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Conceptual Framework and Ecological Considerations for the Study of Birds in Oak Woodlands[1]

William M. Block and Michael L. Morrison[2]

Abstract: The distributions and abundances of birds within oak woodland communities of California are the results of geologic events leading to the formation of the Mediterranean-type ecosystem, and of more recent anthropogenic impacts that have altered the landscape. These human-wrought disturbances to oak woodlands likely are affecting population parameters and distributions of birds throughout California. Because little is known of bird-habitat relationships in oak communities, however, the actual effects of these land-use practices on birds are unknown. Here we present a framework for the study of birds in the oak woodlands of California. The principal objective of this framework is to outline aspects of bird biology, ecology and behavior that must be addressed before assessments of habitat quality can be made. Assessments of habitat quality require that population numbers, reproduction rates, and survival rates be monitored. Further, bird habitats must be studied to determine site characteristics of areas that birds actually use within oak woodlands. Determination of specific patterns of resource use entails intensive study of bird activities. Collection of all of these data requires extensive field work to determine temporal and spatial patterns of habitat and resource use. There are no shortcuts for obtaining this information.

The distributions, abundances, and habitat-use patterns of birds in oak habitats are influenced by numerous factors. Avian settlement patterns and processes of speciation can be traced to the Tertiary and Quaternary periods. During these periods climatic changes, mountain building, and glaciation resulted in the present distributions of hardwoods throughout the state of California, which have in turn strongly influenced the distributions of birds (Hubbard 1973, Axelrod 1977). Proximate and ultimate factors, biotic and abiotic processes, temporal and spatial patterns, and various innate and learned behaviors interacted to shape the patterns of habitat use evident in modern species. Recent anthropogenic pressures have reshaped the landscape and have altered the environments available to birds. These changes have most likely altered the historic habitat-use patterns of birds.

Unfortunately, little is known of bird-habitat relationships in oak woodlands. Early naturalists (e.g., Grinnell and Miller 1944, Leopold 1951, Miller 1951) provided valuable species accounts based on their observations. The information presented by these naturalists was generally in the form of qualitative descriptions of species' distributions and habitat associations. These data are of insufficient detail, however, to allow resource managers to assess habitat quality or to predict the effects of environmental change on bird population parameters. Further, Muick and Bartolome (1985) found few recent studies of bird-habitat relationships in oak woodlands. Consequently, a research program is required to study bird-habitat relationships in oak woodlands that provides information in sufficient detail to allow assessments of habitat quality and predictions of the effects of habitat change on birds.

The purpose of this paper is to present a general framework for the study of birds in oak woodlands. Our primary objective is to outline aspects of bird biology and ecology that researchers must study to provide the baseline information required by managers to determine habitat quality for birds. We begin this framework by suggesting a scenario to describe distributional patterns of birds within oak woodlands. We use the discussion as a basis for explaining ecological and behavioral relationships of birds to their environments, and we conclude by presenting a methodology for the study of birds in oak woodlands.

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[2] Research Assistant and Assistant Professor of Wildlife Biology, respectively, University of California, Berkeley, California.

DISTRIBUTIONAL PATTERNS

Geologic Evolution of Oak Woodland Ecosystems

The evolution of the contemporary Mediterranean ecosystem and associated oak woodlands consisted of an ever-changing environment that enabled biotic speciation to occur. Changing climatic conditions during the Tertiary, and periods of extensive glaciation and mountain building during the Quaternary, strongly influenced patterns of extinction and speciation of both plant and animal life. Axelrod (1973, 1977) developed a theory for the evolution of oak communities based on paleobotanical evidence. That theory suggested that oak diversity decreased as the geographic range of oaks constricted with time from the Miocene through the Pleistocene. Axelrod's theory appears to be consistent with those of avian speciation presented by Rand (1948), Selander (1965), Mengel (1970), and Hubbard (1973). Changing landscapes during the Tertiary and Quaternary periods likely resulted in varying environmental conditions (e.g., temperature, moisture) for different species of birds. As the total area occupied by oaks decreased with time, less habitat was available for many birds. Further, decreases in floristic and structural diversity probably led to a decrease in bird species diversity. Previous studies (MacArthur and MacArthur 1961, Cody 1974, Tomoff 1974) demonstrated that bird species diversity was positively associated with structural vegetative diversity. Others (Robinson and Holmes 1984, Rotenberry 1985) noted that many birds appeared to selectively use plant species. Consequently, as plant species diversity decreased with time, a concomitant decrease in bird species diversity likely occurred.

