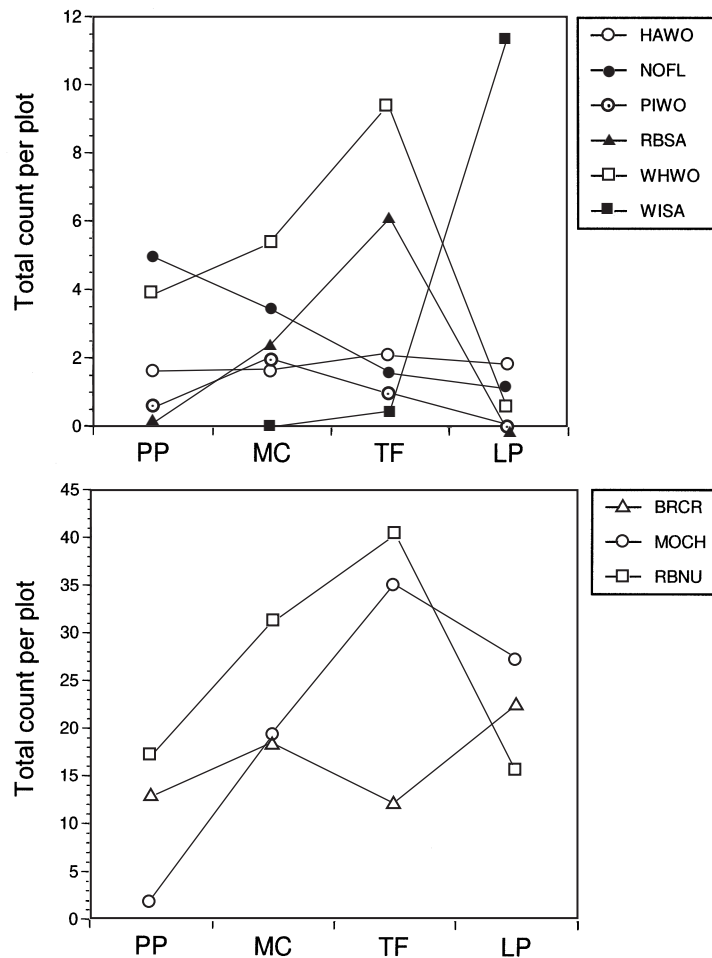


Figure 4—Yearly species richness (number of species detected at unlimited distance) and relative abundance (total count per plots, detected within 50 m.) in four forest types over an elevational gradient (open bars = ponderosa pine, stipled = mixed conifer, cross-hatched = true fir, solid = lodgepole pine).

Figure 5—Relative abundance (total count per plot) of cavity-nesting birds in four forest types over an elevational gradient (PP = ponderosa pine, MC = mixed conifer, TF = true fir, LP = lodgepole pine). HAWO = hairy woodpecker, NOFL = northern flicker, PIWO = pileated woodpecker, RBSA = red-breasted sapsucker, WHWO = white-headed woodpecker, WISA = Williamson's sapsucker, BRCR = brown creeper, MOCH = mountain chickadee, RBNU = red-breasted nuthatch.



showed the reverse pattern, with all but two species attaining their highest abundance in true fir or lodgepole pine sites (fig. 5). The two exceptions were northern flickers (*Colaptes auratus*), which decreased in abundance with increasing elevation, and pileated woodpeckers (*Dryocopus pileatus*), which reached their maximum abundance in mixed-conifer sites (fig. 5). Abundance of open nesters showed no clear trend, as might be expected in such a diverse group.

Abundance of dark-eyed juncos (*Junco hyemalis*) was variable across years (Type III sums of squares, $F_{3,40} = 9.04$, $P = 0.0001$) and across habitats (Type III sums of squares, $F_{3,40} = 6.40$, $P = 0.0012$). Abundance was low in 1997 and 1998, and in mixed-conifer and true fir sites (fig. 6a). Nest success did not differ significantly across years ($P = 0.17$), although variability was high. Nest success increased with increasing elevation ($P = 0.02$), with the highest nest success in lodgepole pine forests ($P = 0.0045$; fig. 6b).

