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HABITAT-USE PATTERNS IN COOPERATIVE AND NON-COOPERATIVE BREEDING BIRDS: TESTING PREDICTIONS WITH WESTERN SCRUB-JAYS

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ABSTRACT.—I propose a method to test extensions of models concerning the maintenance of cooperative breeding systems that examines patterns of habitat use relative to the distribution of habitat components among territories. I analyzed habitat use and behavioral time budget data for a Texas population of the Western Scrub-Jay (*Aphelocoma californica*). As a non-cooperative population, one of two habitat-use patterns was expected: (1) specialist habitat-use patterns in an abundant, widespread habitat type, with little variation among territories in habitat composition or (2) generalist habitat-use patterns with the potential of significant variation in habitat composition among territories. These jays show a combination of habitat-use patterns supporting both predictions. The only resources that males utilize as a specialist, tall oak trees during sentinel behavior, are fairly widespread and would not be considered a limiting resource. In the remaining habitat categories, Texas populations of Western Scrub-Jays act as generalists, using the habitat in relation to its availability, even though variation in habitat composition among territories is considerable. Variation among individuals within a sex was observed but could not be explained using various demographic and ecological correlates. Additional detailed habitat use data when used in a comparative framework can aid determination of subtle ecological differences among populations of Western Scrub-Jays and allow closer examination of intrinsic and extrinsic ecological models concerning the evolution and maintenance of cooperative breeding systems in this group. *Received 27 Aug 1995, accepted 8 April 1996.*

Habitat use and the concept of ecological constraints have played a major role in the development of theories concerning evolution and maintenance of cooperative breeding in birds (Brown 1987, Koenig et al. 1992). Specifically, ecological constraints may serve as both intrinsic and extrinsic reasons for delayed dispersal, setting the stage for the helping behavior seen in cooperative breeding systems. Comparative studies of the genus *Aphelocoma* have been particularly instructive in testing the role ecological constraints play in the evolution of social systems because the genus exhibits extensive geographic variation in social systems and habitat use (Brown 1974, Fitzpatrick and Woolfenden 1986, Peterson and Burt 1992). The success of the comparative method rests on an even and complete sampling of taxa in the study group. To that end, this study documents the habitat use patterns of a non-cooperative population of Western Scrub-Jays (*A. californica,* see American Ornithologists' Union 1995), in central Texas.

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Using behavioral time-budget data, it is possible to test whether each major habitat component is used relative to its availability for each major behavioral category (i.e., individuals act as generalists) or whether certain behaviors are more likely to occur in specific habitats (i.e., individuals act as specialists). When behavioral-habitat specialization patterns are seen, we can then study in more detail the importance and distribution of this target of specialization and see if it is possibly a limiting resource critical in the determination of habitat quality. This study examines habitat composition of territories and habitat use patterns and determines (1) the generalist/specialist habitat use status of this population, (2) the availability and distribution of different habitat components and the presence of potentially limiting resources, and 3) how specific behaviors are related to each habitat component. As a non-cooperative population (Burt 1992), one of two habitat use patterns is expected (see discussion). First, the population may show specialist habitat use patterns, but only if in an abundant, widespread habitat type with little change in habitat composition among territories. Alternatively, the population may show generalist habitat-use patterns with significant variation in habitat composition among territories with individuals using each habitat component in relation to its availability. In the latter case no target of specialization is expected.

STUDY AREA AND METHODS

I conducted this study in oak-juniper woodland in Kerrville-Schreiner State Park, Kerrville, central Texas. The park's dominant woody vegetation was Texas live oak (*Quercus virginiana fusiformis*), Texas red oak (*Q. shumardii texana*), and Ashe Juniper (*Juniperus ashei*) (Miller and Lamb 1985). I partitioned the study area into 231 quadrats, 33.3 m^2 in area. In each quadrat, I characterized the woody vegetation composition in two ways: biodiversity or structural diversity. I characterized biodiversity into four categories by percentage of living oak (LO), dead oak (DO), living juniper (LJ), and dead juniper (DJ). I also characterized structural diversity into four categories by percentage of isolated living (IL), isolated dead (ID), dense living (DL), and dense dead (DD) patches of trees. I calculated percentages by actual counts of trees in each quadrat when possible and by visual estimates to the nearest five percent in dense vegetation. Because percentage estimates of vegetation are not comparable between quadrats of different vegetational density, I multiplied each percentage by the density of vegetation in that quadrat. The resulting number is the standardized, relative abundance of each vegetation type which can then be compared to the relative abundance all other quadrats. The density of vegetation in each quadrat was measured from aerial photographs using the transect method. Evenly spaced transect lines were drawn in each quadrat of the aerial photograph, and the length of line crossing trees was divided by total line length (Avery 1985; 87).

I used mist nets to capture 66 jays and marked them with U.S. Fish and Wildlife Service leg bands and a unique combination of three colored metal bands. I aged adult jays as first-year birds or older based on plumage characters (Pitelka 1945). During the breeding season, jays were sexed by presence or absence of a brood patch. Individuals captured at other times were sexed by behaviors and vocalizations. I determined territory boundaries by observing territorial conflicts and home range use and then mapped each on aerial photographs. I calculated vegetational composition for each territory each year by averaging numbers of each vegetation type for each quadrat in each territory.