These influences and the selective processes of isolation and restricted gene flow during Pleistocene periods of glaciation were largely responsible for extinctions and speciations of birds (Rand 1948, Selander 1965, Hubbard 1973, Diamond 1984). Selander (1965) noted that about 30 percent of the species that occurred during the Pleistocene are now extinct. Although most of the evolutionary processes leading to existing taxa of birds probably occurred during the Miocene and Pliocene (Wetmore 1951), evolution during the Pleistocene continued to differentiate species on subspecific and semi-specific levels (Rand 1948, Selander 1965). Hubbard (1973) traced speciation within the genera *Pipilo* (towhees), *Toxostoma* (thrashers), *Callipepla* (quail), and others as having occurred during the glacial periods of the Pleistocene. He further postulated that many of the species that arose during the Pleistocene had a tendency towards sedentariness. Given this limited motility, these species may be the ones least likely to escape the effects of environmental change.

Human Impact on Oak Woodlands

The evolution of oak-woodland communities occurred over millions of years. More recently, humans have exerted artificial, selective forces that have further altered distributional patterns of oaks. Prior to European settlement, aborigines burned the understory of oak woodlands. These periodic burns influenced the population structure of oaks, and consequently the structure and floristic composition of the stands (Jepson 1910, Rossi 1980). Since European settlement of western North America, changes to oak communities by humans have been more dramatic. Early Spanish settlers cleared expanses of oaks for livestock and agriculture. Increased grazing pressures with the introduction of domestic livestock probably further altered the population structure of oak stands because of the consumption of acorns and seedlings by sheep and cattle. The introduction of livestock also indirectly changed the composition of the understory as many exotic annual grasses displaced natural perennials. Recent fire-suppression programs have allowed conifers to displace oaks as Bonnicksen and Stone (1982) noted for the Sierra Nevada. Bartolome (pers. commun.) speculated that oaks in California are becoming less diverse and proportionally more sclerophyllous owing to historical grazing and cutting practices. He attributed this trend to the tendency of live oaks to sprout after being cut, and to the resistance of live oaks to browsing. In contrast, many of the white oaks [e.g., valley oak (*Quercus lobata*), blue oak (*Q. douglasii*), and Engelmann oak (*Q. engelmannii*)] are not regenerating well, and seedlings and saplings are more heavily impacted by browsing. Thus, the trend described by Bartolome has led to a decrease in white oak populations whereas live oak populations have remained relatively stable.

The cumulative impact of these disturbances has resulted in younger, smaller stands with altered age structures and species compositions. The effects of such large-scale habitat modifications on birds are not well known. However, birds that require extensive stands of large trees or birds that rely on blue, valley or Engelmann oak might be affected adversely by these changes in age and stand structure. Consequently, it is imperative that a protocol be established for the study of birds in oak woodlands. Only through detailed study of these relationships will there be sufficient information to assess environmental impacts on the avifauna of the California oaks and to develop methods to retard or mitigate these losses if judged unacceptable.

STUDY OF ECOLOGICAL RELATIONSHIPS OF BIRDS

Before questions regarding the effects of oak management practices on birds can be addressed, it is necessary to understand the basic biologies, ecologies, and behaviors of birds found in oak woodlands. Whether or not a bird "selects" a given habitat is attributable to a number of proximate and ultimate factors (Hilden 1965, Cody 1985). Proximate factors are cues that induce a bird to settle in a certain area. Examples of proximate factors are song posts, nest sites, and the composition and structure of vegetation. Ultimate factors are those that provide conditions for reproduction and survival. As such, ultimate factors are adaptations resulting from the processes of natural selection. Thus, the study of bird-habitat relationships in oak woodlands is essentially the study of proximate and ultimate factors that allow birds to settle, reproduce, and survive within oak habitats.

