OPERATIVE BREEDING IN THE CALIFORNIA SCRUB-JAY

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This volume is dedicated to Frank A. Pitelka (1916–2003),
Editor of Studies in Avian Biology from 1984 to 1987.

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ABSTRACT

I studied the ecology, behavior, and demography of the noncooperatively breeding Western Scrub-Jay (*Aphelocoma californica californica*) in central coastal California. Cooperative breeding is ancestral in *Aphelocoma* jays and its loss in Western Scrub-Jays presents an opportunity for appropriate phylogenetic and ecological comparisons within the genus to identify key factors selecting for the alternative social systems. My intent was to gather comparative data to test several models for the evolution and maintenance of delayed dispersal and group living in birds, which were developed from long-term studies of cooperative breeders, including the closely related Florida Scrub-Jay (*A. coerulescens*) and Mexican Jay (*A. ultramarina*). The fundamental result of these comparisons is that models for the evolution of delayed dispersal and group living in birds fail as general explanations when floating is ignored or treated as a one-dimensional phenomenon. Factors that lead to delayed dispersal in cooperative species are known to be complex and may differ substantially among species and populations, and even among individuals within populations and groups. Conditions leading to early dispersal and floating may be equally complex. Clearly, opportunities for independent breeding are constrained in both cooperative and noncooperative populations. What then makes early dispersal and floating the preferred strategy in Western Scrub-Jays? Several factors play a part, including (1) the interplay between the pattern of habitat quality and acorn production, (2) the varied behaviors floaters may employ to exploit these resources and acquire breeding space, (3) the behavioral interactions between territorial jays and floaters, and (4) the ability of floaters to settle on low-quality territories and then, as breeders, to move and improve the quality of their territories.

California Scrub-Jays are monogamous, permanently territorial, and noncooperative breeders. Offspring depart from their natal territories at independence, yet breeders tolerate both offspring and unrelated floaters of all ages on their territories except during May and June. Because of this tolerance, juveniles and older floaters aggregate in the highest quality habitats on occupied territories, primarily where acorns are in good supply. Although floaters exhibit diverse dispersal behavior, most remain sedentary throughout the winter and early spring, storing and recovering acorns as do the resident territorial breeders. By late April in most years, the aggregations dissolve and floaters are rarely seen until some of these same individuals return in early July and join large numbers of independent juveniles. The disappearance of floaters is coincidental with increased aggression by territorial jays, but floaters also disappear from areas not occupied by breeders.

Floating in scrub-jays took several forms. Some banded juveniles remained on and around their natal territories until the next breeding season, others joined aggregations a short distance away or disappeared. In four of five years, the study area attracted floaters from a wide area. In the anomalous year (when the acorn crop failed), local juveniles departed and no floaters immigrated. In winter, floaters occasionally established pseudo-territories that were abandoned in the late spring. Other floaters moved widely (up to 35 km) during the winter, but the majority established defined home-ranges from fall to early spring. In April of one year, large flocks of up to 60 jays in transit were observed. The few floaters seen during May and June in most years were individually sneaking through territories or, more rarely, moving in unoccupied habitat. In one year (1985) of high acorn abundance lasting until April, floaters remained on their home ranges (which overlapped an average of nine territories) throughout the breeding season; this was coupled with increased tolerance by breeders.

Breeder survivorship averaged 83% and 79% per year for males and females, respectively, and reproductive output averaged 1.4 fledglings per pair. Reproductive success of jays that acquired territories as yearlings was near zero and did not peak until age four.

Over the five-year period and 215 pair-years, first-year males and females comprised 5% and 10%, respectively, of the breeding population. Of 12 jays that both fledged from and later acquired territories on the study area, five did so as yearlings, four as two-year olds, and three as three-year olds. Nearly all jays gained a territory by pairing with an older, established breeder. Life-table estimates, based upon these and other demographic data, indicate that 19% and 40% of males and females, respectively, acquire territories as yearlings. An analysis of territorial dynamics, including the types of habitats used, occupancy rates of territories, and vegetation characteristics, suggest that all suitable habitat is occupied by breeders in most years and that ecological constraints prevent a sizeable portion of first-year jays from acquiring territories and breeding.

Individual jays cache approximately 7,000 acorns each year. Poor acorn years result in significantly higher mortality, reproductive failure, and territory abandonment. The 1983 crop failure, through the effects of higher mortality and territory abandonment, resulted in a 25% decrease in the number of territories on the study area and the potential for new breeding vacancies. Acorn production by the large and patchily distributed oaks in California is highly variable locally within and among years, and periodic crop failures occur every 4 to 6 years, depending on the number of oaks species in the area.

Early dispersal is favored because floaters are able to aggregate in areas of high acorn abundance, and the tolerance of floaters by breeders allows them access to the best habitats. Floaters appear to be as dependent on cached acorns as breeders and may be closely tied to these stores during the winter. Floaters may spend fall and winter in areas of high acorn production, despite the fact that these areas provide relatively few breeding opportunities. In the spring, near continuous distribution of oak woodland provides lepidopteran larvae and other insects over a wide area. Floaters are then free to move regionally and search out breeding areas, particularly in areas of prior acorn crop failures that may offer more territory vacancies. This pattern of food abundance may also contribute to the tolerance of floaters in the winter (when acorns are superabundant) and intolerance in the breeding season (when insect prey is important and starvation rates of nestlings are high).

Key words: *Aphelocoma*, acorn production, cooperative breeding, dispersal, floating, scrub-jay, social behavior.

INTRODUCTION

Long-term field studies have contributed greatly to our knowledge of the demographic and ecological factors that promote delayed dispersal, larger group size, and increased cooperation in cooperatively breeding birds. Theories based on these studies differ in stressing the relative importance of various demographic and ecological factors both in the maintenance of cooperative breeding and in modeling the evolution of group living and cooperative breeding from an earlier noncooperative state. Similar long-term studies of appropriate noncooperative species are essential for the comparisons required to test these theories and their underlying assumptions. The Western Scrub-Jay (*Aphelocoma californica*) and other species in the genus provide a unique and unparalleled opportunity to make such comparisons. *Aphelocoma* jays are similar in morphology and general aspects of behavior, their social organization ranges from the noncooperative Western Scrub-Jay to the plural-breeding, cooperative Mexican Jay (*A. ultramarina*), and there is a wealth of information on two cooperative members of the genus, the Mexican Jay and the Florida Scrub-Jay (*A. coerulescens*).

APHELOCOMA JAYS

Nearly all races of scrub-jays in western North America breed noncooperatively. Young disperse from their natal territories soon after becoming independent and then, over the ensuing months, attempt to acquire territories and breeding status. Despite their wide geographic range and the diversity of habitats used, only one population (*A. californica sumichrasti*) in the mountains of southeastern Mexico is known to live in family groups (Burt and Peterson 1993).

The insular Island Scrub-Jay (*Aphelocoma insularis*) has been the best studied western population (Atwood 1980a,b; Atwood et al. 1990); it became isolated from the mainland population during the Pleistocene (Pitelka 1951), almost certainly after the western populations had lost traits of cooperative breeding (see below). In contrast to the noncooperative Western Scrub-Jays, the cooperatively breeding Florida Scrub-Jay (Woolfenden 1974, 1975; Woolfenden and Fitzpatrick 1977, 1978, 1984, 1986, 1990; Fitzpatrick and Woolfenden 1986, 1988; Mumme 1992) and Mexican Jay (Brown 1963, 1970, 1974, 1994; Brown and Brown 1981a, 1984, 1990; Brown et al. 1997; Trail et al. 1981) have been intensively studied for 25+ years. In Florida Scrub-Jays, offspring from a single breeding pair may delay dispersal for one to several years, forego breeding, and help in defending the territory and raising offspring in subsequent breeding efforts. Roughly one-half of all pairs have helpers in any given year. The Mexican Jay exhibits geographic variation in group size and social behavior (Strahl and Brown 1987, Brown and Horvath 1989) ranging from singular breeding (one breeding female per group) to up to five breeding pairs on a single group territory. Offspring may delay dispersal and breeding for up to six years and help; some offspring never disperse but become breeders on their natal territories. Both nonbreeders and breeders participate in territory defense and care for young at all group nests. Less is known of the Unicolored Jay (*Aphelocoma unicolor*), but it does breed cooperatively and exhibits behavioral characteristics intermediate between those of Florida Scrub-Jays and Mexican Jays: intermediate group sizes, a single female breeder, and possibly more than one breeding male per group (Pitelka 1951, Webber and Brown 1994).

The occurrence of cooperative breeding in the Florida Scrub-Jay, Mexican and Unicolor jays, in one population of Western Scrub-Jay (*A. californica sumichrasti*), and in some or all species studied in closely related genera (*Cyanolyca*, *Cyanocorax*, *Cissilopha*, and *Calocitta*; reviewed in Brown 1987), suggests that cooperative behavior is a primitive character state shared with other Middle and South American jays (Edwards and Naeem 1993). Indeed, even other more distantly related corvids exhibit varying aspects of group living and cooperative breeding (e.g., Gray Jays, *Perisoreus canadensis* [Waite and Strickland 1997]; western American Crows, *Corvus brachyrhynchos hesperis* [Caffrey 1992]), and a wide variety of other avian taxa show at least facultative or incidental helping behaviors (see Brown 1987). If group living and cooperative breeding are ancestral and Western Scrub-Jays have lost the behavior (Pitelka 1986, Peterson and Burt 1992; but see Brown and Li 1995), why then are California Scrub-Jays so adamantly noncooperative?

OVERVIEW

Proposed hypotheses and models have invoked a variety of ecological, demographic, and behavioral processes as key factors in the evolution and maintenance of group living and cooperative breeding. Most theories for the evolution of group living and cooperative breeding postulate that social groups form because individuals lack opportunities to disperse and breed successfully themselves. Such opportunities may be limited by a shortage of mates (Rowley 1965, Pruett-Jones and Lewis 1990); by the ability of groups, but not pairs, to breed successfully (Rabenold 1984, 1985; Austad and Rabenold 1985, 1987); and by a high variance in resource levels and carrying capacity, leading to either a high cost of independent breeding (Emlen 1982), to closures of intermittently open breeding vacancies (Brown 1987), or a general lack of suitable breeding territories (Selander 1964; Brown 1974, 1978). Other theories stress the importance of the distribution of habitat quality (Koenig and Pitelka 1981) or the variance in territory quality (Stacey and Ligon 1987, 1991) in selecting for delayed dispersal and group living. Others point out that where resource renewal is slow, group size may be limited to pairs, despite other factors favoring retention of offspring (Waser 1981, Brown 1982). Finally, virtually every study of cooperative breeders suggests significant direct or indirect inclusive fitness benefits, or both, accruing to individuals that delay dispersal and assist their parents or siblings in some manner. Although California Scrub-Jays do not delay dispersal and help, ancestral populations almost certainly did so, and the loss of the fitness benefits associated with group living and cooperative breeding must be taken into account.

Examining the importance of these factors requires data on food resources and foraging, territorial behavior and territory quality, dispersal, reproduction, and survivorship. Such information for the California Scrub-Jay is presented in the central sections of this monograph. An essential part of the comparisons among populations must focus on nonbreeders: helpers in cooperative species, floaters in noncooperative ones. Acquiring data on nonbreeding floaters is notoriously difficult, and floaters have most often been ignored or written-off as "surplus population." Floaters are, of course, as integral to a population as nonbreeding helpers, and are a primary focus of this monograph.

The penultimate section of this volume uses these data to draw comparisons among *Aphelocoma* jays and to test the predictions of the various models and hypotheses. It should be noted that these models approach the evolution of group living and cooperative breeding as proceeding from an earlier noncooperative state. Here, the transition is from an ancestral cooperative state to a noncooperative one, and there is no a priori reason to suspect that evolutionary factors are symmetrical in their effects. This may also complicate comparisons among populations in that certain behaviors may be relics of an ancestral cooperative social system.

In the final section, I show how specific factors affect Western Scrub-Jays in California —from the pattern of acorn production to the suite of strategies available to floaters for gaining a territory—and contribute to the loss of cooperative breeding while favoring early dispersal and floating.

STUDY AREA AND METHODS

LOCATION OF STUDY AREA

The 900-ha Hastings Natural History Reservation lies in the outer coast range of central California at the upper end of the Carmel Valley, 36 km from the Pacific Ocean. To the southwest the Santa Lucia Range rises to 1,538 m on Chews Ridge, and to the east Palo Escrito Peak tops the Sierra de Salinas at 1,362 m (Fig. 1).

I studied scrub-jays primarily on Big Creek, in the lower portion of the Reservation.