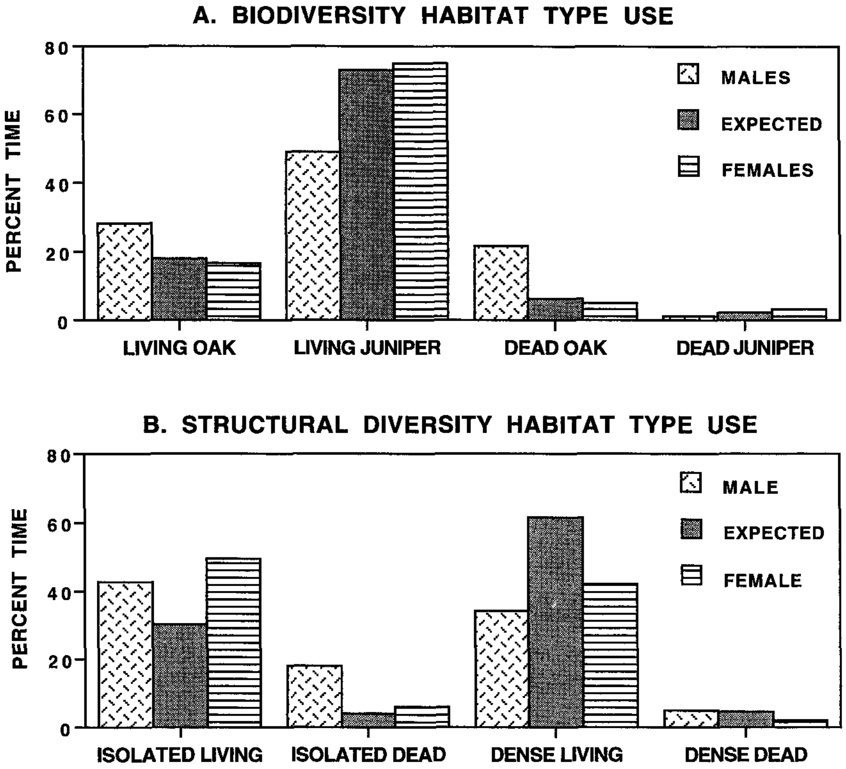
I collected focal sampling data from 7 June to 6 July 1989 on four breeding pairs and from 14 June to 29 June 1990 on five breeding pairs. All behaviors were recorded to the nearest second in 15-min sampling sessions or until the bird was lost from sight. Sessions where the bird's behavior was affected by observer presence were excluded from analysis. I categorized behaviors as sentinel, foraging, inactive/preening, territorial, or other (begging, caching, sunning, etc.). Sentinel behavior included any behavior engaged in when an individual was perched on a tall exposed branch, and its designation overrides concurrent behaviors such as preening or territorial calling. I recorded the following data in addition to behavior: general weather, time of day, substrate used (same vegetation categories as in quadrat sampling), location in territory, the presence/absence of other jays, and food type eaten (when possible). I collected data from 07:00 to 20:00 CST using a stop watch, tape recorder, and 10 × 40 binoculars. An effort was made to observe marked individuals for equal amounts of time, evenly spaced throughout the time of day and season. Individuals to be sampled were predetermined each day to avoid observer biases that could result in simply observing the first bird seen.

For each individual in each year, I calculated percentages of time spent in each behavior in each main vegetation type listed above. These observed values were then compared to the availability of this habitat in the individual's territory. Time spent on substrates other than woody vegetation (i.e., buildings, fences, the ground) was excluded from analyses. Data were checked for normality (Lilliefors' test) and homogeneity of variances (F-max test), and then either paired comparison t-tests, t'-tests (comparisons of groups with unequal variance), Mann-Whitney U tests, or two-way ANOVAs were used to examine statistical significance where appropriate (Sokal and Rohlf 1981, Neave and Worthington 1988). Percentage data were arcsine transformed for parametric tests. All tests are two-tailed. Bonferroni's correction is applied to probability values for multiple tests that share portions of the data set. Statistical values and associated probabilities are given for all comparisons, but because of the conservative nature of these tests when dealing with small sample sizes, trends for values approaching significance are considered for potential biological importance.

Methodological limitations.—Two approaches to studying habitat use and behavioral time budgets were considered for this study. One approach is to follow many individuals and have fewer sampling sessions per individual. This method might reduce the variance among individuals for each behavioral category, but it is impractical if behaviors vary temporally (i.e., within a day, month, season). This variation would require equal sampling through time for all individuals. Behavioral patterns show temporal variation in the Florida Scrub-Jay (*A. coerulescens*; DeGange 1976). The approach in this study was to follow fewer individuals for more sampling periods, more or less regularly spaced through time (day and season). The difficulties with this approach are limited sample sizes for statistical tests and the potential for large among-individual variation.