The abundance of dusky flycatchers (*Empidonax oberholseri*) was lower in 1997 and 1998 than in other years (Type III sums of squares, $F_{3,30} = 9.28$, $P = 0.0002$; fig. 7) and lowest in true fir habitat (Type III sums of squares, $F_{3,30} = 9.53$, $P = 0.0006$; fig. 7). Nest success, on the other hand, was highest in true fir habitat ($P = 0.0359$; fig. 7), yielding a negative, although nonsignificant, relationship between abundance and nest success ($r = -0.41$, $P = 0.19$; fig. 8).

Clutch size of dusky flycatchers did not differ across forest types (fig. 9), but the number of young fledged per attempt was highest in true fir (fig. 9). After removing small sample sizes for year/forest type combinations ($n < 8$), the correlation between abundance and clutch size was nonsignificant ($r = -0.57$, $n = 6$, $P = 0.24$; fig. 10), but abundance and number fledged per attempt was significantly negatively correlated ($r = -0.78$, $n = 8$, $P = 0.02$; fig. 10).

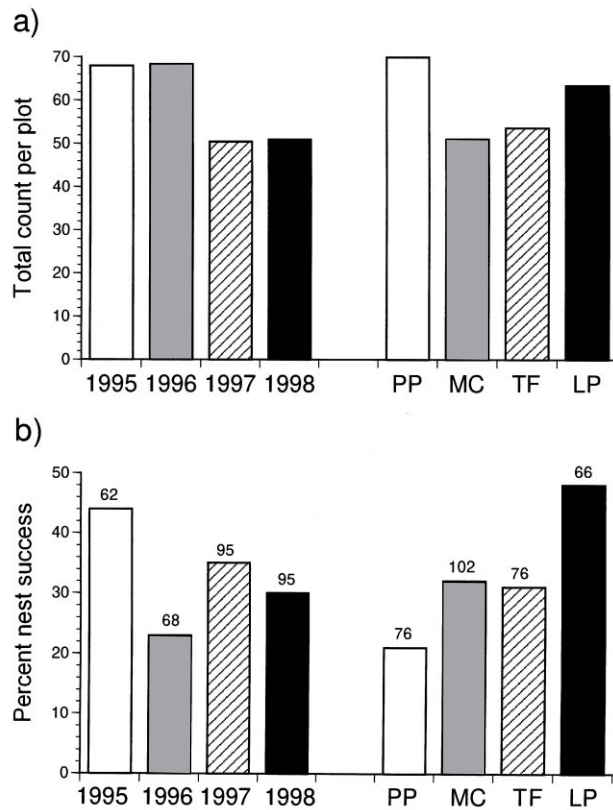


Figure 6—Relative abundance (total count per plot) and nest success of dark-eyed juncos by year and forest type (PP = ponderosa pine, MC = mixed conifer, TF = true fir, LP = lodgepole pine), from low to high elevation. Sample sizes for nest success are shown above columns.

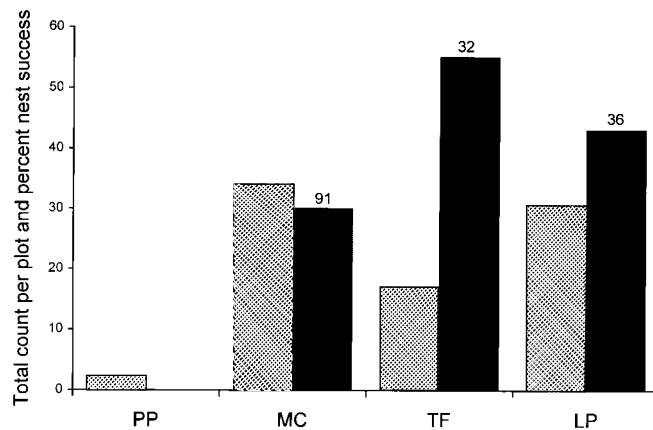


Figure 7—Dusky flycatcher abundance (cross hatched columns) and nest success (solid columns) by forest type (PP = ponderosa pine, MC = mixed conifer, TF = true fir, LP = lodgepole pine) from low to high elevation. Sample sizes for nest success are shown above columns.