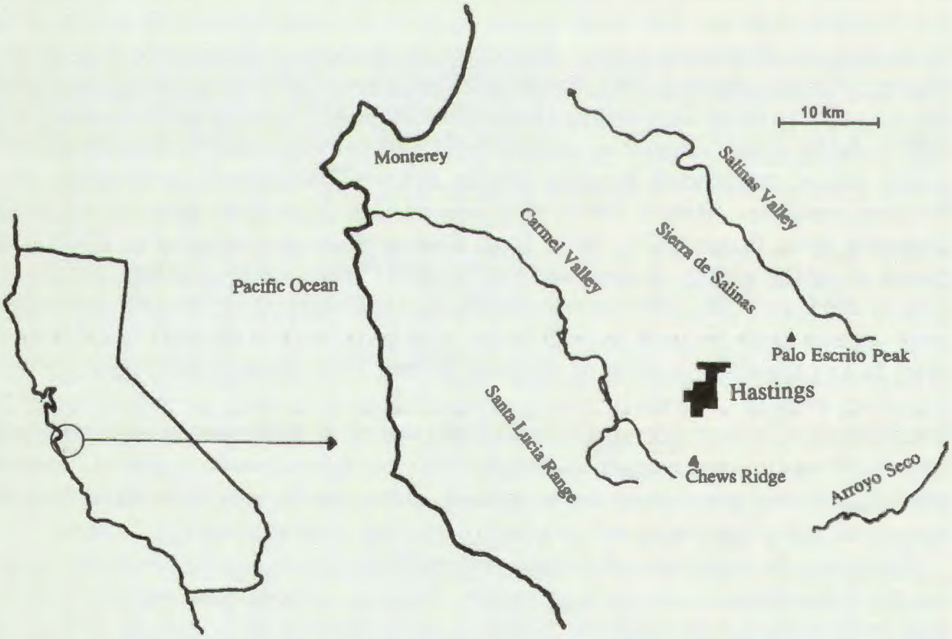

FIGURE 1. Location of the Hastings Reservation in relation to local geographic and topographic landmarks.

Big Creek flows through the center of the site, and four hills (470–637 m) rise nearby (Fig. 2). In 1981, the first year of the study, the study area covered 83 ha, and in 1982 through 1985, 197 ha. Within the study area all major vegetation and habitat types found in the surrounding area are represented. Other parts of the Reservation, and neighboring ranches, were surveyed occasionally for floaters and to monitor dispersal.

CLIMATE

The Reservation has a Mediterranean climate; the summers are dry and warm, and the winters wet and cold. Almost no rain falls between May and October, and late summer and early fall are extremely hot and dry. Rainfall over the last 40 years has averaged 52 cm. Mean monthly temperature and precipitation are roughly inversely related. July is the hottest and driest month; the wettest months are December through March. Figure 3 presents 40-year averages for temperature and precipitation at the Reservation headquarters, at the center of the study area. The creeks stop flowing in late summer in most years; Finch and Robertson creeks always hold some pools through the summer whereas Big Creek dries up completely. Snow falls on the higher elevations of the Reservation several times in most winters, but rarely persists for more than a day.

VEGETATION

Vegetation is predominantly oak woodland and is similar to foothill vegetation found throughout the central coast ranges. Six important plant communities, as defined in

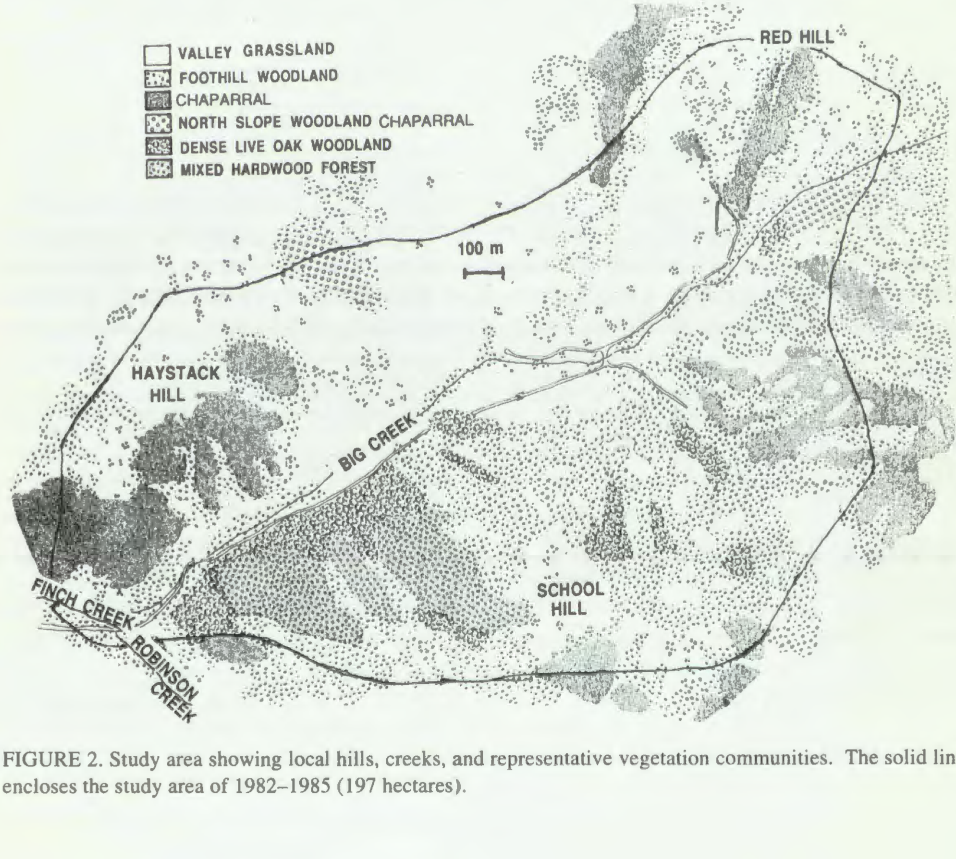

FIGURE 2. Study area showing local hills, creeks, and representative vegetation communities. The solid line encloses the study area of 1982–1985 (197 hectares).

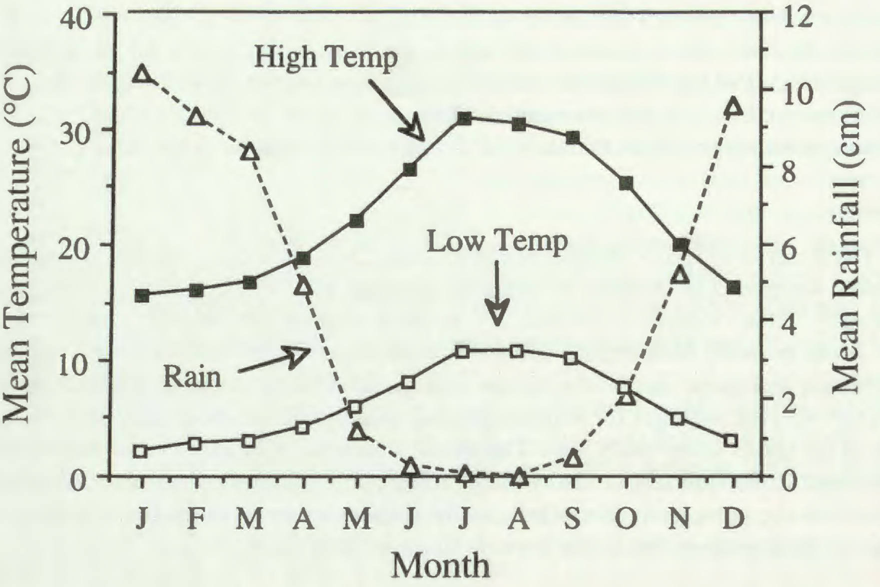

FIGURE 3. Forty-year mean rainfall and mean maximum and minimum temperatures at the Hastings Reservation (1938–1978).

Barbour and Major (1977), are found on the scrub-jay study area:

1) Mixed hardwood forest (*Quercus agrifolia-Arbutus*).
2) Foothill woodland (*Q. lobata-Q. douglasii*).
3) North slope woodland-chaparral (*Aesculus californica-Q. agrifolia* phase).
4) Chaparral (*Adenostoma fasciculatum-Ceanothus cuneatus*).
5) Riparian forest (*Salix-Platanus* phase).
6) Valley grassland (*Bromus-Avena-Erodium*).

The distribution of these communities on the study area (except for the riparian communities) is mapped in Figure 2. By far the most dominant trees, and most important to the scrub-jays, are the oaks. On the Reservation there are six species representing all three oak subgenera. On the study area, three of these species are common (*Q. agrifolia*, *Q. lobata*, and *Q. douglasii*) whereas *Q. kelloggii* is rare and *Q. chrysolepis* and *Q. wizlizenii* are absent; however, *Q. kelloggii* and *Q. chrysolepis* are abundant within 1 km.

METHODS

Banding

Between July 1977 and March 1981, prior to the start of this study, 43 jays were banded, either with color bands or with U.S. Fish and Wildlife Service (USFWS) bands only. Eleven of these jays were found as breeders on the study area in April 1981 at the start of the study. Beginning in 1981, my field assistants and I banded 779 scrub-jays: 106 as breeders, 350 as nestlings, and 323 as nonbreeding floaters. I use the terms "breeder" and "territorial jay" interchangeably; floaters are nonterritorial and nonbreeding individuals. Jays were given unique band combinations consisting of three plastic colored bands (8 colors) and a USFWS aluminum band. The plastic wrap-around color bands were sealed with acetone.

I captured breeders and floaters almost exclusively with ground traps baited with acorns, but a small percentage was captured with mist nets at water sources in July through September. Nestlings were banded at 10 days of age.

Age determination

When first caught, scrub-jays were aged according to molt and feather wear (Pitelka 1945). I use the following terminology to describe age classes:

1) juveniles (up to five months old): individuals between fledging and near conclusion of post-juvenile molt (approximately 1 October). Juveniles have gray heads and other less obvious plumage characteristics that separate them easily from other age classes.

2) first-year birds (up to 12 months old): individuals from fledging through the next spring (31 May). Thus I refer to jays breeding in the spring following hatching as first-year birds. In the post-juvenile molt, jays molt their body feathers, but most flight feathers (and coverts) are retained (Pitelka 1945). This allows first-year jays to be distinguished from adults easily in the hand and, with practice, in the wild.

3) adults (+12 months old): all individuals after the first spring (1 June) following hatching. Between June and September three age classes could be identified: juveniles (young of the year), second-year jays (hatched the previous spring, entering their second year and undergoing their first complete molt), and jays entering their third year or older.

Sex determination

All breeders were sexed by behavioral criteria; only females incubate, brood young, and give the sex-specific "rattle call." Females are also slightly smaller, duller in plumage, and weigh less than their mates. Side by side, the sexes of a known pair are usually easily recognized.

Floaters could not be sexed in the field unless a female gave a rattle call, or a male engaged in courtship feeding with a known female floater. To ascertain the sex of floaters I performed discriminant function analyses, based upon weight and wing-cord measurements on breeders and floaters from the study area, all of known sex. The single discriminant function ($N = 150$, $\chi^2 = 133.9$, $df = 2$, $P < 0.001$) correctly classified 89% of 79 females and 89% of 71 males. An independent data set was taken from museum specimens (University of California Museum of Vertebrate Zoology) collected on or near the Hastings Reservation. These 36 females and 25 males included only adults and first-year birds. The discriminant function derived from the first sample correctly classified 93.4% of the independent data set (94.4% of females and 92% of males) and was then used to sex the floaters captured on the study area.

Nest checks

I attempted to find every nest each year as early as possible in the breeding season. Beginning in late February, I began monitoring the banded breeders and tried to locate nests during nest building, when the task is easiest. After egg laying, the jays become secretive and locating nests often took hours or several days. Locating nests was difficult because jays may nest from 0.5 to 15 m above the ground in shrubs, lichens, mistletoe, old magpie nests, and in oak canopies. My attempts to entice nest-building females with nesting material in order to follow them back to the nest, as is sometimes possible with Florida Scrub-Jays (G. Woolfenden, pers. comm.), proved unsuccessful.

Nearly all nests were found before or soon after egg laying. A few nests were lost to predators before they were located, but even in those cases I knew, from the pair's behavior, whether the pair had a nest with eggs. For example, prior to egg-laying the pair would be vocal and easily observed; after egg-laying the female would rarely be seen, and the male would be comparatively unobtrusive and would collect food to feed to the female. I failed to locate only one nest that successfully fledged young (out of 215 pair-years and a total of 315 nests).