Because habitat selection by birds is largely behavioral (Morse 1980), investigators often take indirect approaches to discern patterns of habitat and resource use. These approaches include monitoring population parameters, characteristics of bird habitats, and resource abundances. Measures of population parameters are required to understand the viability of species in relation to habitat conditions (Van Horne 1983). Detailed quantitative descriptions of macro- and microhabitats of species are needed by resource managers to determine habitat quality (Capen 1981). It is also necessary to measure resource abundance--in particular prey abundance--and relate these measures to bird population parameters to more fully understand the extrinsic factors that regulate bird distributions and abundances. We detail below parameters that should be included in the study of birds in oak woodlands.

Study Areas

In our discussion we present examples from the Tejon Ranch, Kern County, California and Blodgett Forest Research Station (University of California, Berkeley), El Dorado County, California. The Tejon Ranch is a 100,000-ha corporate landholding in the Tehachapi Mountains. Approximately 35,000 ha of the Ranch are oak woodlands dominated by blue oak, valley oak, and California black oak (*Quercus kelloggii*), with lesser amounts of canyon live oak (*Q. chrysolepis*), interior live oak (*Q. wizlisneii*), and Brewer's oak (*Q. garryana* var. *brewerii*). The Ranch is managed for multiple uses including livestock production, firewood cutting, and game hunting. Cutting of oaks is restricted to selected stands of blue, valley, and black oaks, leaving large areas of the Ranch uncut. Elevation on the Ranch ranges from 1,000 to 1,700 m, and aspects include all directions. Because of the variety of land-use practices that occur on the Ranch, it provides an excellent opportunity for study of the effects of oak removal and livestock grazing on bird habitat.

Blodgett Forest Research Station is located in the central Sierra Nevada at an elevation of 1300 m. Vegetation of the forest is characteristic of mixed-conifer forests of the Sierra Nevada, and is dominated by white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), incense-cedar (*Calocedrus decurrens*), and California black oak. Tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), and golden chinquapin (*Castanopsis chysophylla*) are major hardwood components of the subcanopy. The 1,200-ha forest is divided into compartments 5-35 ha in size. Compartments have been subjected to various forest management practices. Thus, Blodgett affords an opportunity to study the use of hardwoods by birds within a managed mixed-conifer forest.

Methods

Monitoring Populations

Although monitoring population parameters of species is time- and labor-intensive, these data are integral to understanding bird-habitat relationships in oak woodlands. Commonly, only species abundances are measured by researchers. Van Horne (1983) discussed the shortcomings of this approach and showed that population abundance alone may be an inadequate measure of habitat quality. Whether or not a habitat is suitable for a species depends largely on the species' ability to survive and/or reproduce there. Thus a population-monitoring program should not only be directed at estimating abundances, but it should also attempt to estimate rates of survival and reproduction.

Numerous techniques are used to measure the numbers of birds (Ralph and Scott 1981, Verner 1985). No technique, however, has been shown to yield accurate estimates of bird numbers, as all techniques contain inherent biases. Counting birds can provide measures of absolute abundance or indexes of relative abundance. We will not review the advantages and disadvantages of the various techniques because these have been reviewed amply elsewhere (Ralph and Scott 1981, Verner 1985, Verner and Ritter 1985). It is important to note, however, that the choice of counting technique depends on several factors and should not be haphazard. Further, comparisons of abundances using most methods should be restricted to the same species, location, and season (J. Verner, pers. commun.).