RESULTS

General habitat use.—This first analysis examines whether each sex uses each habitat component relative to its availability when all behaviors are examined together. Bonferroni's corrected probabilities needed for statistical significance in this test are $P = 0.05/2$, or $P = 0.025$. When considering biodiversity habitat categories (Fig. 1A), males used living



A. BIODIVERSITY HABITAT TYPE USE

B. STRUCTURAL DIVERSITY HABITAT TYPE USE

FIG. 1. Observed and expected time percentages birds spent in each biodiversity (A) and structural diversity (B) habitat category in 1989.

juniper (LJ) significantly less than expected on the basis of its availability in 1989 ($t = 7.7$, $P = 0.0045$), and possibly in 1990 ($t = 3.03$, $P = 0.039$), but used living oak (LO), dead juniper (DJ), and dead oak (DO) in proportion to their availability (1989: LO, $t = 1.06$, $P = 0.37$; DJ, $t = 2.0$, $P = 0.14$; DO, $t = 2.8$, $P = 0.068$ df = 3. 1990: LO, $t = 1.4$, $P = 0.22$; DJ, $t' = 1.2$, $P = 0.29$; DO, $t' = 1.8$, $P = 0.14$), although dead oak approaches a statistically significant increase in use for 1989. Females use each habitat in proportion to its availability (1989: LJ, $t = 0.45$, $P = 0.68$; LO, $t = 0.58$, $P = 0.60$; DJ, $t = 0.0086$, $P = 0.94$; DO, $t = 0.66$, $P = 0.56$. 1990: LJ, $t = 0.73$, $P = 0.50$; LO, $t = 0.0084$, $P = 0.99$; DJ, $t' = 1.3$, $P = 0.27$, DO, $t' = 0.19$, $P = 0.86$).

Relative to woody vegetation structural diversity, males in 1989 used isolated living (IL) habitat significantly more than expected ($t = 22.9$, $P = 0.0002$) and dense living (DL) significantly less than expected ($t =$

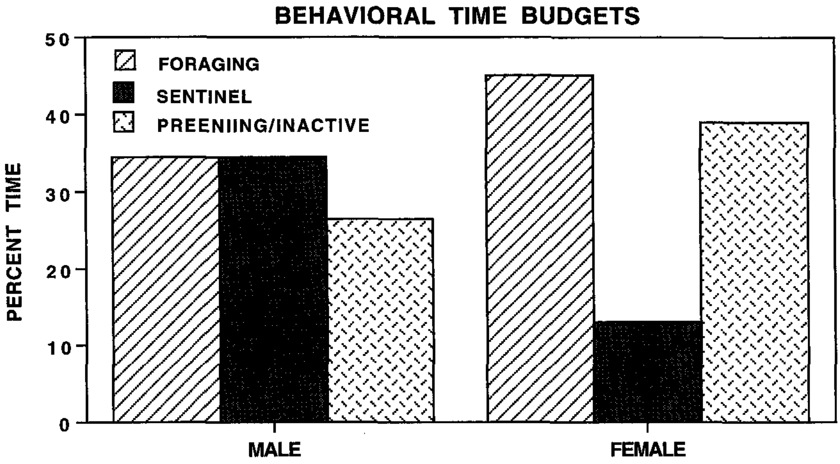
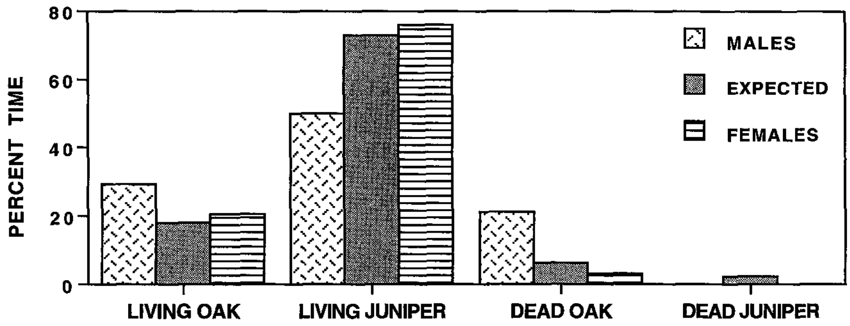


FIG. 2. Percentages of time spent in the three main behavioral categories in 1989.

5.5, $P = 0.012$) (Fig. 1B). Females had a similar pattern for 1989 (IL, $t = 5.2$, $P = 0.014$; DL, $t = 2.8$, $P = 0.067$) although this pattern was not statistically significant. Neither use of isolated living nor dense living habitats were different from expected in 1990 for males (IL, $U = 14.5$, $P > 0.2$; DL, $U = 16$, $P > 0.2$) or females (IL, $U = 16.5$, $P > 0.2$; DL, $U = 12.5$, $P > 0.2$). Use of isolated dead (ID) habitat was greater than expected by males in both years (1989, $t = 2.45$, $P = 0.092$; 1990, $t = 2.45$, $P = 0.070$) but not by females in either year (1989, $t = 0.72$, $P = 0.52$; 1990, $t = 0.61$, $P = 0.57$). In each year, use of dense dead (DD) habitat did not differ from expected for either males (1989, $t = 0.25$, $P = 0.82$; 1990, $t' = 0.98$, $P = 0.38$) or females (1989, $t' = 1.95$, $P = 0.15$; 1990 $t' = 1.15$, $P = 0.31$).