Once located, nest checks were kept at a minimum. I visited only to determine first egg date (FED), clutch size, and hatching brood size, and to band the nestlings. The jays vociferously defend their nests and thus may attract any of a suite of predators. My activities, primarily in 1981, led to the loss of nests by attracting other scrub-jays, American Crows, Yellow-billed Magpies (*Pica nuttalli*), and Cooper's Hawks (*Accipter cooperii*). To minimize the impacts of my activities, nests were checked with a mirror attached to a 1-m staff, and in many cases I did not need to approach the nest closely until banding. Nests that were difficult to reach were checked only at the estimated hatching date and at banding, or just at banding to minimize the chance of attracting predators. This resulted in some loss of data, but minimized bias due to human interference; in cases where I thought my activities caused nest or nestling loss, I excluded the record from all analyses.

Nests were visited on the estimated day of fledging to count the number fledging, and then one month and two months later to count the number of independent young. Although young may be fed up to three months after fledging, they usually disperse from their natal territories 7 to 8 weeks after fledging. Between nest checks, pairs and nests were watched to confirm whether the nests were still active. If not, the nest was examined to determine cause of loss, and the new nest (if any) subsequently located. Local scrub-jays fledge only one brood per year but will renest up to three times if earlier nests fail.

Territory mapping

Beginning in March of each year, locations of the banded breeders were recorded on aerial photographs (1 cm = 12.5 m) of the study area. In addition, defended boundaries were marked where disputes occurred. By August, the accumulated locations and defended boundary locations were used to delineate territories. Although I mapped territories only during the breeding season, pairs defended their territories throughout the year. Changes in boundaries may occur at any time, usually as a result of breeder death; such changes and their presumed cause were noted. Throughout this volume specific territory names are indicated in capitals, e.g. BURNT, 2400R, NTN, and can be located on the territory maps.

Operationally, I use both defended area (Noble 1939) and exclusive use (Pitelka 1959) to define the territory boundaries. In some cases, especially where territories were not apparently contiguous, I used a tape recorder to play vocalizations to attract breeders and locate borders. Territory size was measured by tracing boundaries with a digital planimeter; no compensation was made for differences in slope.

Vegetation sampling

Two methods were used to sample vegetation characteristics. First, vegetation throughout the Reservation was measured (W. Koenig, unpubl. data) employing the methods of James and Shugart (1970). On 0.04 ha plots (N = 246) placed every 60 m on a grid, the following were recorded: (1) the species and diameter at breast height (DBH) of all trees; (2) estimates of percent coverage of tree canopy, shrubs, and grass; and (3) the species of trees observed within the 60 m grid unit but not within the 0.04 ha plot. Each sample covered approximately 10% of the total area of a grid unit.

Second, on aerial photographs of the study area, I used a digital planimeter to measure the following on 24 territories: (1) total area; (2) area of canopy cover of oaks; (3) area of canopy of other trees; (4) area of chaparral; (5) area of other brush; and (6) area of open grassland. These data were used to relate vegetation characteristics to occupied and unoccupied habitats and to the overall quality of territories.

Breeder censuses

The study population of banded breeders was censused periodically to acquire data on survivorship and breeder movements. Censuses occurred in early October, early January, early April, and early July, and pairs were monitored on a weekly basis from mid-March to mid-July in conjunction with nest checks. Each complete census took 10–14 days.

Floater censuses

During 1981–1982 and 1982–1983, monthly surveys were conducted on all territories and unoccupied areas on the study area. In each location the number of floaters (nonterritorial jays) was estimated. Floaters, especially during the nonbreeding season, tended to aggregate and to be vocal, bold, and easily observed. Many were banded, and I remained on an area until most sightings were repeats. In areas with no apparent floaters, I remained at least 1 h, during which I played vocalizations from a tape recorder to attract any jays in the area.

Floater sightings

In the course of the study, floaters were identified by their color bands, and their location was noted. Over 2,196 resightings of 276 color-banded floaters (including jays born on the study area and immigrants) were recorded. These data were used to examine juvenile dispersal, floater associations, floater movements, and the transition from floater to breeder status.

Behavioral observations

Between August 1981 and March 1984, I collected time-activity budgets on territorial breeders. Focal-animal sampling (Altmann 1974) on each individual lasted for 1 to 4 h (mean of 3 h). A composite day for each individual was completed over a one- or two-day period. I made a continuous record of all behaviors, with transitions between behaviors recorded to the nearest 10 s. Each hour was considered an individual sample period, and percentage of time in different activities was calculated as a percentage of time the jay was in view. Particular attention was focused on foraging behavior and method (e.g., leaf gleaning, hawking, caching acorns, recovering acorns), and territorial behavior (e.g., breeder-breeder and breeder-floater interactions). Data were collected every month (mean of 35 h per month) between July 1981 and March 1984, except for January through March and October through November 1983. Because I was able to follow individual floaters for only short periods, I quantified foraging behavior by recording the second foraging movement after initial contact on each individual. This was also done for breeders so that breeder and floater foraging behavior could be compared directly.

Radio-tracking

Floaters were radio-tracked to acquire data on juvenile dispersal, home-range movements, and habitat use. Radio backpacks were glued to the backs of jays and further secured with a harness (5 g total weight). Radio batteries lasted from 4 to 10 weeks. Radios were placed on 16 birds: (1) three juveniles five weeks post-fledging, just prior to dispersal in 1984; (2) two first-year floaters during the winter, 1984–1985; and (3) 11 floaters during the breeding season in 1985 (one adult, 10 first-year jays). Jays were followed for 3-h periods, and locations marked on aerial photographs every 10 min. From observations over one- or two-day periods, composite days were compiled from morning, midday, and evening watches. During the watches, in addition to locations, data were collected on interactions with breeders, other floaters, and foraging behavior. The tagged jays became accustomed to observers and could usually be kept in sight. In all, 618 h of radio-tracking data were collected on tagged jays. I also performed 27 "simultaneous" locations on all of the tagged jays during the breeding season in 1985 to detect grouping.

Food assessment

Scrub-jays eat a wide variety of foods, which makes sampling resources difficult. I settled on several methods to estimate the relative abundance of two important foods: insects during the breeding season, and acorns in the fall. The relative abundance of flying insects was measured with a series of 9 yellow pan traps filled with water and surface tension broken with a drop of liquid dish soap (Southwood 1978). The yellow pans were emptied weekly, and the collected insects classified to order, dried, and weighed (W. Koenig, unpubl. data). Data on relative abundance of ground and grass dwelling insects were provided by P. Williams, who performed weekly sweep-net samples during the breeding season. These samples consisted of 100 sweeps of a butterfly net across an open field (valley grassland community) at the center of the study area. Collected insects were dried and weighed. I attempted to estimate the relative abundance of lepidopteran larvae, the major food of young nestlings (Verbeek 1970; pers. obs.) by examining 1,000 oak leaves weekly (Perrins 1976). Even when the jays were gleaning large numbers of larvae, the only kind I counted in sufficient numbers were those of the California oak moth (*Phryganidia californica*), which is not eaten by jays. The relative abundance of acorns was visually estimated each fall (Carmen et al. 1987, Koenig et al. 1994a). We sampled 250 oaks of five common species. On each tree, two observers counted as many acorns as possible in 15 s and the two counts were combined for "acorns per 30 s." Each tree was also scored on a scale from 0 (no acorns) to 4 (a bumper crop). In addition, four traps were placed under each of two trees of each species to determine the temporal pattern of acorn fall.

FOOD AND FORAGING

Food abundance and foraging behavior have fundamental influences on the social behavior of birds. Verbeek (1970) and Brown (1974) hypothesized that the differences in social behavior in jays and other corvids were primarily the result of the various exploitation patterns resulting from patterns of food abundance and foraging behavior. A distinct and important behavior that all jays share is food caching; numerous species of birds, including *Aphelocoma* jays, cache food (Smith and Reichman 1984, Vander Wall 1990), primarily seeds, and studies have shown that differences in annual seed abundance affect the timing of reproduction, reproductive success, and behavior of seed caching birds (Perrins 1970, Vander Wall and Balda 1977, van Balen 1980, Koenig and Mumme 1987). In this section, I examine how food abundance and foraging behaviors of scrub-jays varied seasonally and annually, and how this variation affected their social behavior.

SEASONAL ABUNDANCE OF FOOD

Many studies at Hastings have measured food resources thought to be important to several avian species. These data give a broad picture of average seasonal variation in scrub-jays' food availability. Early in the breeding season, jays forage predominantly by leaf-gleaning when oak-leaf arthropods are available, especially on live oaks (*Q. agrifolia*; Fig. 4a). Grasshoppers are important later in spring and early summer, and their abundance shows an abrupt rise in May and decline in July in most years (Fig. 4b). During this study, other research workers and I quantified the relative abundance of ground-dwelling invertebrates (P. Williams, unpubl. data; Fig. 4c) and flying insects (W. Koenig, unpubl. data; Fig. 4d). These data indicate that invertebrate abundance is typically low in March through mid-April, increases sharply in late April, and peaks in May and early June. By August, with the onset of the late summer dry period, all samples of invertebrate abundance decrease.

Although seasonal buildup and total relative abundance of invertebrates differed among years, variation in acorn abundance was even greater. In a 12-year study of acorn production patterns at the Hastings Reservation, the oak species tended to produce acorns asynchronously, with crop failures occurring every 4 to 7 years; the probability of an poor acorn crop was directly related to the number of oak species in the area (Carmen et al. 1987, Koenig et al. 1994b). Between 1971 and 1987 three crops failed; two (1973 and 1983) were localized and affected lower elevations of the Reservation (MacRoberts and MacRoberts 1976, Carmen et al. 1987), one in 1978 was extensive (Koenig and Mumme 1987). Over the study period, acorn production was good in four years and poor in one (1983, Fig. 5). In the poor year, however, acorns were abundant within 3 km of the study area.

Another important factor in acorn availability is the length of time acorns are retained on the trees, being greatest in *Q. agrifolia* (Fig. 6). Once acorns fall they are rapidly lost to acorn consumers; in contrast, those on the tree are available to just a few seed eaters, and therefore represent a valuable and long lasting food resource for jays, both for immediate consumption and for caching.

SEASONAL FORAGING BEHAVIOR OF BREEDERS AND FLOATERS

Foraging of breeders

A total of 2,456 foraging observations on territorial jays (minimum of 100 observations in any month) were recorded between July 1981 and December 1982, years with good acorn crops. Foraging activity was expressed as a proportion of all observations, with observations from the same month in different years pooled (Fig. 7). Beginning in August and continuing through February, acorns eaten directly off the tree or from the ground ranged from 16% of all recorded foraging events in February to 31% in October. Jays began storing acorns and, to a lesser degree insects, worms, and other foods, in large numbers in September (25% of all foraging activity), and continued to do so into March