We used the variable-radius circular plot method (Reynolds and others 1980, Verner and Ritter 1985) to estimate numbers of birds at the Tejon Ranch. Eighty points were placed at 300-m intervals using a systematic-random sampling design. We chose 300-m intervals to ensure sampling independence among points. Censusing was done by only one observer to remove observer differences. The observer remained at the point for 5 min and recorded all birds detected by sight or sound. Counts were replicated at each point three times. Censuses were done between 05:30 and 09:30 from 29 May to 24 June 1986. We used a Fourier series estimator from the computer program TRANSECT to calculate density estimates (Laake and others 1979). We calculated densities only for species for which we accumulated >40 detections. Density estimates ranged from 4.8/40 ha (Nuttall's woodpecker), to 47.2/40 ha (plain titmouse) (table 1). Coefficients of variation ranged from 3.8 percent (acorn woodpecker) to 20.9 percent (northern flicker) (table 1). Although we cannot evaluate the accuracy of these density estimates, the shapes of the probability density functions met the shape criterion of Burnham and others (1980), and the coefficients of variation for most of the density estimates were less than 20 percent, suggesting that the estimates were within ranges of precision generally accepted by wildlife biologists.

Estimates of bird numbers generally have been restricted to the breeding season under the assumption that the breeding season is the most important in a bird's life history. The breeding season is not the only time of the year when oaks are used by birds, however. Many species are year-long residents, and others may use an area during nonbreeding periods as short-term migrants or as wintering birds. If birds change their patterns of resource use, then studies restricted to the summer may not detect shifts in some critical aspects of resource use. Consequently, use of oaks by nonbreeding birds might be as important for their ultimate survival as the oaks are for the survival of breeding birds. Lack (1954) and Wiens (1977) noted that the nonbreeding season might be the most critical period of a bird's annual cycle. Consequently, it is critical that bird numbers are monitored throughout the year and not only during the breeding season.

As an example of the temporal variation in avifaunal composition, we recorded the species present in the oak woodlands of the Tejon Ranch from 14 to 20 April 1986 and from 18 May to 20 June 1986. Although there was extensive overlap of the species present during both periods, we recorded 13 species during April that were not present during May and June, and 9 species detected during May and June were not detected during April (table 1). Most of the species detected only during April were probably migrants (with exception of California condor) which used Tejon Ranch woodlands as foraging and resting sites. The species detected in May-June but not during April were probably late-arriving breeding birds. Thus, if surveys or censuses were restricted to only one of these periods, many species would have gone undetected. These data are only preliminary, but they serve as examples of the dilemma faced by resource managers attempting to construct bird-habitat models: different sets of species use a particular area during different seasons. Further, if habitat-use patterns by birds change over time, then changes to the environment might differentially affect the species present during different times. An increasing body of literature indicates that different tree species are differentially preferred by birds based on the season (Travis 1977, Conner 1980, Hutto 1981, Morrison and others 1985). In New Hampshire, for example, Kilham (1970) showed that in winter downy woodpeckers (*Picoides pubescens*) were attracted to birches (*Betula papyifera*) that were infested with a scale insect. Therefore, managers must provide adequate habitat for a variety of situations.

Many studies of bird populations are restricted to estimating densities during a single year. Wiens (1981), however, cautioned against single-sample surveys because the numbers estimated during any one year may not be representative of long-term population trends. Fretwell and Lucus (1970) and Van Horne (1983) noted that once the preferred habitat of a species becomes saturated, the surplus population will occupy marginal habitats. Theoretically, the relative densities of the species in marginal habitats may exceed the numbers found in superior habitats, leading to erroneous conclusions if population densities alone are used to index habitat quality. A more appropriate method for monitoring habitat quality must include estimates of reproduction and survival rates for species found in the oak woodlands, as well as numbers. Further, the monitoring program should occur over a timeframe encompassing temporal variations in population parameters in response to various biotic and abiotic factors.

Study of Habitats

Descriptions of bird habitats are central to the study of birds in oak woodlands. The study of habitats involves two major steps. The first step is to associate birds with macrohabitats such as blue-oak savanna or canyon-live-oak woodlands. These general associations have been provided by early naturalists (e.g., Grinnell and Miller 1944, Leopold 1951, Miller 1951); Verner (1980) summarized regional associations. These descriptions provide useful summaries and serve to narrow the range of possible hardwood communities where a species might be found. Much of the information provided by these naturalists is used to construct models of wildlife-habitat relationships. These wildlife-habitat models are matrices that qualitatively rate the suitability of various seral stages of common vegetation types for selected species of wildlife. Because these models are based mostly on general descriptions, many existing models of wildlife-habitat relationship have been found to be inaccurate when tested with empirical data (Dedon and others 1986). Further, the descriptions of habitats and distributions provided by these models are only very general in nature. For instance, a blue oak stand may exhibit certain structural or floristic characteristics that are used disproportionately

Table 1. Species of birds present within the oak woodlands of the Tejon Ranch during the 1986 breeding season. Estimates of the densities (#/40 ha) given for common species.