Behavioral time budget.—In this analysis, the pair studied only in 1990 was excluded to create a balanced two-way ANOVA for comparisons of each of the three main behavioral categories (Fig. 2). The ANOVA tests differences between sexes and years for each behavior. For the preening/inactive category no differences existed between sexes ($F_{1,12} = 0.11$, $P > 0.50$), or between years ($F_{1,12} = 0.044$, $P > 0.75$), and no interaction effect existed ($F_{1,12} = 0.38$, $P > 0.50$). Males spent more time in sentinel behavior than did females ($F_{1,12} = 8.6$, $P = 0.012$) but no significant difference existed between years ($F_{1,12} = 1.6$, $P = 0.23$) nor was an interaction effect seen ($F_{1,12} = 0.63$, $P > 0.25$). Foraging data had significant heteroscidacity and therefore a test of equality of means (Games and Howell method, Sokal and Rohlf 1981) was performed in lieu of a two-way ANOVA. Unplanned comparisons among all means showed no

A. PREENING/INACTIVE, BIODIVERSITY HABITAT TYPE



B. PREENING/INACTIVE, STRUCTURAL DIVERSITY HABITAT TYPE

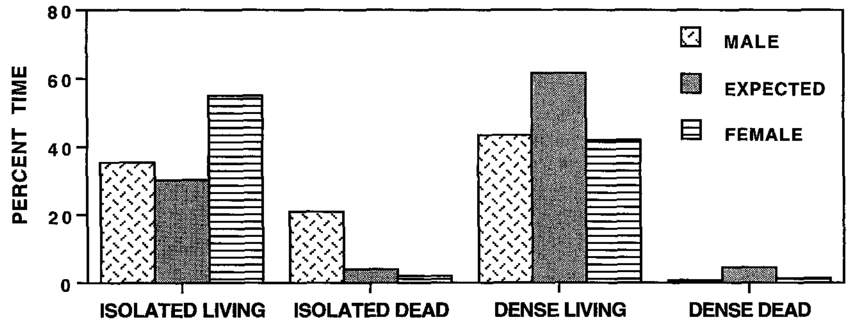


FIG. 3. Observed and expected percentages of time birds spent in each biodiversity (A) and structural diversity (B) habitat category in 1989 while preening/inactive.

significant differences in time spent foraging between either sexes or years at $P \leq 0.05$.

Behavioral differences in habitat use.—The next series of analyses examine whether each sex uses each habitat component relative to its availability during each specific behavior. Bonferroni's corrected probabilities needed for statistical significance in these tests are $P = 0.05/6$, or $P = 0.0083$. For both years, neither males nor females spent more or less time than expected preening or inactive in any category of habitat classified by either biodiversity or structural diversity (Fig. 3). Four values do, however, approach $P = 0.05$ in the biodiversity categories (male LJ, 1989, $t = 2.55$, $P = 0.084$, 1990, $t = 2.05$, $P = 0.11$; male and female DJ 1989, $U = 16$, $P = 0.05$) and four values approach significance for the

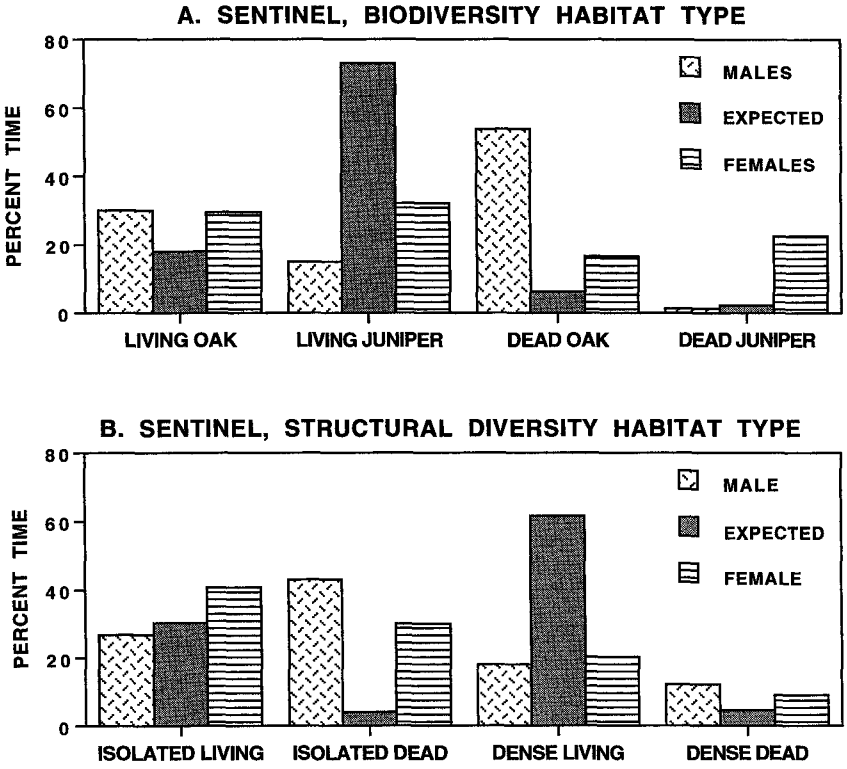


FIG. 4. Observed and expected percentages of time birds spent in each biodiversity (A) and structural diversity (B) habitat category in 1989 while sentinel.

structural diversity categories (male DL 1990, $t = 2.98$, $P = 0.041$; female IL 1989, $t = 3.14$, $P = 0.052$; male and female DD 1989, $t = 3.46$, $P = 0.04$).