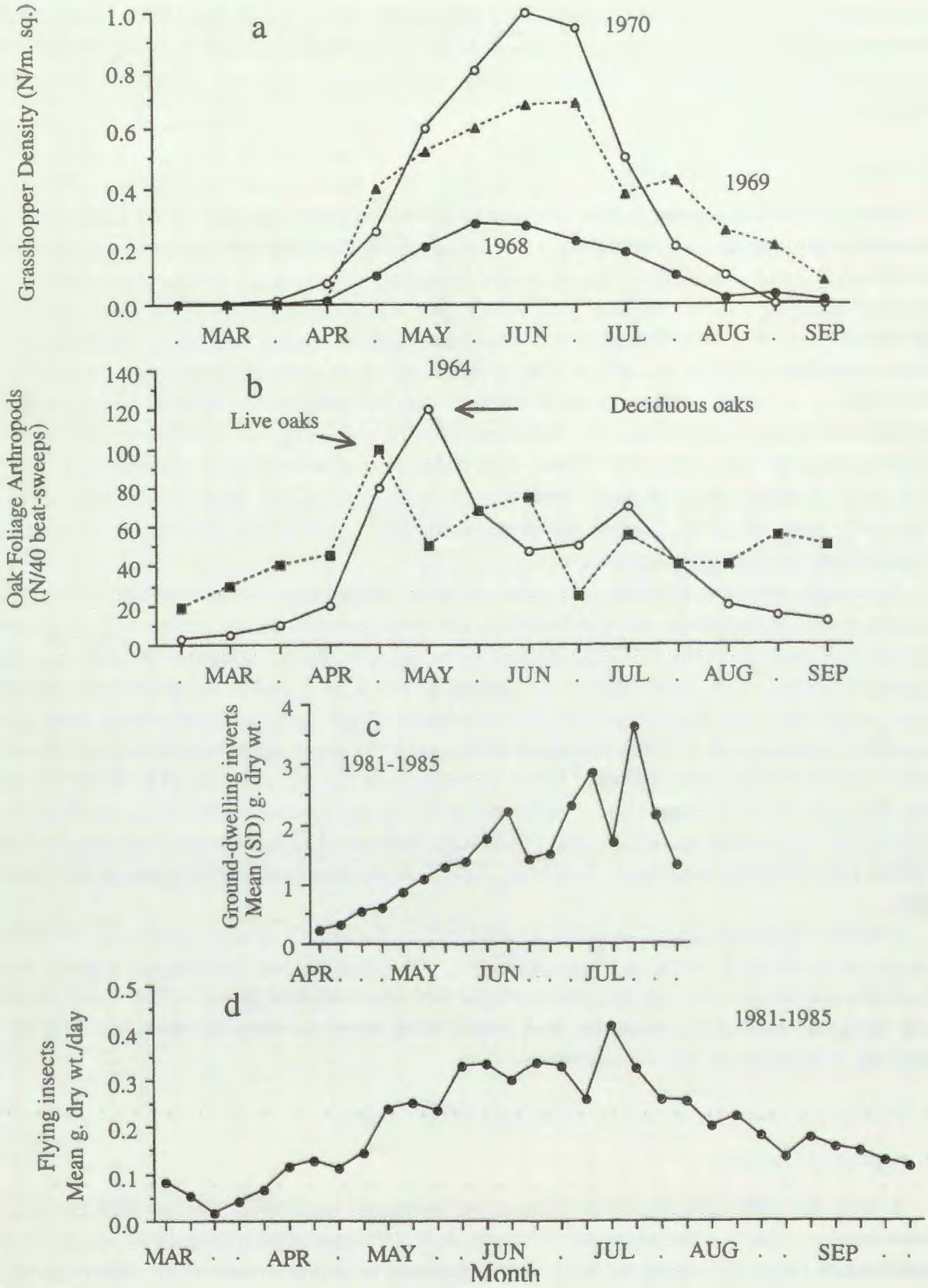

FIGURE 4. Relative abundance and seasonality of invertebrates at the Hastings Reservation: a) grasshopper density 1968–1970 (Verbeek 1970); b) oak-foliage arthropods from beat-sweep samples in 1964 (Root 1967); c) ground-dwelling invertebrates from sweep-net samples 1981–1985 (P. Williams, unpubl. data); and d) flying invertebrates from yellow-pan catch traps, 1981–1985 (W. Koenig, unpubl. data).

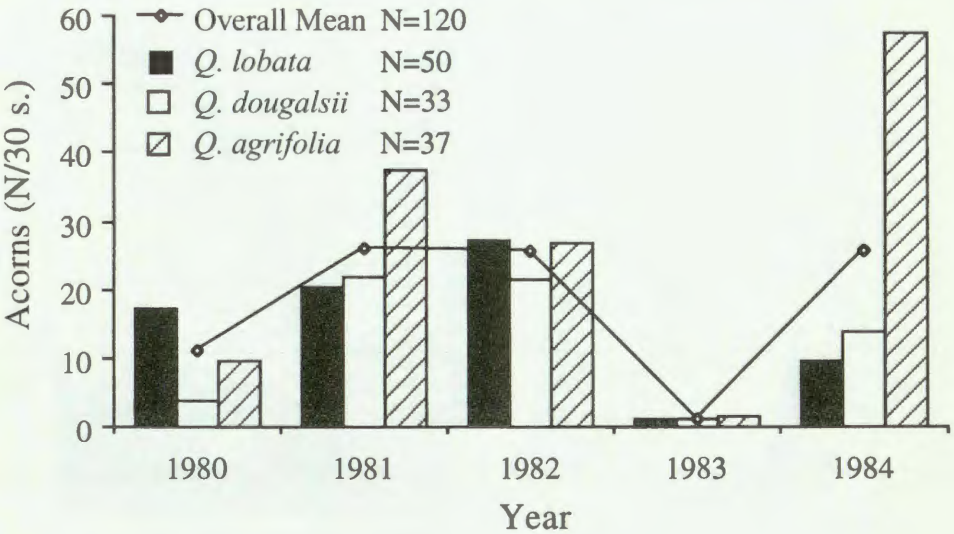

FIGURE 5. Relative abundance (30-s counts) of acorns produced by the three common species of oaks on the scrub-jay study area from 1980–1984. The line indicates overall mean for the three oak species.

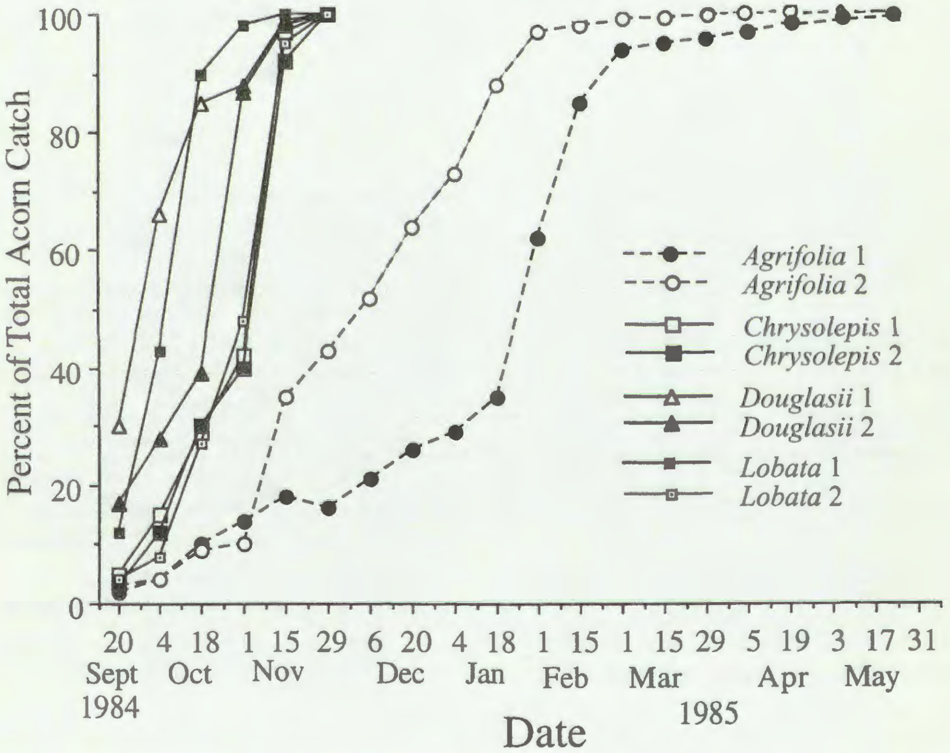

FIGURE 6. Seasonal pattern of acorn fall for two individuals each of four oak species shown as the cumulative percentage of total fall. Data are from acorns collected in acorn traps on a weekly basis, with four traps under two trees of each species.

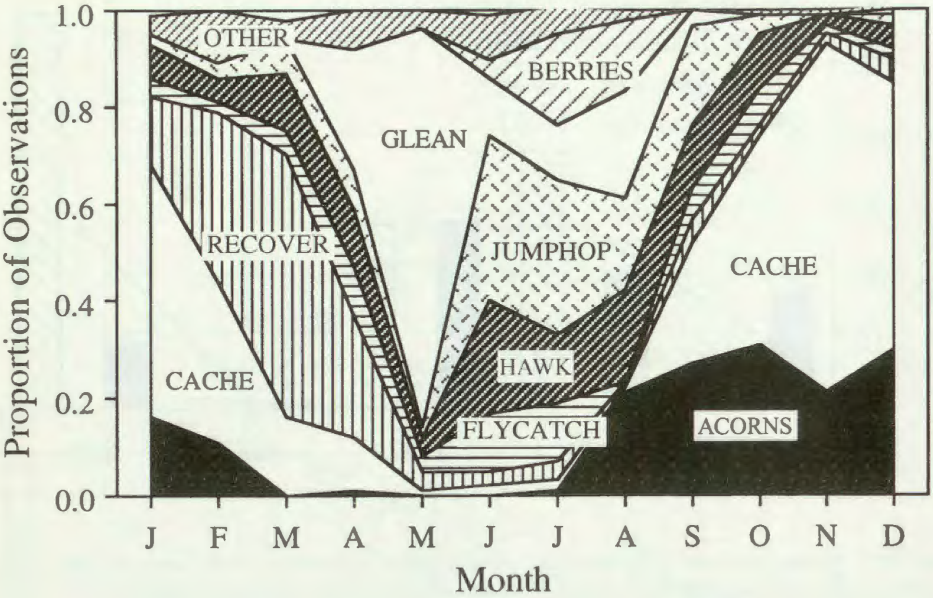

FIGURE 7. Seasonal change in foraging activities of territorial jays over the year expressed as a proportion of all foraging activity (see text for explanation).

(16%). Jays scatterhoarded intact acorns in the ground on their territories; perishable foods (e.g., partially eaten acorns, insects, earthworms, parts of animals) were cached off the ground in lichens and bark. The vast majority of food stored (>90%) was acorns, but jays might store any temporarily abundant food, such as swarming ants and bees. Jays did not recover much stored food until January (14% of foraging activities), but in February and March recovering stored food comprised the better part of foraging effort (Fig. 7). Acorns made up the vast majority of food items recovered during this period.

In April, jays shifted to invertebrate foods, primarily by gleaning lepidopteran larvae from oak leaves; by mid-April and May this constituted 79% of all foraging events, suggesting that such larvae are abundant earlier than other invertebrate foods (see Fig. 4). Lepidopteran larvae, which have a relatively high protein content compared to plant material, constitute approximately 60% of the nestling diet (Verbeek 1970). Jays recovered cached acorns even in May and fed acorns to their older nestlings (Verbeek 1970; pers. obs.). Acorns contain mostly carbohydrates and moderate amounts of lipids (Wainio and Forbes 1941, Ofcarcik and Burns 1971), but high tannin levels (Ofcarcik and Burns 1971), and their detrimental effects on growth rate (Marquardt and Ward 1979) and bone development (Elkin et al. 1978) may make them unsuitable for younger nestlings.

By June and through July, jays used several different foraging methods, such as hawking (flying from low perches to capture insects on the ground), jump-hopping (hopping through the grass and leaf-litter, scaring up insects), and flycatching (aerial sallies), reflecting the wider array of foods available to them.

Acorn use, foraging behavior, and time budgets

I studied time-budgets of territorial jays from August 1981 through February 1984. This period included two years of good acorn production (1981 and 1982) and one (1983) of local failure. Time budgets from April through July were similar in all years, and breeders spent an average of 71% of all daylight hours foraging (Fig. 8). This sample excludes incubating and brooding females as well as breeders without eggs or nestlings. The high percentage of foraging time, therefore, reflects the high demands of the male foraging for himself and his incubating mate, and both adults foraging for young. In good years, jays reduced their foraging time beginning in August, when acorns became available and began to make up a large part of the diet, and from August through March spent only 36% of the day foraging. In contrast, during the poor acorn year, jays foraged significantly longer, averaging 64% of daylight hours in August and December through February (Fig. 8).

In good years, jays spent an average of 70% of their foraging time (or 25% of total time) from October through March looking for, eating, and caching acorns, compared to less than 10% in 1983–1984 (Fig. 9). Estimated from the time-budget data, each territorial jay cached 5,000 to 7,000 acorns in a good acorn year and spent 16% of foraging time in January, 30.4% in February, and 43% in March recovering and eating them (Fig. 10). In the poor year jays spent less than 1.2% of their foraging time in January and February recovering acorns, and turned to less profitable foods, such as *Avena* grass seeds, and other foraging methods, such as searching through leaf litter, which has been shown to be energetically costly in Black-billed Magpies (*Pica hudsonia*; Mugaas and King 1981). Cached food may be crucial as the breeding season approaches. In good years, scrub-jays laid as early as 15 March, well before most invertebrates were abundant (see Fig. 4). Stored food may be specially important for incubating females that spent long periods on the nest. In another corvid, the Northwestern Crow (*Corvus caurinus*), James and Verbeek (1984) found that without cached food incubating females were unable to maintain normal incubation periods and spent long periods foraging.

Effect of acorn supplementation

Beginning in December 1983 and continuing through March following the acorn crop failure, I experimentally fed four pairs of jays 200 acorns per week. The acorns were placed on feeding platforms at the center of each territory, and the jays removed and stored them within 30 min. The time budgets of these jays closely matched those of jays during the good acorn years and were significantly different compared to unfed jays. For example, foraging time in January was 37% of total time for jays in the good years, and in the poor year 39% for experimentals and 62% for unfed jays; jays spent significantly more time foraging during the poor year (Kruskal-Wallis ANOVA, $df = 2$, $\chi^2 = 10.2$, $P < 0.01$). The difference was due to the lack of readily available stored food; jays in good years spent 15.7% of their foraging time in January recovering stored acorns compared to 15.3% for experimentally fed jays and 1.2% for unfed jays in the poor year. These differences are probably even more pronounced in March, when in good years jays spent only 25% of their total time foraging and 43% of that foraging time recovering stored acorns. Unfortunately, I did not collect time budget data in March of the poor acorn year (1983).