Species	Presence Status[1]	Density[2] n	D	pct CV
California condor (Gymnogyps californianus)	1			
Cooper's hawk (Accipiter cooperii)	3			
Red-tailed hawk (Buteo jamaicensis)	3	45	7.7	18.5
Golden eagle (Aquila chrysaetos)	3			
American kestrel (Falco sparverius)	3	9		
California quail (Callipepla californica)	3	38		
Mountain quail (Oreortyx pictus)	3	10		
Band-tailed pigeon (Columba fasciata)	3			
Mourning dove (Zenaida macroura)	3	263	20.1	7.5
Western screech owl (Otus kennicottii)	3			
Great-horned owl (Bubo virginianus)	3			
Northern Pygmy-owl (Glaucidium gnoma)	3	1		
Long-eared owl (Asio otus)	3	1		
Anna's hummingbird (Calypte anna)	3	26		
Acorn woodpecker (Melanerpes formicivorus)	3	1120	39.6	3.8
Lewis' woodpecker (Melanerpes lewis)	1			
Nuttall's woodpecker (Picoides nuttallii)	3	55	4.8	15.3
Hairy woodpecker (Picoides villosus)	2	4		
Northern flicker (Colaptes auratus)	3	49	11.7	20.9
Olive-sided flycatcher (Contopus borealis)	2	1		
Western wood-peewee (Contopus sordidulus)	2	111	13.8	10.3
Dusky flycatcher (Empidonax oberholseri)	1			
Black phoebe (Sayornis nigricans)	2			
Say's phoebe (Sayornis saya)	1			
Ash-throated flycatcher (Myiarchus cinerascens)	3	244	30.3	11.0
Western kingbird (Tyrannus verticalis)	3	11		
Purple marten (Progne subis)	2	1		
Violet-green swallow (Tachycineta thalassina)	3	226	33.6	8.6
Stellar's jay (Cyanocitta cristata)	3			

Table 1. Continued.

Species	Presence Status[1]	Density[2] n	D	pct CV
Scrub jay (Aphelocoma coerulescens)	3	195	22.4	11.4
Common raven (Corvus corax)	3	5		
Plain titmouse (Parus inornatus)	3	346	47.2	8.6
Bushtit (Psaltriparus minimus)	3	5		
White-breasted nuthatch (Sitta carolinensis)	3	174	28.0	8.3
Brown creeper (Certhia americana)	2	1		
Bewick's wren (Thryomanes bewickii)	1			
House wren (Troglodytes aedon)	3	348	44.2	8.3
Blue-gray gnatcatcher (Polioptila caerulea)	3	8		
Western bluebird (Sialia mexicana)	3	34		
American robin (Turdus migratorius)	3	25		
Phainopepla (Phainopepla nitens)	2	1		
Loggerhead shrike (Lanius ludovicianus)	1			
European starling (Sturnus vulgaris)	3	46	18.5	19.1
Hutton's vireo (Vireo huttoni)	1			
Warbling vireo (Vireo gilvus)	1			
Yellow-rumped warbler (Dendroica coronata)	3	3		
Townsend's warbler (Dendroica townsendi)	1			
Hermit warbler (Dendroica occidentalis)	1			
Western tanager (Piranga ludoviciana)	2	1		
Black-headed grosbeak (Pheucticus melanocephalus)	3	130	19.9	13.6
Rufous-sided towhee (Pipilo erythrophthalmus)	3	7		
Brown towhee (Pipilo fuscus)	3	99	24.7	14.9
Chipping sparrow (Spizella passerina)	3	10		
Lark sparrow (Chondestes grammacus)	3	2		
Golden-crowned sparrow (Zonotrichia atricapilla)	1			
White-crowned sparrow (Zonotrichia leucophrys)	1			
Dark-eyed junco (Junco hyemalis)	3	1		
Red-winged blackbird (Agelarus phoenueus)	3	5		

Table 1. Continued.