For sentinel time in biodiversity categorized habitats (Fig. 4A), males spent less time in living juniper in 1989 ($t = 6.28$, $P = 0.0082$) and possibly in 1990 ($U = 25$, $P = 0.01$). Females also may have spent less sentinel time in living juniper in both years (1989, $U = 16$, $P = 0.05$; 1990, $U = 25$, $P = 0.01$). A pattern of more than expected use of dead oak during sentinel behavior is suggested, but only the value for males in 1990 is significant ($t' = 7.611$, $P = 0.0016$). In all other categories and years, observed percentages do not differ from those expected based on habitat availability. Sentinel time in structural diversity categories (Fig. 4B) indicates males, and possibly females, used isolated living trees less than expected in 1990 (male, $t = 4.62$, $P = 0.01$; female, $U = 25$, $P =$

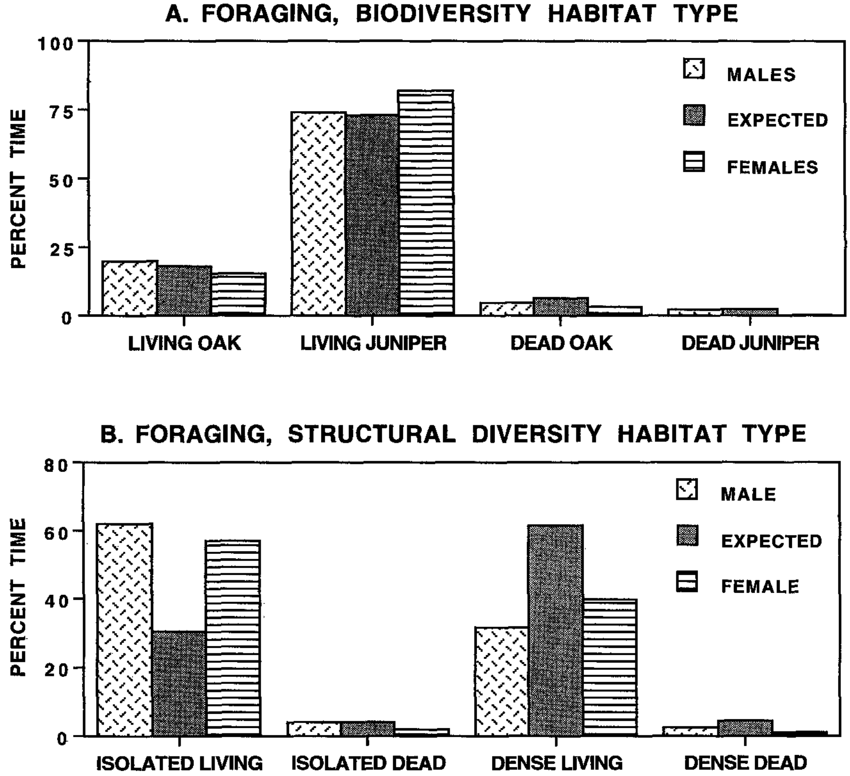


FIG. 5. Observed and expected percentages of time birds spent in each biodiversity (A) and structural diversity (B) habitat category in 1989 while foraging.

0.01) but not 1989. Increased use of isolated dead vegetation for both sexes in each year is suggested by the data, but values are not significant. All other comparisons for sentinel time in structural diversity categories do not differ from expected.

Foraging time does not differ from expected for either sex in either year in any biodiversity categories of vegetation (Fig. 5A). Five values approach significance in some of the rarer habitat categories (male and female DO 1990, $t' = 4.50$, $P = 0.011$ and $t = 3.59$, $P = 0.023$; female DO 1989, $t = 2.72$, $P = 0.073$; male DJ 1990, $U = 21$, $P = 0.1$; female DJ 1989, $U = 16$, $P = 0.05$). Foraging time in structural diversity categories of vegetation shows males, and possibly females, used isolated living vegetation more than expected in 1989 (male, $t = 7.78$, $P = 0.0044$; female, $t = 2.43$, $P = 0.094$) but not in 1990 (Fig. 5B). Males, and possibly females, also used the fairly rare category of isolated dead trees less than expected in 1990 (male, $t = 5.63$, $P = 0.0049$; female, $t = 2.79$, $P = 0.049$) but not in 1989. Three other values approach significance in rare habitats (male and female DD 1990, $t = 3.55$, $P = 0.024$ and $t = 2.77$, $P = 0.05$; female DD 1989, $t = 5.074$, $P = 0.015$).

DISCUSSION

Habitat use and the concept of ecological constraints are central to many theories concerning the evolution and maintenance of cooperative breeding in birds. Specialization in habitat use in long-lived birds and the resulting potential to saturate this habitat is central to both the habitat saturation and marginal habitat models. The habitat saturation model states that suitable breeding habitat slots become filled, forcing young individuals to delay dispersal (Selander 1964, Brown 1974). The marginal habitat model builds on this concept by adding an additional constraint, namely scarcity of habitats of marginal quality. Scarcity of marginal habitats reduces the possibility of individuals dispersing and roaming as nonbreeding floaters (Verbeek 1973, Koenig and Pitelka 1981, Emlen 1982, Woolfenden and Fitzpatrick 1984, Fitzpatrick and Woolfenden 1986). One prediction of the marginal habitat model is a high proportion of territories of high-quality habitat relative to those of marginal quality in cooperative breeding populations. As an alternative to these extrinsic constraint models, the benefits-of-philopatry (BOP) model stresses the importance of intrapopulational variation in territory quality and is not dependent on complete saturation of either breeding or marginal/floating habitats but is instead based upon the intrinsic decision making processes of young birds regarding their dispersal options relative to the quality of their natal territory (Stacey and Ligon 1987, 1991). According to this model, individuals born in high quality natal territories choose to delay dispersal and remain at home, thereby increasing their chances of inheriting the natal territory or occupying another nearby territory of equal quality. These individuals also may avoid increased chances of mortality associated with breeding or floating in lower quality habitats. Koenig et al. (1992) introduced an elegant, more inclusive model, which more formally distinguishes between extrinsic and intrinsic factors influencing an individual's decision on whether to delay natal dispersal. This delayed dispersal threshold model identifies five parameters that are many times jointly involved in the probability of an individual delaying dispersal. A complete explanation of this model is not possible here, however, in regard to this paper, one of its parameters is the distribution of territory quality as modeled in either the marginal habitat or BOP models.