Foraging of floaters

The foraging behavior of floaters was sampled from June 1981 through December 1982 (total $N = 2987$, minimum of 129 per month). This sample includes only juveniles in June and juveniles and older floaters in other months. No data were collected in May 1982 because all floaters disappeared.

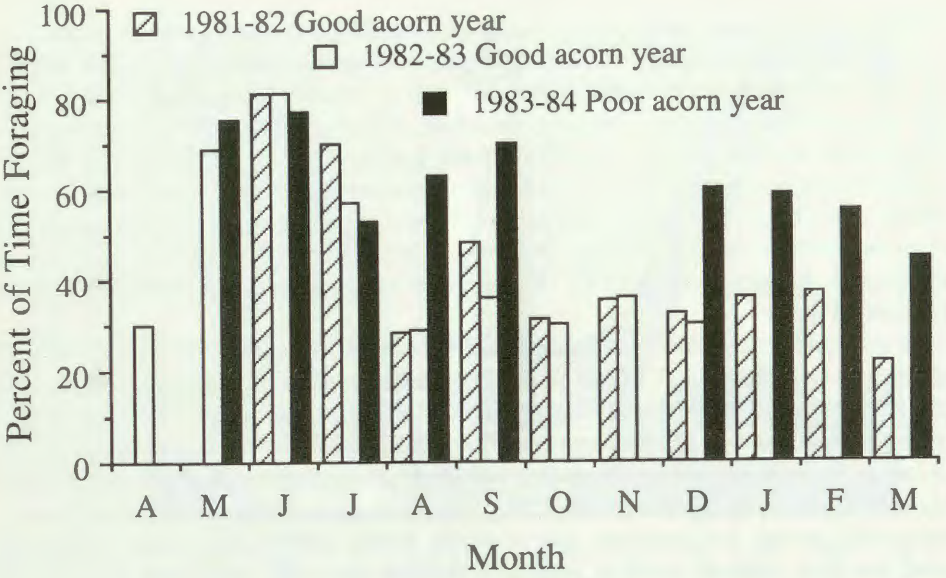

FIGURE 8. Percentage of time territorial scrub-jays spent foraging in two good acorn years and in one poor acorn year. Months without bars indicate no data were taken. Scrub-jays significantly increased their foraging time from August through March in the poor acorn year (Mann-Whitney U, $P < 0.05$ for each paired month). Total sample = 875 h, with a minimum of 18 h per month.

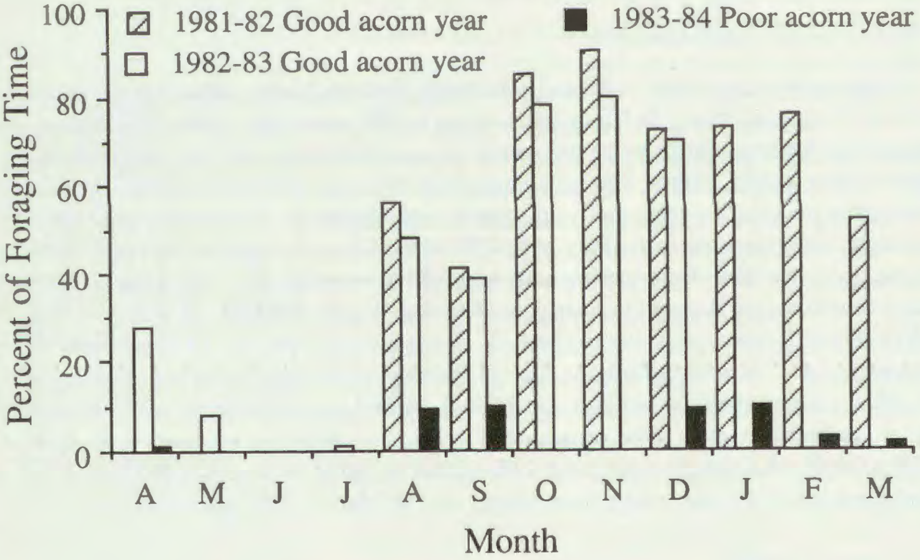

FIGURE 9. Percentage of foraging time territorial scrub-jays spent looking for, eating, caching, and recovering stored acorns in two good acorn years and a poor acorn year. Months without bars indicate no data were taken.

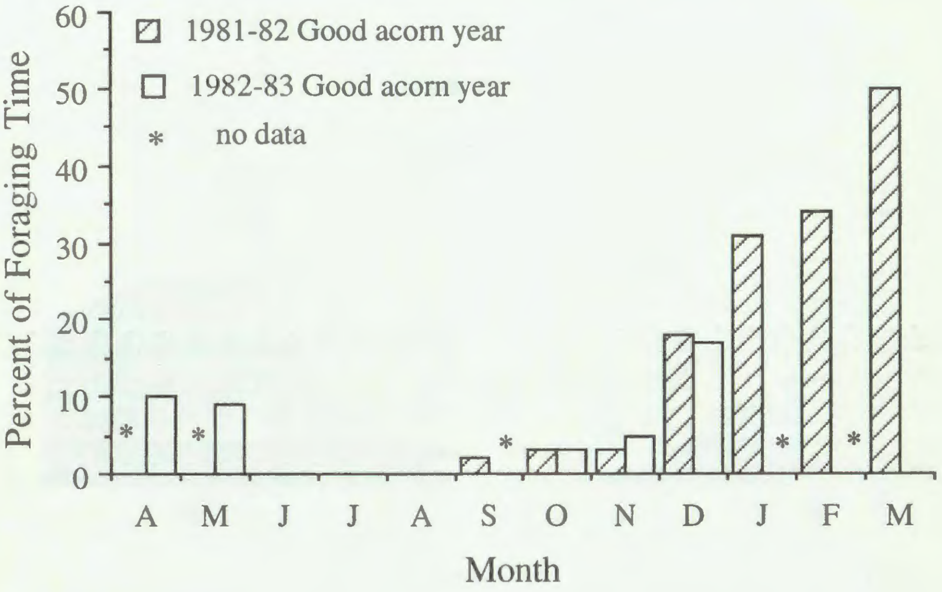

FIGURE 10. Percentage of foraging time territorial scrub-jays spent recovering and eating cached acorns and other cached food during the good acorn years (see text for explanation). Months without bars indicate no data were taken.

The foraging behavior of territorial adults and floaters is similar throughout the year (compare Figs. 7 and 11). The major difference is that young juveniles make heavy use of berries (blue elderberry, *Sambucus caerulea,* and fuschia-flowered gooseberry, *Ribes speciosum*), to which they directed 19% and 52% of total foraging activity in June and July, respectively. Floaters used acorns, stored food, and recovered food in nearly the same proportion as territorial jays and thus seem to be equally dependent on acorns. In 1982 and 1983, floaters disappeared from the study area beginning in April at about the time that territorial jays shifted from stored acorns to lepidopteran larvae. In 1985, when floaters did remain on the study area during the breeding season, foraging behavior of breeders and floaters was identical.

TERRITORIES AND TERRITORIAL BEHAVIOR

Aphelocoma jays are permanently territorial, and those unable to secure a territory are unable to breed. In cooperative species, nonbreeders delay dispersal, live in family groups on their natal territories, and help. In noncooperative populations, nonbreeders float. Differences in territorial behavior, habitat and habitat tolerance, variation in territory quality, and the degree of habitat saturation determine, in large part, the dispersal options available to newly independent young and older nonbreeders, and therefore play crucial roles in selecting for delayed or early dispersal.

TERRITORIAL BEHAVIOR

Scrub-jay breeders at Hastings rarely left their territories. In several thousand hours of field work I resighted 276 color-banded floaters 2,196 times, but I recorded breeders off their territories only 59 times. Of these, 33 (56%) occurred during the year of an acorn

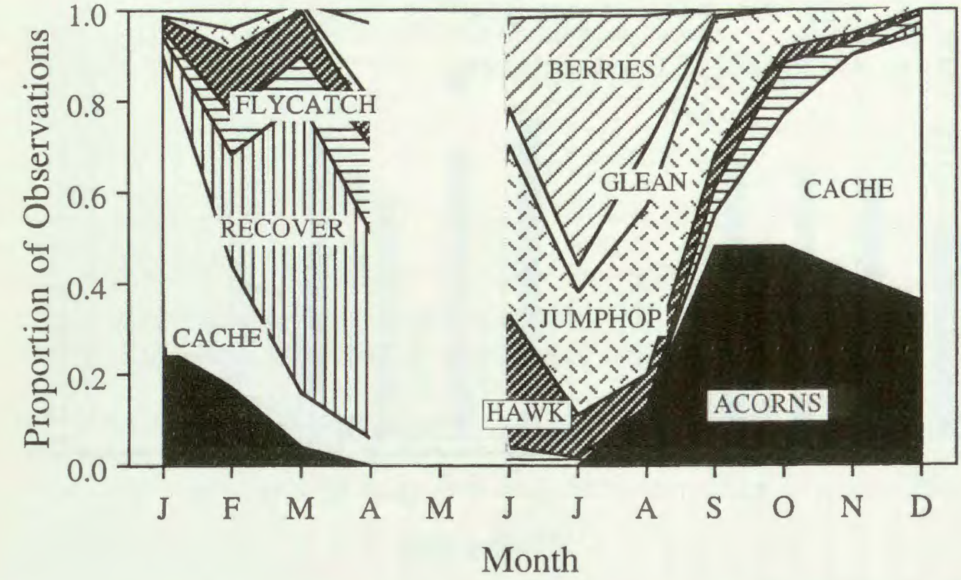

FIGURE 11. Seasonal change in foraging activities of nonbreeding floater scrub-jays, primarily first-year birds, over the year expressed as a proportion of all foraging activity (see text for explanation).

crop failure when jays abandoned their territories. Of the remaining 26, five were at water sources during July and August (see also Williams and Koenig 1980), 10 were at acorn-laden oaks in late winter, six were in large aggregations of floaters, three were in "power struggles" during mate replacements, one was in an unoccupied area with its fledglings, and three were off their territories for no discernable reason.

To quantify breeder movements and survivorship, I made quarterly surveys (see METHODS). Excluding the year of the acorn crop failure, only one individual (CR male), absent from its territory and counted as dead, later returned. In contrast, in 1983–1984 when the acorn crop failed, breeders began leaving in August. At first these movements were short and brief, with pairs joining into small groups in unoccupied habitat. Later in August up to 15 breeders and several nonbreeders formed loose groups that moved through both occupied and unoccupied areas, as breeders began abandoning their territories. By December 1983, 57% (59 of 103) of the banded breeders could not be located, although 64% (38) subsequently returned, the majority in late March and early April. Males and females were equally likely to abandon their territories in the poor acorn year; of the 103 banded breeders present in summer of 1983 (55 males and 48 females), 30 males and 29 females were not found on their territories in December, and 20 males and 18 females later returned. Where acorns were available at higher elevations, breeders did not abandon their territories and floaters were common (pers. obs.). I sighted one of the banded absentee breeders in such an area.

Features of territorial interactions

Breeder-breeder territorial interactions and agonistic "*wek*" vocalizations in 1981–1982 are shown in Figure 12. *Wek* vocalizations were fewest in July and August, and most numerous in September and October when jays began harvesting large numbers of acorns and intrusions by floaters were common, whereas border interactions remained uniform over the year. Because scrub-jays remain aggressive toward their neighbors throughout the year, it appears that they are always at risk of losing all or part of their territories.

I emphasize that only territorial neighbors were evicted because unfamiliar territorial jays, like all floaters, were tolerated, at least during the nonbreeding season. For example, during August 1983, when some breeders abandoned their territories, male MB was observed for several hours over two consecutive days on the BURNT territory, 1.3 km distant. He was clearly visible to the residents, often foraging within 3 m, but was not challenged. Yet territorial neighbors, and even banded, known breeders from two territories distant, were quickly chased off.

Territorial interactions included vocalizations at borders, flight displays, and chases. These could be triggered simply by the approach of neighbors to a shared boundary as well as by active intrusion. Responses by the occupants could include any of the following: vocalization and body "pumping" on an exposed perch, flying to the border, "*wek*" vocalizations, "rattle" vocalizations (females only), display flights, supplants, and chases. Intrusions by neighbors were consistently met with agonistic behavior, followed by hasty retreat of the trespassers. Border disputes lasted from seconds to more than 30 min, and were substantially longer when new individuals were attempting to become established as breeders on adjacent territories. Neighboring pairs seemed to have specific areas where border disputes and territorial interactions were common and females frequently left the nest to participate.