		Density[2]		
		n	D	pct CV
Western meadowlark (<u>Sturnella neglecta</u>)	3	22		
Brewer's blackbird (<u>Euphagus cyanocephalus</u>)	3	11		
Brown-headed cowbird (<u>Molothrus ater</u>)	3	8		
Northern oriole (<u>Icterus galbula</u>)	3	221	35.1	8.2
Purple finch (<u>Carpodacus purpureus</u>)	1			
House finch (<u>Carpodacus mexicanus</u>)	3	76	15.8	15.5
Lesser goldfinch (<u>Carduelis psaltria</u>)	3			
Lawrence's goldfinch (<u>Carduelis lawrencei</u>)	2	147	27.7	18.0

[1] 1-detected only between 14 and 20 April; 2-detected only between 18 May and 20 June; 3-detected both between 14-20 April period and 18 May-20 June.

[2] n = number of detections; D = density (1//40 ha) estimates; pct CV = percent coefficient of variation. All densities calculated using Fourier series estimator from the computer program TRANSECT.

by a species. Thus it is instructive to examine in more detail aspects of the areas a species actually uses (i.e., microhabitat) within the macrohabitat where it is found. Microhabitat includes the size and shape of leaves, branches, bark, and other subtle features of the vegetation present in the macrohabitat. These features vary with the size and age of the tree, for example. Thus, the density--or even mere presence--of a bird may be related not only to the plant species present, but their size, shape, and vigor. The failure of existing wildlife-habitat models to incorporate these fine-scaled aspects of species' microhabitats may be one reason why the models perform poorly.

Two primary techniques are used to describe the microhabitats of species. One method correlates the abundance of a species to combinations of physiognomic and floristic characteristics. This method entails estimating relative or absolute numbers of a species at a set of fixed census points and correlating these abundances to physiognomic and floristic characteristics measured at the points. Morrison and others (1987) used stepwise multiple regression (Draper and Smith 1981) to relate relative abundances of species to habitat characteristics. They used fixed-radius circular plots to obtain indexes of relative abundance, and measured habitat characteristics within the radius of the census plot. Thus, if a species is strongly associated with certain habitat features and those features are measured by the investigator, this method is potentially effective. Other investigators use variable-radius circular plots to census birds. However, the area over which these birds are recorded can be greater than the area within a fixed-radius plot, and thus may contain greater habitat heterogeneity. Thus using regression techniques to discern relationships between a species and habitat components might yield weaker associations than using fixed-radius plots because the species might not be closely associated with the location where the habitat measurements were taken.

An alternative method of quantifying habitats is to center habitat plots at the locations where birds are found. Larson and Bock (1986) found that organism-centered plots provided better descriptions of a species' habitat than using the regression techniques described above. There could be little question as to whether or not the bird was associated with the habitat, because by definition habitat is where the organism is found. There is a risk, however, that only the more conspicuous members of a population will be sampled by this method. This effect might be lessened if the observer moves slowly through the area, using care not to disrupt bird activity patterns. Separate plots could be centered at locations used for perching, singing, foraging or nesting. Collins (1981) showed that the characteristics of areas used by a species for different purposes (e.g., nest sites vs. perch sites) may differ. The strength of this type of analysis is that an investigator could more accurately predict habitat components of areas used for specific functions by a species.

Measuring habitat plots can be accomplished in many different ways. Considerations include plot shape and size, and the techniques used to measure them. James and Shugart [1970; see also James (1971)] presented a methodology commonly used in eastern deciduous forests; this was refined by Noon (1981). Whether or not the James and Shugart method is appropriate for western oak woodlands is unknown. Plot size can vary with the habitat and the activity range of the species studied. The objective of plot size is to include a representative sample of the variation found within the habitat of a species. James and Shugart's (1971) plots were 0.04 ha in size, whereas Gutierrez (1980) found that 0.02 ha plots were sufficient for describing mountain quail habitat in the sclerophyllous oak woodlands of the central California Coast Range. Morrison and Meslow (1983) used 0.01-ha plots to describe the habitats of brush-inhabiting birds in clearcut Douglas-fir habitats of the Oregon Coast Range.