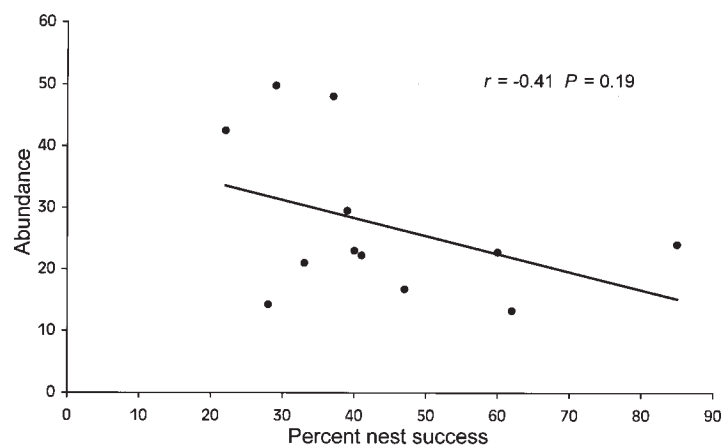


Figure 8—Relative abundance (total count per plot) vs. nest success of dusky flycatchers.

Figure 9—Clutch size (stippled columns) and number of young fledged per nesting attempt (solid columns) by dusky flycatchers by forest type (PP = ponderosa pine, MC = mixed conifer, TF = true fir, LP = lodgepole pine) from low to high elevation. Sample sizes are shown above columns.

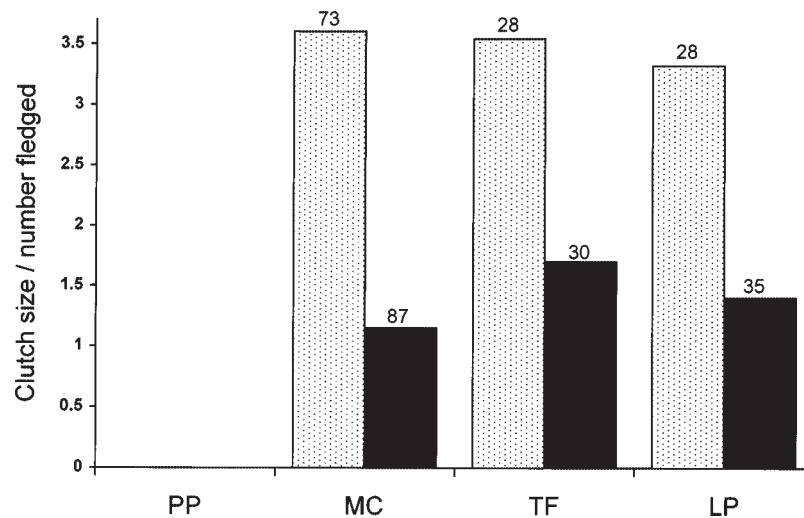


Figure 10—Relative abundance (total count per plot) vs. clutch size (open circles) and number of young fledged per attempt (closed circles) for dusky flycatchers. Small sample sizes ($n < 8$) for year/forest type combinations were deleted.