Males were generally more aggressive, instigating the majority of interactions and continuing them longer. Territorial females were dominant over all other jays except their mates, including intruding neighboring males and adult male nonbreeding floaters.

Upon the death of a breeder, either sex was able to defend its territory prior to and

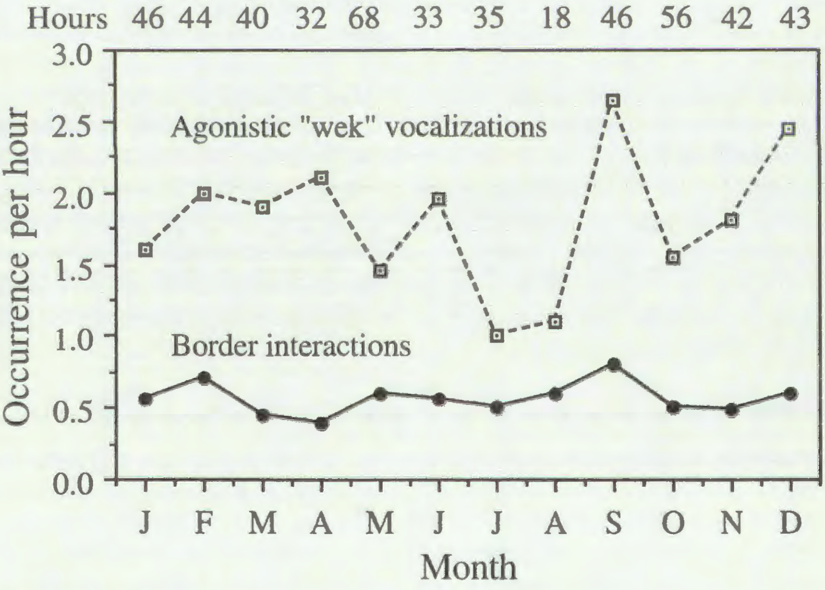

FIGURE 12. Rate of border interactions and aggressive "*wek*" vocalizations territorial scrub-jays directed towards territory neighbors. Numbers at top of figure are hours of observation of territorial scrub-jays.

during mate replacement, and both males and females quickly acquired new mates from the floater pool. Mate replacement varied from a quiet and increasingly close association between a resident and a new jay, with mutual courtship feeding over a several-day period leading to a closely bonded pair, to highly charged contests involving floaters, which resembled the "power struggles" described in the Acorn Woodpecker (*Melanerpes formicivorus*; Koenig 1981). Mate replacement could be extremely rapid, and I recorded most replacements after the fact. I witnessed six of the "quiet," and probably more common, replacements, and five "power struggles." The latter occurred in winter or early spring, when large numbers of floaters were nearby; up to 20 jays, primarily floaters, engaged in loud vocalizations, constant flights, including slow undulating display flights, chasing, contact, and even grappling to the ground. The participants, including the widowed bird, could carry on their dispute far from the territory of interest, and when they passed through other territories the residents also made undulating display flights, vocalized, and participated in the group melee. The nearly constant activity in these "power struggles" could last over two days, until a floater filled the breeding vacancy.

The pair bond and separation

Scrub-jays generally pair for life. I recorded 12 separations in 182 breeding-pair years (6.6%). However, if the sample is restricted to pairs in which both members were alive at the beginning of the next breeding season (a more critical measure of pair fidelity because it excludes mortality as a causative factor; Woolfenden and Fitzpatrick 1984), the separation index was 11.2%.

Of the 12 separations, five occurred during the fall or winter of the acorn crop failure, or early the following spring when birds returned to their territories. Some of the fall separations may really be territory abandonment. For example, female 2400R left her territory (and mate) in fall, and returned to the study area in April and paired with a different male; in her absence her former mate had paired with a neighboring territorial female. Excluding those observed in 1983–1984 leaves seven separations in 87 pair-years (8.0%).

Of these seven separations, five involved either: (1) adult, experienced breeders divorcing inexperienced or first-year mates to pair with experienced, established mates (two cases); (2) jays on intermittently occupied territories moving to adjacent permanently occupied territories (two cases); and (3) separation from an unsuccessful breeder (one case). Of the remaining two separations, one pair split their former territory and each acquired a new mate. In the other, a male separated from his mate and moved to and paired with a newly widowed female on the adjacent territory. Such divorces and movements may increase the reproductive success of the divorcer, as Baeyens (1981) showed for Eurasian Magpies (*Pica pica*).

Breeders and offspring

Prior to eight weeks postfledging, breeders actively fed young, and offspring remained in close associations with their parents. Offspring begged and followed adults, and near the end of the association males occasionally threatened or supplanted begging young. After eight weeks the young began wandering off, unaccompanied by parents, although some were fed up to 12 weeks after fledging. Territorial jays did not evict offspring (or unrelated floaters) from their territories until the onset of the following breeding season. In 875 h of time-budget observations (1981–1983) and 240 h following radio-tagged fledglings and juveniles (1985), I never observed parents in full chase of offspring in fall and winter; but in two interactions between breeders and their yearling offspring in May, the offspring were chased away. In approximately 50 h of nest watches, no offspring or other jays other than the pair were observed near nests or fledglings.

Breeders and floaters

The tolerance of independent offspring by breeders also extended to unrelated nonbreeders. As early as June, a few juveniles began wandering from their natal territories; these were ignored by other breeders, even those with young fledglings. By early July, loose aggregations of juvenile floaters were tolerated by breeders, who were still aggressive toward territorial neighbors, and from late July through April adult nonbreeding floaters also were tolerated.

The monthly rate of different types of aggressive interactions that breeders directed at nonbreeders (Table 1) was determined from time-budget observations, during which I estimated the number of floaters on the focal jay's territory every 10 to 20 min. As virtually all floaters disappeared from the study area in May–June of both 1982 and 1983, I have few data from the breeding season. However, during the nonbreeding season breeders used mostly low-level aggressive behaviors, such as "supplants," and few high-level aggressive behaviors such as "chases" or "chases off the territory." Most of the few interactions were a result of floaters either approaching too closely (< 1 m), or storing food in the same locations as the residents. Although floaters on territories tended to aggregate into loose groups of up to 20, even singles were tolerated or ignored during the nonbreeding season. My observations indicated that breeders preferentially supplanted unfamiliar floaters and, in effect, established dominance at first meeting, indicating that tolerance by breeders is based on subservient behavior of floaters. Floaters that remained on one or two territories for several months were rarely bothered.

Tolerance decreased as nest building began, and nests with eggs were defended. However, in every year floaters could be found on territories throughout April, even though the mean first egg date was 6 April. Although their disappearance in May coincided with increased aggression when breeders switched from supplants to long chases and chases off the territory (Fig. 13), many places existed on the study area where floaters could have settled at least temporarily, including some temporarily unoccupied

TABLE 1. TYPES AND FREQUENCIES OF AGGRESSIVE BEHAVIORS DIRECTED AT FLOATERS BY BREEDERS BY MONTH

Month	Hours observed	Floater-hours (FH)[a]	Supplant		Chase		Chase off	
			N	N/FH	N	N/FH	N	N/FH
Jan	46	444	94	0.21	41	0.0	3	0.01
Feb	44	394	99	0.25	26	0.07	1	0.02
Mar	40	242	90	0.37	23	0.09	4	0.02
April	32	105	38	0.36	15	0.14	12	0.12
May	68	<1	6	—	8	—	5	—
June	33	<<1	0	—	0	—	4	—
July	35	148	11	0.07	3	0.02	0	0
Aug	18	141	21	0.14	9	0.06	0	0
Sept	46	219	63	0.29	37	0.17	3	0.01
Oct	56	213	100	0.47	33	0.15	4	0.02
Nov	42	343	141	0.41	59	0.17	4	0.01
Dec	43	383	136	0.36	29	0.08	0	0

[a] FH = floater-hour: mean number of floaters on the territory during each observation hour, summed over the total number of observation hours.

territories. In addition, large aggregations of floaters disappeared from temporarily unoccupied territories where they were free from disturbance by breeders.

In May and June of most years, floaters were evicted from territories. In 1985, however, many floaters remained on the study area and breeders were more tolerant (interactions not quantified) as long as they remained away from the nests, territory centers, and the residents. This is similar to the interactions between Florida Scrub-Jay breeders and helpers prior to when helpers feed the nestlings (G. Woolfenden, pers. comm.). This extended period of tolerance occurred in a year when acorns remained available on the oaks well into May. During May and June 1985, 93% of 914 locations of 11 radio-collared floaters occurred on territories, mostly near the margins.

Why do breeders defend against neighbors during the nonbreeding season but tolerate floaters? First, a small investment in territorial defense throughout the year prevents neighbors from usurping territory space, a real threat as shown during the acorn crop failure; in at least three cases jays that abandoned their territories failed to recoup them the following spring because neighboring pairs that remained took them over. Second, tolerance of floaters suggests that exclusivity of territorial space is not critical during the nonbreeding season, but floaters are easily expelled at the onset of the breeding season through the dominance established earlier.

TERRITORY ACQUISITION

To gain a territory and breeding status, juveniles and older floaters have three options: (1) to pair with an established breeder upon the death of its mate; (2) to pair with another floater and establish a territory de novo; or (3) to pair and establish a territory in an unoccupied area. Option 1 was used by 62 of 90 (69%) jays, options 2 and 3 by 15% each.

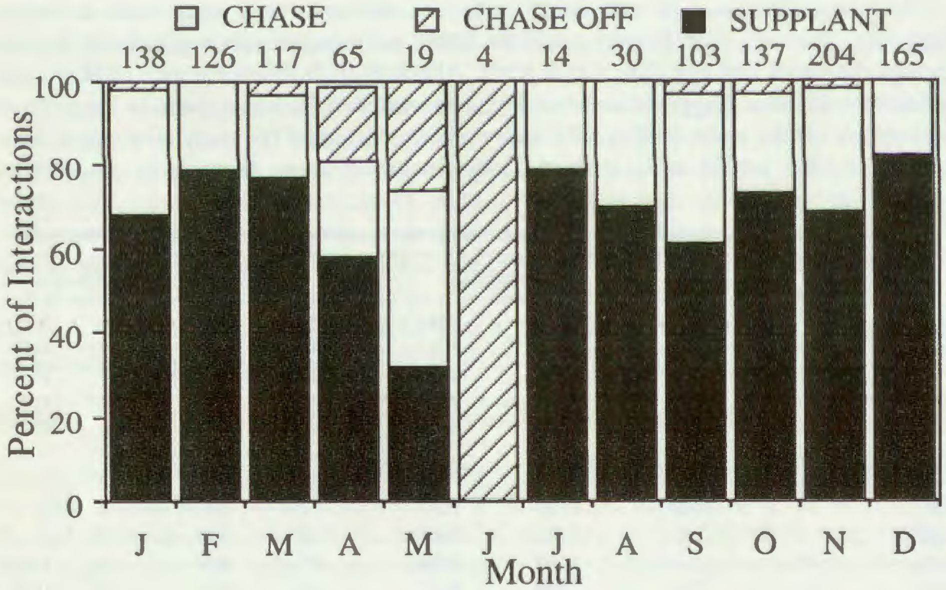

FIGURE 13. Seasonal change in aggressive behaviors breeders directed at floaters. Numbers above bars are total number of interactions recorded in each month.

First-year jays acquired territories almost exclusively by pairing with established adults. In five years (215 breeding-pair years), only one pair of first-year jays successfully defended a territory throughout a breeding season. In five other cases, first-year males established temporary, small, and intermittently defended "pseudo-territories" that overlapped portions of two or three adjacent territories. The males paired with first-year females and three pairs built nests, but never laid eggs. The pairs were dominant over floaters but not over the neighboring, true territory holders. In every case by early May, the females disappeared, followed shortly by the males. One of the five males was the offspring of an adjacent territorial pair; the other four were banded as juveniles and were not natal to the study area. Four of the five males returned to the same area the following autumn and reestablished their pseudo-territories and paired with a first-year female. Again the pairs failed to lay and defend or remain on their territories through May. Three of these five males returned and eventually acquired true territories, two as three-year olds and one at age four. In two cases, the territories claimed included the original pseudo-territory.

The age at which true territories are acquired is a crucial demographic variable. While a complete analysis is given below, here I present data for calculating this variable. The sample includes novice jays filling territories using all three options listed above. On established territories only replacements of banded breeders were included. Figure 14a gives the age distribution of these jays, separating exact and minimum ages. In Figure 14b, the data are presented with jays in the minimum age classes placed in the distribution in proportion to the exact age jays. For example, of the 14 females in the 2+ age category in Fig. 14a, 66% were placed in the age 2 category and 34% in the age 3 category in Fig. 14b, representing the proportion of two- and three-year old females in the sample whose age was known exactly. This underestimates the age of jays filling the vacancies, but provides conservative figures for later calculations.