Plot size will likely vary with the species studied and with the type of vegetation present. Pilot studies should be done to determine appropriate plot sizes for different birds and vegetation types.

The choice of habitat characteristics to be measured and the techniques used to measure them are integral to describing the habitat of a species. An investigator must have some prior knowledge of the biology and habitat-use patterns of the bird. James (1971) used the term "niche gestalt" to refer to how an organism perceived the environment, but a more appropriate explanation of this concept is that the "niche gestalt" is how an investigator perceives the species' environment. The closer the investigator's gestalt is in accord with how the organism perceives the environment, the more accurate the description of the habitat. Unfortunately, data on the biology and "niche gestalt" of many species are lacking; thus the investigator must rely on her or his field expertise to determine which components of the environment should be studied. Various techniques are used to quantify these habitat characteristics. These techniques range from ocular estimates to rather meticulous and often labor-intensive measurements. Each technique contains certain inherent biases and different techniques vary with regards to accuracy. Block and others (in press) compared habitat measurements with ocular estimates of the same characteristics and found that measurements provided more accurate estimates with greater precision than ocular estimates. Moreover, measurements tended to vary less among observers than did estimates. Consequently, actual measurements would be expected to yield a more accurate estimate of a species' niche gestalt than values obtained by estimation (i.e., "guessing").

Study of Bird Activity Patterns

To understand the modes of resource use by birds in greater detail, it is useful to measure activities of birds (Holmes 1981). Quantifying foraging activity has been the object of many studies. From a theoretical standpoint, this seems appropriate because food availability is generally acknowledged as a key factor in whether a bird survives and/or reproduces. In a more practical sense, foraging involves a large proportion of a bird's activity time, thus making it easier for an observer to obtain adequate numbers of samples. This does not negate the importance of other aspects of bird activity, since most bird activity is likely adaptive and certainly merits study. Studies should be flexible and designed to collect data measuring all aspects of bird behavior. Unfortunately, the costs of a study to determine all aspects of bird activity probably exceed the budgets of most projects, because adequate samples for many bird activities are precluded by the infrequency or secrecy of the activity.

Birds forage throughout the year, although the prey and methods used to capture prey vary across both time and space. Spatial and temporal variations might be attributed to differences in the phenologies of vegetation and of the prey available to birds. Consequently, studies should sample behavior across a range of conditions and times. The types of information that should be collected include general characteristics of the plant or object where foraging occurred, details of the perch and foraging substrates, and the foraging maneuver. These types of data provide detailed information about modes of resource use by species. Further, the patterns of microhabitat use by birds can be used by resource managers to determine how even fine-scale habitat alterations will affect selected species.

We observed activity locations and foraging behaviors of birds at the Tejon Ranch from 15 May to 20 June 1986. A bird was observed from 10-30 sec while foraging. We recorded the characteristics of the tree (when applicable) where the bird foraged (species, height, diameter, and vigor of the tree), characteristics of the foraging and perch substrates, and the foraging maneuver. Simple analyses of these data suggested that some birds used certain tree species with greater frequency than others (table 2). For example, northern orioles were observed using valley oak with greater frequency than other oak species, whereas Nuttall's woodpeckers, plain titmice, and white-breasted nuthatches used blue oak with greater frequency (table 2). In contrast, black-headed grosbeaks rarely were observed foraging on oaks and appeared to use California buckeye (*Aesculus californicus*) more frequently than any other foraging substrate (table 2).

The use of oaks and other hardwoods by birds is not restricted to oak woodlands. We used the same general methods as those used at the Tejon Ranch to study activity patterns of birds found in the mixed-conifer habitats of Blodgett Forest. All species studied used California black oaks for part of their foraging activities, with the Nashville warbler making heavy use of oak (table 3). The red-breasted sapsucker, pileated woodpecker, solitary vireo, warbling vireo, and black-headed grosbeak used hardwood species for at least 20 percent of their foraging activities; the Nashville warbler did so for almost 50 percent of its activities. Thus, alteration of the hardwood resource in the mixed-conifer zone may affect adversely some or all of these species.