An extension of current models.—I believe the logic outlined in each of these models can be extended to predict specific habitat use patterns

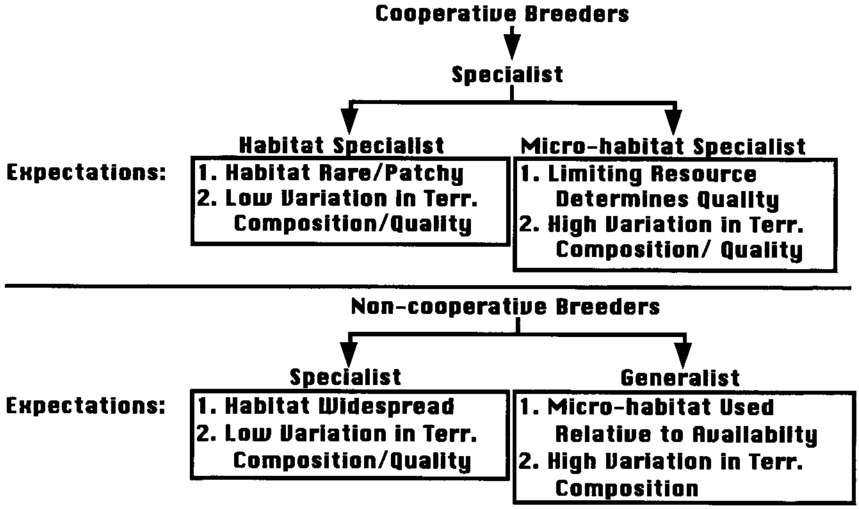


FIG. 6. Model of habitat-use expectations for cooperative and non-cooperative breeding populations.

for cooperative and non-cooperative breeding populations (see Fig. 6). One might expect cooperative populations to show restricted, habitat specialist patterns of habitat use in one of two ways. First, a population may show a strict requirement to live in a habitat characterized by a certain vegetation assemblage. This habitat-use inflexibility would lead to demographic conditions favoring the evolution of cooperative breeding only if the habitat in question is either rare in comparison to other assemblages in the same geographic region or is very patchily distributed. With such broad habitat-use specificity, variation among usable territories in habitat composition and quality may be small. In extreme cases, all habitat patches in an area are either acceptable or unacceptable for breeding or floating, with no intermediaries. These predictions fit the habitat saturation model and, depending on the degree of habitat specificity (i.e., does marginal habitat even exist for the species), the marginal habitat model. The second habitat-specialist pattern to be expected from a cooperative population is the required use of a *particular* aspect of the habitat, a target of specialization, that serves as a limiting resource while other aspects of habitat composition have reduced importance and may vary independently among territories. In this case, general habitat composition may vary greatly but be of little importance. The presence of the limiting resource is the crucial feature of successful breeding in this situation and is the currency by which territory quality is measured. Examples of such targets of specialization in cooperative species include cavities for both Green Woodhoopoe (*Phoeniculus purpureus,* Ligon and Ligon 1988) and Red-cockaded Woodpecker (*Picoides borealis,* Kulhavy et al. 1995) for roosting and nesting, and granary trees for acorn storage by Acorn Woodpeckers (*Melanerpes formicivorus,* Koenig and Mumme 1987). If territory quality varies greatly and is tightly correlated with reproductive success, as predicted by the BOP model, a cooperative breeding system may evolve as a queue of non-dispersing individuals builds to fill the small number of high quality breeding territories. In this latter case, it is necessary to demonstrate that individuals utilize the limiting resource disproportionately to its availability in the territory.

Non-cooperative populations also would be expected to show one of two habitat-use patterns (Fig. 6). First, non-cooperative populations also may show specialist habitat-use patterns but only in a super-abundant, widespread habitat type. In this case, territory composition should not change much among territories. Alternatively, the population may show generalist habitat-use patterns with significant variation in habitat composition among territories. In the latter case, it is expected that individuals use each habitat component in relation to its availability and no target of specialization is expected.

Measuring territory quality has proven difficult and is flawed in many studies because reproductive success is used as the primary currency which fails to distinguish between habitat quality and the quality of individuals (Koenig et al. 1992). However, I believe documentation of habitat-use patterns allows closer examination of the mechanisms leading to changes in breeding systems. This approach must first classify populations as habitat specialist/generalist relative to other populations based on knowledge of the distribution of each major habitat component across territories and detailed habitat-use patterns of these major components. Then, given the two predictions concerning patterns of habitat-use for both cooperative and non-cooperative populations and information on population variation in breeding systems, we can examine the models concerning the ecological bases of cooperative breeding systems more closely.