Many jays did not acquire a territory for several years and females filled vacancies at a younger age than males. But are these jays really novice territory holders? One complication is that breeders occasionally shift territories, most often a result of death of a mate or divorce, which could result in misclassifying a new arrival as a novice. If one counts unbanded breeders that moved into the study area as first-time territory holders, the age distribution may be artificially shifted to older age classes. Of 57 vacancies filled by jays ≥2 years old (thus excluding yearlings), breeders filled 20, of which 15 were on adjacent territories; 11 of the 20 occurred during the acorn crop failure. Of the 20 vacancies filled by established breeders, 15 (75%) moved to an adjoining territory. Three long-distance movements occurred during the acorn crop failure; the longest one was three intervening territories. Excluding the 11 cases during the crop failure, 88% of movements by breeders were to adjacent territories, and 100% within only one intervening territory. Throughout the study, I periodically searched nearby locations, including at least one territory beyond the study area. Only one former breeder was found, a male that had disappeared during the acorn crop failure. If movement by breeders onto the study area is as rare as movement off, the bias imposed by possible long-distance movement of breeders in calculating the age at onset of breeding is negligible.

Another method for determining age of first breeding is by following the fate of banded nestlings. Of those banded as nestlings in 1981–1983 that eventually acquired territories on the study area (N = 12), 42% did so their first year, 33% their second, and 25% their third (Table 2).

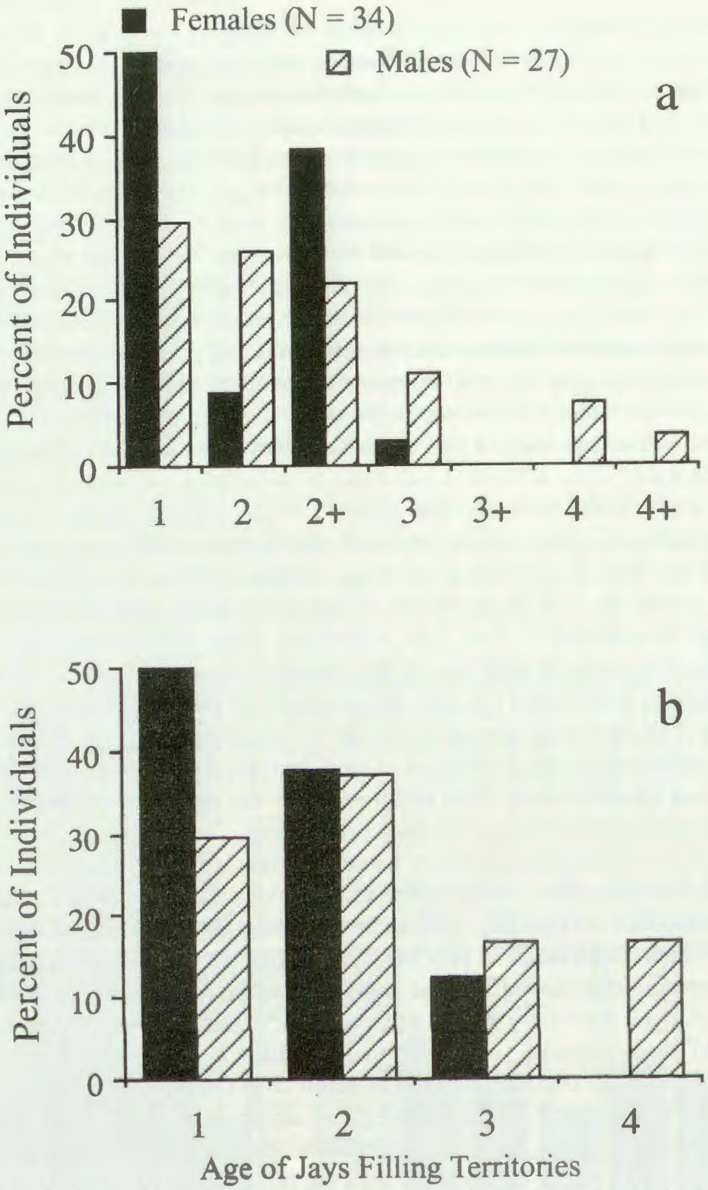

FIGURE 14. Age distribution of first-time breeders filling territory vacancies: a) age distribution includes exact and minimum ages; b) age distribution with minimum age scrub-jays included in age categories in proportion to the distribution of exact age scrub-jays filling territories.

TERRITORY CHARACTERISTICS

Between March and August over five breeding seasons I mapped 194 territories and determined territory size; maps were made in the period from nest building through dispersal of young. In 1981 the study area encompassed 83 ha and I mapped 23 territories. From 1982–1985 it was 173 ha and held from 40 (1984) to 53 (1982) territories (Figs. 15–19).

TABLE 2. AGE AT WHICH SCRUB-JAYS HATCHED ON THE STUDY AREA (1981–1983) FIRST ACQUIRED A TERRITORY

Year	Number	Number acquiring breeding status in					
hatched	independent	1982	1983	1984	1985	Total	Unaccounted
1981	33	3	1	1	0	5	28
1982	54	—	2	3	2	7	47
1983	23	—	—	0	1	1	22
Total	110					13	97

Jays breeding at age (year)	N	(%)	Males	Females
1	5	(38%)	2	3
2	5	(38%)	2	3
3	3	(23%)	3	0

Territory size and population density

The 194 territories averaged 2.53 ha, and ranged from 0.66 to 6.5 ha. Average territory sizes were smaller in 1981 through 1983 (range 2.16–2.46 ha), increased significantly in 1984 (3.18 ha), and then decreased significantly in 1985 (2.64 ha; ANOVA, $F = 5.62$, df = 5, 205, $P < 0.001$; Fisher's LSD test, $P < 0.05$; Table 3).

Breeder density ranged from 9.2 pairs/40 ha in 1984 to 12.2 pairs/40 ha in 1982 (Table 3). Mean territory size was inversely related to breeder population density (Fig. 20). The relative stability in both the number of territories and territory size in the first three years of the study contrasts with 1984 (after the acorn crop failure) when many territories were abandoned and the number of territories decreased 20% and mean territory size held by breeders increased 57% (Table 3). In 1985, five new territories were established and the average size decreased 17%. Despite this fluctuation, the area actually covered by territories remained essentially unchanged at 60 to 66% throughout the study.

Habitat features: habitat suitability and territory quality

Despite the change in breeder density and number of territories, four habitat types were consistently avoided: (1) dense mixed hardwood forest; (2) coast range blue oak foothill woodland; (3) large unbroken areas of chaparral; and (4) sparse coast valley oak foothill woodland. Jays whose territories included portions of these habitats did use adjacent areas of chaparral, blue oak woodland, or oak savannah on occasion, but rarely mixed hardwood, open grassland, and oak savannah. Comparisons of vegetation attributes between scrub-jay territories and the study area as a whole, unoccupied areas only, and each of the four habitat-types scrub-jays avoid, revealed that preferred habitat consists of patches with intermediate oak density and canopy cover, interspersed with

TABLE 3. STUDY AREA SIZE, TERRITORY SIZE, BREEDER DENSITY, AND AREA OCCUPIED (HA), 1981–1985

Year	Study area (ha)	Number of territories	Mean territory size (ha)	Pairs/40 ha	Area occupied, ha (%)
1981	83	23	2.46	11.1	—[a]
1982	173	53	2.16	12.2	103.6 (60%)
1983	173	50	2.37	11.5	113.6 (66%)
1984	173	40	3.18	9.2	114.3 (66%)
1985	173	45	2.64	10.4	113.5 (65%)
Mean ± SD:			2.59 ± 0.4	10.9 ± 1.1	111.3 ± 5.1

[a] Area occupied could not be accurately calculated for 1981.

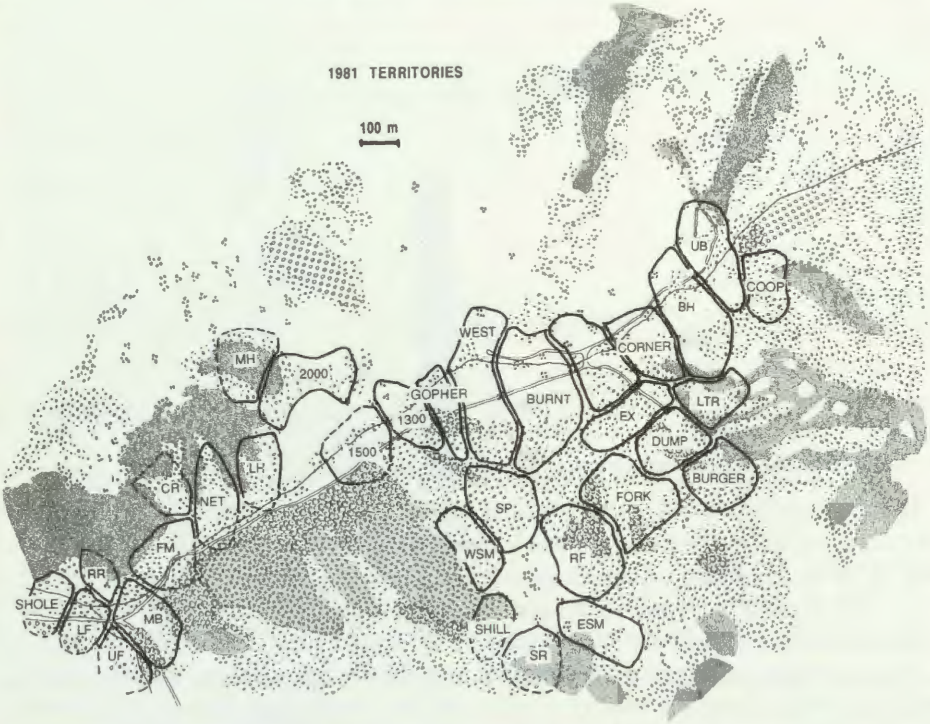

FIGURE 15. Location of scrub-jay territories in 1981. Vegetation key as in Figure 2.

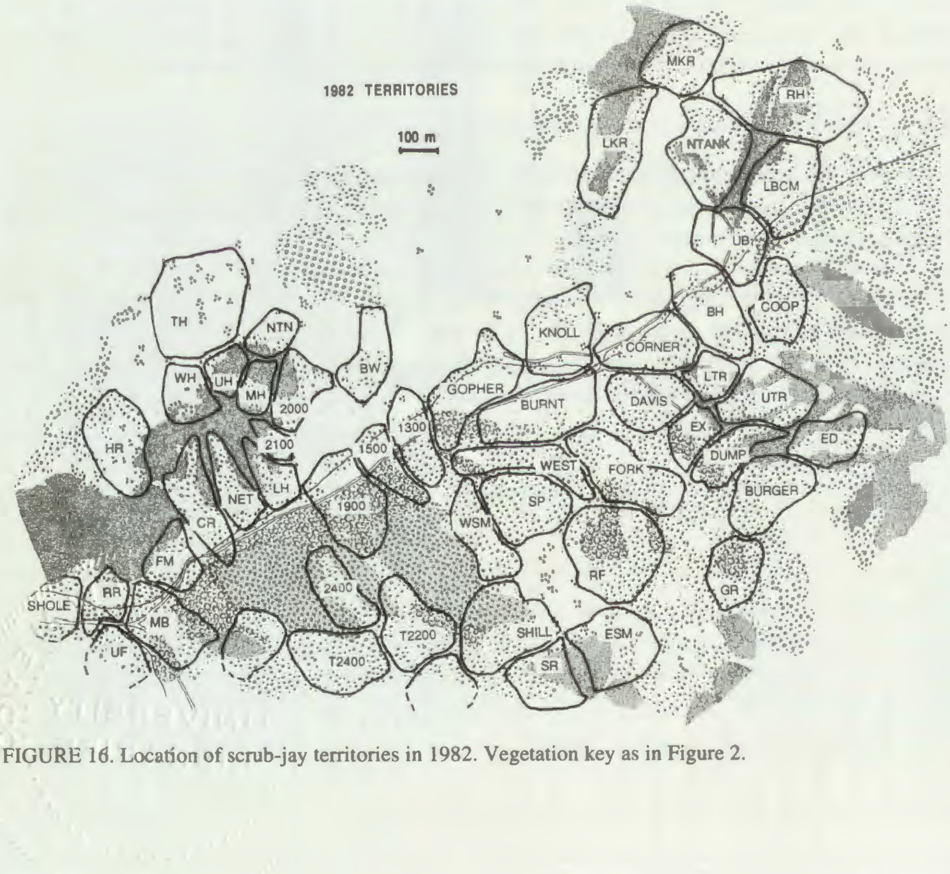

FIGURE 16. Location of scrub-jay territories in 1982. Vegetation key as in Figure 2.