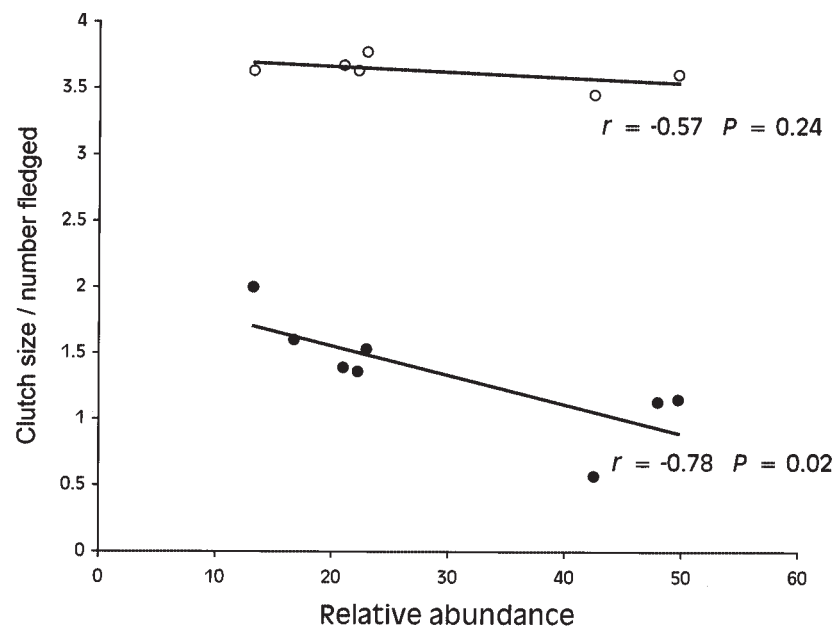
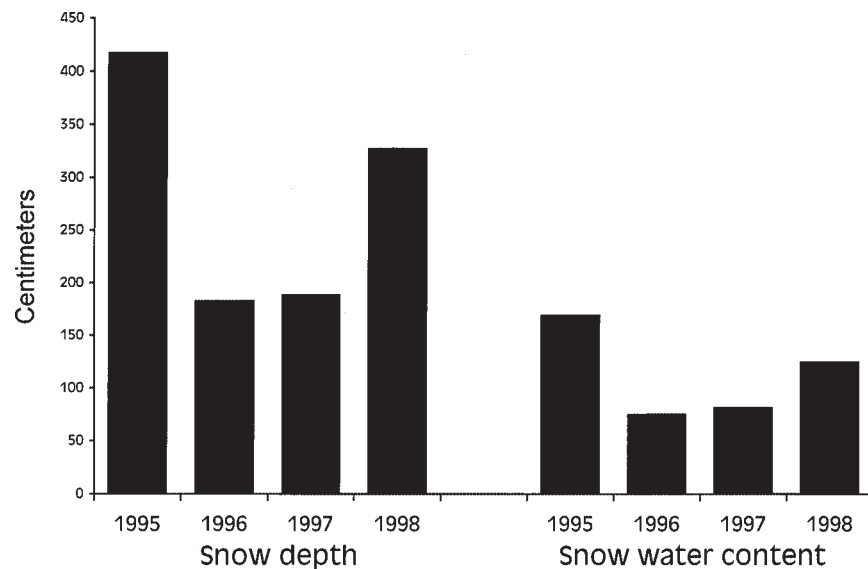


Figure 11—Snow depth and snow water content recorded 1 April each year at Courtright Reservoir (elevation 2,570 m).



The 1995 and 1998 breeding seasons followed severe winters, with snow remaining on the ground until well into the breeding season. Snow-depth data from Courtright Reservoir (elevation 2570 m) showed high snow depths on 1 April of 1995 and 1998, compared to 1996 and 1997 (fig. 11). Field personnel did not record snow data in 1995, but 38-46 percent of the census markers had snow during the census period in mixed-conifer, true fir, and lodgepole pine forest types in 1998. No snow was recorded at the census markers in 1996 or 1997.

We expected to observe downslope shifts in populations of some species in years with heavy precipitation. Looking only at presence/absence data and examining species that either disappeared from habitats where they had occurred or appeared in habitats where they were absent in 1996 and 1997, I found 15 downslope shifts of species in 1995 and 1998 compared with six

Table 1—Downslope and upslope shifts of species of species in the breeding season after the severe winters of 1994-95 and 1997-98, based on presence/absence data and disappearance of species from forest types where they had occurred in the previous year, or their appearance in forest types where they were absent in the previous year