Behavioral patterns in biodiversity habitat categories.—Texas Western Scrub-Jays use the biodiversity categories of woody vegetation as generalists with one exception: males use living juniper less than expected with the excess time transferred to dead and living oaks (Fig. 1A). The behavioral explanation for this deviation is the large fraction of time males engage in sentinel behavior and the relatively poor visibility attributes of (usually short) living juniper and the good visibility attributes of (usually tall) oak trees. Females also use these habitat categories in this pattern, but because so little of their time is spent in sentinel behavior, deviations from general use of this habitat type are not as large (Figs. 2, 4A). Males also may have used living juniper while preening/inactive less than expected (Fig. 3A). The habitat in which this behavior occurs may be influenced by the habitat in which the behavior preceding it occurred. Individuals may simply preen wherever they find themselves and, in general, males spent little time in living juniper. Values approaching significance in differential use of several of the rarer biodiversity categories should not be given much weight because of the potential for sampling error in categories where behaviors appear also to be rare (e.g., foraging in DO and DJ, Fig. 5A).

Behavioral patterns in structural diversity categories.—Observed values deviated from expected values in more structural diversity categories than in biodiversity categories (Fig. 1B). As noted above, males and females used isolated living vegetation more than expected at the expense of dense living trees in 1989 but not in 1990. Similarly males, and possibly females, used isolated living vegetation while foraging more than expected in 1989 but not 1990 (Fig. 5B). This pattern could have been due to a food resource shift between years; however, no data exist to test this possibility. The two most frequently captured prey items were large katydids (probably *Microcentrum* sp.) and walking sticks (probably *Megaphasma* sp.), but their distribution among the different habitat categories is unknown. Deviations from expected in habitat use of preening/inactive behavior seem to mirror those of foraging behavior in females but not in males (Fig. 3B). Again, if individuals preen wherever they find themselves, foraging would influence where the preening/inactive behavior occurred in females more than in males, because females spent a large fraction of their time foraging, while males were influenced by both foraging and sentinel behaviors (Fig. 2).

Males also may have used isolated dead vegetation more than expected in both years (Fig. 1B). Both sexes increased use of this habitat for sentinel behavior (Fig. 4B); however, not all deviations from expected are close to statistical significance. Much of the isolated dead habitat is equivalent to the dead oak category of the biodiversity categorization, and a functional relationship of isolated dead trees to sentinel behavior probably exists. Both males and females also used isolated living vegetation for sentinel behavior less than expected in 1990 but not 1989. This difference is not observed in general habitat use (Fig. 1B), and reasons for this deviation while in sentinel behavior are not apparent.

Habitat use patterns of other scrub-jay populations.—Peterson and Vargas (1992) provide a thorough analysis of the diversity of habitat types used by birds in the scrub-jay species complex. Scrub-jays use a wide range of habitats including: oak, juniper, pinyon and desert woodlands; riparian brush; oak-palmetto scrub; pine-oak, alpine pine-spruce, tropical thorn forests; and mangrove swamps. This level of variation in habitat use is that which occurs *across populations.* Levels of variation in habitat use *within populations* is highly population specific. Florida, coastal California, and Great Basin populations are very habitat specific. This specificity was hypothesized to be related to the importance of either acorns or pinyon seeds in the diet of these populations. Baja California and southern Mexico populations are more general in habitat use, and these habitats frequently have no obvious replacements for acorns or pinyon seeds. Koenig et al. (1992) discuss the importance of mast production relative to differences in social systems in scrub-jays. In the non-cooperative California population of Western Scrub-Jays, years of poor acorn abundance result in increased reproductive failure, adult mortality and territory abandonment. Oaks are distributed in patches in California and floaters typically move freely among breeding territories in search of areas of high acorn abundance (Carmen 1988). Concerning the Florida Scrub-Jay, mast production is more stable in Florida and this predictable, evenly distributed, resource is easily defended and floaters are not tolerated in breeding territories. Koenig et al. (1992) also speculate that differences in mast production partially explains differences in jay use of the optimal, recently burned oak patches and unoccupied, dense, unburned patches of oaks.

Presence of other jay species affects range of habitat use in Florida (Blue Jays, [*Cyanocitta cristata*]), central California (Steller's Jays [*C. stelleri*]), and New Mexico/Arizona (Gray-breasted Jays) but does not limit use in southern Mexico (Magpie-Jays [*Calocitta* spp.]). However, the diversity of habitats utilized by Scrub-Jays in Baja California cannot be solely explained by the absence of other jay species because this population uses habitats that are not used on the mainland by any jay species (Peterson and Vargas 1992).

Habitat use and predictions of models for the Texas population.—In most habitat-use categories examined in this study, the central Texas population of Western Scrub-Jays appears to use its habitat as a generalist. The only clear exception to this statement is the apparent specialization by males in using oak, particularly isolated snags, for sentinel behaviors. As a non-cooperative population, one of two habitat-use patterns was expected (1) specialist habitat-use patterns in an abundant, widespread habitat type, with little variation among territories in habitat composition (matching the habitat saturation or marginal habitat models), or (2) generalist habitat-use patterns with the potential of significant variation in habitat composition among territories (as predicted under the BOP model). Texas Western Scrub-Jays show an interesting combination of habitat-use patterns supporting both predictions. The only resources that males utilize as a specialist, oak trees during sentinel behavior, are fairly widespread and would not be considered a limiting resource. In the remaining habitat categories Texas Western Scrub-Jays act as generalists, using the habitat in relation to its availability, even though variation in habitat composition among territories is considerable. Mast production, an important resource to many jay populations, was not measured in this study because of the season in which data were collected.