Intensive observations of bird activities are therefore critical to understanding actual modes of habitat use by species. These data allow managers to more specifically assess tree species and substrate preferences by the birds. For example, a species might use a plant species in

Table 2. Relative frequency (percent) of use of foraging substrates by birds within oak woodlands at the Tejon Ranch, Kern County, California during the 1986 breeding season.

Species	n	Blue oak	Valley oak	California Black oak	Canyon live oak	Interior live oak	California buckeye	Other plants	Ground	Air
Nuttall's woodpecker	39	61.9	17.9	5.3	5.3	5.3	5.3			
Acorn woodpecker	22	18.2	31.8	18.2	4.5		4.5			22.7
White-breasted nuthatch	57	56.1	26.3	8.8	7.0	3.5		1.8	1.8	
Plain titmouse	81	57.3	9.7	4.9	2.4	9.8	7.3	3.7	4.9	
House Wren	22	13.6	31.8	4.5				13.6	37.5	
Ash-throated flycatcher	23	21.7	21.7			4.3		4.3	17.4	30.4
Black-headed grosbeak	29		13.7		6.9	10.3	31.0	17.2	13.7	6.9
Northern oriole	46	11.4	50.0	13.6	4.5	6.8	11.4		11.4	

Table 3. Tree species used (pct) by foraging birds at Blodgett Forest Research Station, El Dorado County, California during spring-summer 1983-85[1].

Species	N[2]	Black oak	Tan oak	Other Hardwood[3]	Coniferous[4]
Red-breasted sapsucker (Sphyrapicus ruber)	91	15	1	7	76
Hairy woodpecker	89	14	0	3	81
Pileated woodpecker (Dryocopus pileatus)	48	23	0	1	76
Dusky flycatcher	45	16	4	5	72
Mountain chickadee (Parus gambeli)	62	8	3	2	87
Chestnut-backed chickadee (P. rufescens)	129	13	0	1	84
Brown creeper	124	10	2	-	86
Red-breasted nuthatch (Sitta canadensis)	126	14	0	1	84
Solitary vireo (Vireo solitarius)	79	23	0	1	77
Warbling vireo	50	26	0	6	68
Nashville warbler (Vermivora ruficapilla)	98	38	1	8	48
Yellow-rumped warbler	84	11	1	2	84
Black-headed grosbeak	86	19	0	7	71

[1]Percentages do not total 100 percent because not all foraging substrates are given.

[2]Number of individuals observed; sexes combined.

[3]Primarily madrone, chiquapin (sic), and white alder (Alnus rhombifolia).

[4]Douglas-fir, white fir, incense cedar, and ponderosa and sugar pine.

much greater frequency than it occurs in the macrohabitat. Detailed observations may indicate, however, that the bird concentrates foraging activities on stems of a certain size or exhibiting a certain vigor (e.g., live, dying, dead). These types of data are critical for the formulation of species-specific management plans, as they indicate the species and relative vigor of trees and substrates used by birds.

CONCLUSIONS

The study of birds within any habitat requires first a conceptual understanding of the processes that influenced their distributions, and second, intensive field research to determine viability and patterns of resource use of the species. Much research is restricted to a single season or within a particular site. Although this approach provides useful information, the results of such study may be valid only for the place and time the data were collected. More extensive data are required to determine year-round patterns of habitat and resource use by birds. There are no shortcuts for obtaining the information.

Determining population parameters, habitat quality, and resource-use patterns of species are both time- and labor-intensive. These data are essential for the development of species-specific models to assess habitat quality and to predict the effects of various land-use practices on the viability of oak woodland birds. These models must be based on empirical field data that include characteristics of the habitat thought to be critical to the survival of the species. Once developed, these models must be scrutinized to determine their temporal and spatial applications through rigorous testing and refinement. Only through such integrated study of avian-habitat-resource relationships will researchers begin to understand the processes that underlie bird distributions and abundances, and to provide managers a basis from which positive management approaches can be advanced.

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