Forest type	Bird species	Year	Direction of shift
Ponderosa pine	Ash-throated flycatcher (<i>Myiarchus cinerascens</i>)	1998	down
	Western scrub-jay (<i>Aphelocoma californica</i>)	1995	down
	Winter wren (<i>Troglodytes aedon</i>)	1995	up
	Bewick's wren (<i>Thryomanes bewickii</i>)	1998	up
	Song sparrow (<i>Melospiza melodia</i>)	1998	up
	Fox sparrow (<i>Passerella iliaca</i>)	1998	down
	Cassin's finch (<i>Carpodacus cassinii</i>)	1995, 1998	up
Mixed-conifer	Mourning dove (<i>Zenaidura macroura</i>)	1995, 1998	down
	Wrentit (<i>Chamaea fasciata</i>)	1995, 1998	down
	Brown-headed cowbird (<i>Molothrus ater</i>)	1998	down
True fir	Brown-headed cowbird (<i>Molothrus ater</i>)	1995, 1998	down
	Williamson's sapsucker (<i>Sphyrapicus thyroideus</i>)	1995, 1998	down
	Pacific-slope flycatcher (<i>Empidonax difficilis</i>)	1995, 1998	up
	Ruby-crowned kinglet (<i>Regulus calendula</i>)	1998	down
	Lincoln's sparrow (<i>Melospiza lincolni</i>)	1995	down
Lodgepole pine	White-headed woodpecker (<i>Picoides albolarvatus</i>)	1998	down
	Western wood-pewee (<i>Contopus sordidulus</i>)	1998	down
	Golden-crowned kinglet (<i>Regulus satrapa</i>)	1995	down
	Hermit warbler (<i>Dendroica occidentalis</i>)	1995	up
	White-crowned sparrow (<i>Zonotrichia leucophrys</i>)	1998	down
	Purple finch (<i>Carpodacus purpureus</i>)	1995, 1998	down

upslope shifts (table 1). Abundance of dusky flycatchers in ponderosa pine habitat in 1995 and 1998 was more than twice that in 1996 and 1997. The spotted towhee (*Pipilo maculatus*), a species found only in ponderosa pine and mixed-conifer types, was only half as abundant in the mixed-conifer type in 1995 and 1998 as it was in 1996 and 1997. Dusky flycatchers nested in ponderosa pine habitat for the first time in 1998, and one nest of the mountain chickadee (*Poecile gambeli*) was found in a ponderosa pine site in both 1995 and 1998.

Discussion

A consensus has emerged in recent years that the appropriate focus for wildlife issues by the Forest Service is on maintaining native biodiversity. Conservation of biological diversity depends on identification and preservation of habitat conditions that sustain healthy populations of coexisting species. Results obtained from this research are important to resource specialists and agency biologists in managing for and maintaining biodiversity. Identification of source and sink habitats and understanding their dynamics are crucial for maintaining healthy populations of these species.

Among the four forest types under study, ponderosa pine provides habitat for the most species and the most individuals. Many of the species found there are more typically found at lower elevations in vegetation types that are not well represented on public lands.

Abundance and nest success have varied significantly across years and forest types, underlining the need for long-term studies. Some of the variability in abundance and nest success appeared to be related to winter weather conditions preceding the breeding season. The lower nest success at lower elevations found in some species might be compensated by the longer breeding seasons at lower elevations and the possibility of multiple breeding attempts.

A lack of correlation between abundance and nest success suggests that individuals are not able to judge the probability of nesting successfully in a particular habitat. A negative relation suggests inappropriate choices. This pattern is consistent with density-dependent predation, where, at high densities, predators can specialize on the nests of a particular species, resulting in low nest success. At low densities, nest predators cannot specialize on the more rare nests, leading to low rates of nest predation (Major and others 1994; Martin 1988a, 1988b, 1996). If density-dependent predation is acting, dusky flycatchers cannot make appropriate choices regarding nesting habitat, as they will experience low nest success wherever they settle in high densities. Social interference might also cause low nest success at high densities (Jones and Leopold 1967, Tompa 1964), if adults are forced to spend more time away from their nests defending territories and mates, leaving the nest undefended and exposed to predation. Poor post-fledging survival in true fir sites could also account for a lack of recruitment in high-quality habitat, although no a priori reason exists to expect lower survival in fir than in other habitats.

Although I did not report analyses of habitat data here, the accumulating vegetation and nest-site data will be important for describing habitat characteristics of nest sites used by birds, it will allow identification of variables important to successful nesting, and it will allow prediction of the effects of forest management practices on forest birds.

After 10 years, when these sites are to be managed according to the silvicultural prescription appropriate to each of the two watersheds, the efficacy of these approaches for maintaining biodiversity will be assessed. The hope is that, by maintaining a mosaic of forest stand structures using uneven-aged management practices and reintroducing fire into the ecosystem, all species will be retained. "To keep every cog and wheel is the first precaution of intelligent tinkering" (Leopold 1966).

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