Areas in need of future research.—Comparisons between cooperative and non-cooperative populations using more detailed habitat-use studies, when combined with demographic and phylogenetic information, will allow closer examination of the various models of the evolution and maintenance of cooperative breeding in birds. It is clear that habitat constraints are important in the Florida Scrub-Jay and examining habitat use in their relict scrub habitat may reveal why very dense, unburned scrub and other habitats are inadequate for maintaining populations (Woolfenden and Fitzpatrick 1984). This subject is the focus of a detailed habitat-use study currently underway (R. Curry, pers. commun.) This type of detailed study also would be most valuable for examining correlations between ecological constraints and cooperative breeding in the southern Mexico population of the Western Scrub-Jay. This population appears to use a wide range of habitat types which do not appear saturated (Burt and Peterson 1993). A detailed habitat-use study might identify specific microhabitats that limit where successful territories can be maintained. These microhabitats may be found to exist within several of the more broadly defined habitat types. As shown in this study, habitat-use patterns can be used to test predictions concerning the role ecological constraints play in determination of individual dispersal patterns and, potentially, the evolution of breeding systems.

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LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1995. Fortieth supplement to the American Ornithologists' Union Checklist of North American Birds. Auk 112. (in press)

AVERY, T. E. 1985. Interpretation of aerial photographs, fourth ed. Burgess Publ. Co., Minneapolis, Minnesota.

BROWN, J. L. 1974. Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. Am. Zool. 14:63–80.

———. 1987. Helping and communal breeding in birds: ecology and evolution. Princeton Univ. Press, Princeton, New Jersey.

BURT, D. B. 1992. Comparative Scrub Jay behavioral ecology. M.A. thesis, Univ. of Kansas, Lawrence, Kansas.

——— AND A. T. PETERSON. 1993. Biology of the cooperative-breeding Scrub Jays (*Aphelocoma coerulescens*) of Oaxaca, Mexico. Auk 110:207–214.

CARMEN, W. J. 1988. Behavioral ecology of the California Scrub Jay (*Aphelocoma coerulescens californica*): a noncooperative breeder with close cooperative relatives. Ph.D. diss., Univ. of Calif., Berkeley, California.

DEGANGE, A. R. 1976. The daily and annual time budget of the Florida Scrub Jay. M.A. thesis, Univ. of South Florida, Tampa, Florida.

EMLEN, S. T. 1982. The evolution of helping behavior. I. An ecological constraints model. Am. Nat. 119:29–39.

FITZPATRICK, J. W. AND G. E. WOOLFENDEN. 1986. Demographic routes to cooperative breeding in some New World jays. Pp. 137–160 *in* Evolution of animal behavior (M. Nitecki and J. Kitchell, eds.). Univ. of Chicago Press, Chicago, Illinois.

KOENIG, W. D. AND R. L. MUMME. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Princeton Univ. Press, Princeton, New Jersey.

——— AND F. A. PITELKA. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. Pp. 261–280 *in* Natural selection and social behavior: recent research and new theory (R. D. Alexander and D. Tinkle, eds.). Chiron Press, New York, New York.

———, ———, W. J. CARMEN, R. L. MUMME, AND M. T. STANBACK. 1992. The evolution of delayed dispersal in cooperative breeders. Quart. Rev. Biol. 67:111–150.

KULHAVY, D. L., R. G. HOOPER, AND R. COSTA (EDS.). 1995. Red-cockaded Woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Nacogdoches, Texas.

LIGON, D. J. AND S. H. LIGON. 1988. Territory quality: key determinant of fitness in the group-living Green Woodhoopoe. Pp. 229–253 *in* The ecology of social behavior (C. N. Slobodchikoff, ed.). Academic Press, San Diego.

MILLER, H. A. AND S. H. LAMB. 1985. Oaks of North America. Naturegraph Publishers Inc., Happy Camp, California.

NEAVE, H. R. AND P. L. WORTHINGTON. 1988. Distribution-free tests. Unwin Hyman Ltd., Boston, Massachusetts.

PETERSON, A. T. AND D. B. BURT. 1992. Phylogenetic history of social evolution and habitat use in the *Aphelocoma* jays. Anim. Behav. 44:859–866.

——— AND N. VARGAS. 1992. Ecological diversity in Scrub Jays (*Aphelocoma coerules-*

cens). Pp. 309–317 *in* Selected faunistic groups of Mexico (T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, eds.). Oxford Univ. Press, New York, New York.

PITELKA, F. A. 1945. Pterylography, molt, and age determination of American jays of the genus *Aphelocoma.* Condor 47:229–260.

SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhyncus*. Univ. Calif. Publ. Zool. 74:1–224.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry. 2nd ed. Freeman Press, San Francisco, California.

STACEY, P. B. AND J. D. LIGON. 1987. Territory quality and dispersal options in the Acorn Woodpecker, and a challenge to the habitat saturation model of cooperative breeding. Am. Nat. 130:654–76.

——— AND ———. 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. Am. Nat. 137: 831–846.

VERBEEK, N. A. M. 1973. The exploitation system of the yellow-billed magpie. Univ. Calif. Publ. Zool. 99:1–58.

WOOLFENDEN, G. E. AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird, Monogr. Pop. Biol. No. 20. Princeton Univ. Press, Princeton, New Jersey.