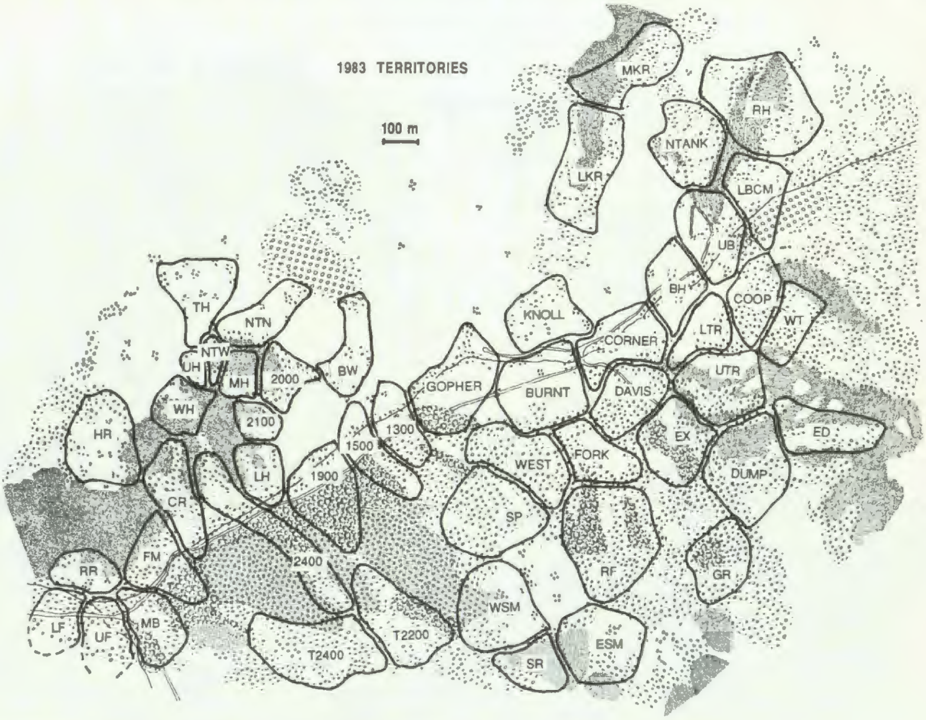

FIGURE 17. Location of scrub-jay territories in 1983. Vegetation key as in Figure 2.

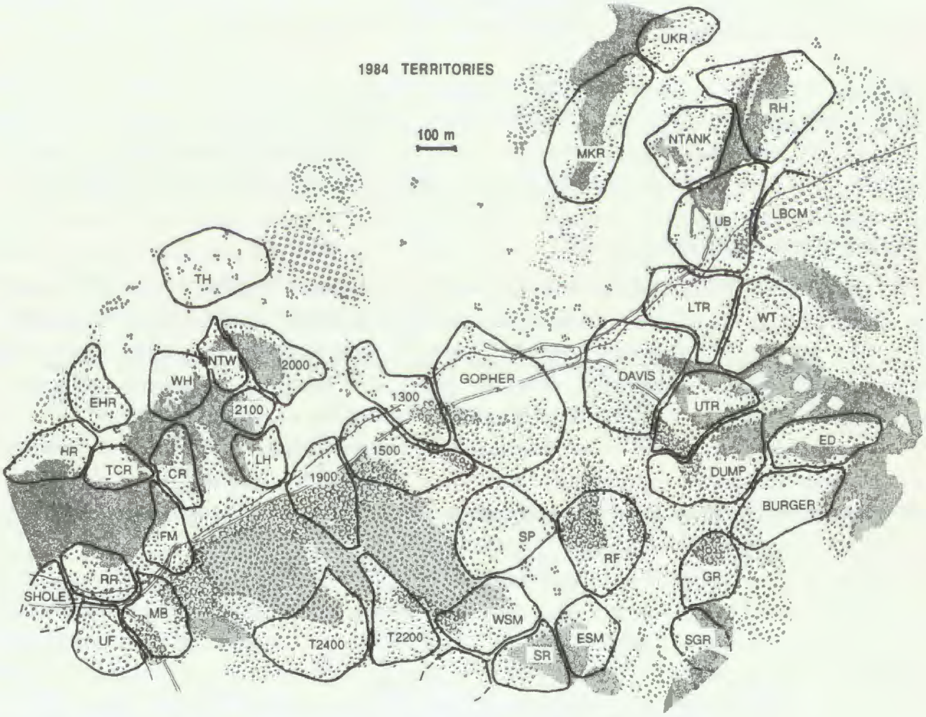

FIGURE 18. Location of scrub-jay territories in 1984. Vegetation key as in Figure 2.

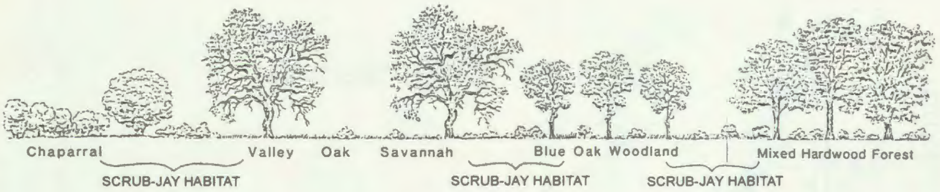

FIGURE 21. Schematic representation of habitat types and plant communities on the study area illustrating preferred, occupied scrub-jay habitat.

The amount and spacing of shrubs, which provide nest sites and cover, was by far the most important variable. Type 1 territories contained more shrubs (mean of 0.90 vs. 0.39 and 0.26 ha for Types 1, 2 and 3, respectively; Table 5). Of the five Type 3 territories, two had no shrubs, one had 0.01 ha, one had 0.1 ha, and the fifth 1.2 ha, the latter misclassified by the DFA as a Type 2 territory. The lack of shrub cover evidently explains why unoccupied areas that appeared suitable, such as the large area of blue oak woodland between the GR and RF territories (see territory maps, Figs. 15–19), were not used. Percentages of grass and of oak canopy were greatest on Type 3 territories (Table 5), suggesting that extensive open grassland and dense woodland habitats are avoided.

Territory size varied in relation to several variables. Partial correlation analysis indicates that area of grassland was positively correlated with territory size (R = 0.60, P = 0.003), again indicating that open grassland does not provide suitable resources. No relationship was found between area of shrub cover and territory size. Oak canopy—a critical resource for jays—did not vary independently with territory size; a minimum of 0.16 ha occurred on even the smallest territories. However, overall oak density and number of oak species are not evenly distributed; while all territories included at least two species, some territories held predominately one species and others three. Because *Q. agrifolia* retains acorns for much longer periods, it is a relatively more valuable resource. Because oak species tend to produce crops synchronously, and variation in production is high even within species (Carmen et al. 1987, Koenig et al. 1994b), territories with greater numbers of oak species and individual trees are more likely to produce good acorn crops in any given year.

DISPERSAL AND FLOATING

Knowledge of the behavior of floaters is essential to understanding the evolution of reproductive strategies (Stutchbury and Robertson 1986). Rather than being merely a

TABLE 5. CHARACTERISTICS OF TERRITORIES (MEANS ± SD) OF HIGH (TYPE 1), MEDIUM (TYPE 2), AND LOW QUALITY (TYPE 3)

	Type 1	Type 2	Type 3
N	11	8	5
Size (ha)	2.8 ± 1.7	2.0 ± 1.0	2.8 ± 0.9
Canopy oaks (ha)	0.68 ± 0.48	0.48 ± 0.40	0.83 ± 0.37
Area shrub (ha)	0.90 ± 0.43	0.39 ± 0.21	0.25 ± 0.51
Area grass (ha)	1.2 ± 1.1	1.1 ± 0.8	1.6 ± 1.2
Proportion canopy	0.24 ± 0.13	0.23 ± 0.12	0.35 ± 0.23
Proportion shrub	0.39 ± 0.14	0.32 ± 0.21	0.17 ± 0.26
Proportion grass	0.40 ± 0.14	0.50 ± 0.17	0.55 ± 0.29

Note: Territory quality classified by occupancy rate during study period, 1982-1985.

surplus, floaters may show complex social organization and exhibit various strategies to become breeders (Smith 1978, 1984), which in turn affects the behavior of existing territorial breeders. For example, females in Red-winged Blackbirds (*Agelaius phoeniceus*) defend territories against nonbreeding females (Hurly and Robertson 1984). The presence of floaters in Bank Swallows (*Riparia riparia*) induces males to mate-guard (Beecher and Beecher 1979), and in Eastern Bluebirds (*Sialia sialis*) they affect seasonal patterns of territorial behavior (Gowaty 1985). Floaters can evict male and female territorial tropical House Wrens (*Troglodytes aedon*; Freed 1986) and male Song Sparrows (*Melospiza melodia*; Arcese 1987), but floaters do not challenge territorial Rufous-collared Sparrows (*Zonotrichia capensis*; Smith 1984). Floaters may live singly, sneaking through territories as do male Song Sparrows (Arcese 1987) and both sexes of Rufous-collared Sparrows (Smith 1978), or in aggregations off territorially held areas (Atwood 1980a). Within groups, the status of floaters may determine their access to resources and chance of eventually breeding (Eden 1987; Smith 1978, 1984). Floaters may also engage in extrapair copulations as shown in Tree Swallows (*Tachycineta bicolor*) and may be responsible for at least some extrapair young (Barber and Robertson 1999).

Given the diversity and importance of floater behavior and social organization, the first step in assessing the trade-offs between early independent breeding, delayed dispersal and helping, and floating, is acquiring detailed data on dispersal and movement patterns. Especially important are parent-offspring and breeder-nonbreeder interactions, the types of habitats available for dispersing individuals, and the social relationships among nonbreeders. Such detailed data are available for nonbreeders of cooperative species, including Florida Scrub-Jays (e.g., Woolfenden and Fitzpatrick 1984, Fitzpatrick and Woolfenden 1986) and Mexican Jays (Brown 1963, 1970; Brown and Brown 1984), but are rare for noncooperative species (Smith and Arcese 1989). Most commonly, floater presence is inferred from replacement of breeders (Watson and Moss 1970, Rutberg and Rohwer 1980, Sæther and Fonstad 1981, Stutchbury and Robertson 1986). Floaters have been found in a few cooperative breeders, such as Red-cockaded Woodpeckers (*Picoides borealis*; Walters 1990), Acorn Woodpeckers (Koenig and Mumme 1987), Mexican Jays (Brown 1986), Hoatzins (*Opisthocomus hoatzin*; Strahl and Schmitz 1990), Groove-billed Anis (*Crotophaga sulcirostris*; Koford et al. 1990), Pukekos (*Porphyrio porphyrio*; Craig and Jamieson 1990), and White-throated Magpie-Jays (*Calocitta formosa*; Innes and Johnston 1996, Langen 1996b). However, floaters (when their numbers were estimated) comprised less than 5% of these populations and appear either to be "losers" (*sensu* Fitzpatrick and Woolfenden 1988) or the product of chance events rather than individuals exercising a viable alternative dispersal strategy. (Alternatively, floaters in these and other cooperative breeders may be difficult to detect and monitor, as is the case in most noncooperative species). An interesting exception is the Australian Magpie (*Gymnorhina tibicen*), in which delayed dispersal and floating are both conspicuously expressed dispersal options (Carrick 1972). In studies that explicitly compared closely related cooperative and noncooperative species, floaters were rarely, if ever, seen (Zack and Ligon 1985a,b; Bell and Ford 1986) or not followed in any detail (Atwood 1980a, Leighton 1986).

In the following discussion, "juvenile dispersal" is defined as the initial, usually one-way, movement away from the natal territory, as contrasted with individual "movements" of independent floaters either on defined home-ranges or directionally over long distances.

JUVENILE DISPERSAL

In 1984, I radio tracked three juvenile scrub-jay males from two territories. Two male fledglings from UB territory (jays 570 and 025) and one male from 1300 territory (jay 640) were fitted with radio backpacks five weeks after fledging. The jays were followed until the transmitters failed, from four to eight weeks later. Focal animal point samples every 10 min (Altmann 1974) on each individual lasted 3 h, and morning, midday, and evening watches over a one- or two-day period were combined for composite full-day samples. During the watches the jays' foraging behavior, microhabitat use, behavioral interactions, and location were monitored. I collected 13 representative full-day watches on jay 640 (114 h), 8 days on 025 (72 h), and 6 days on 570 (54 h).

The movements of jays 570 and 640 illustrate the salient points of juvenile dispersal (Figs. 22 and 23). Each map represents a full-day sample consisting of three 3-h samples with a total of 57 location points; hence, both home range and activity centers can be identified. Prior to six weeks post-fledging juveniles associated closely with parents and remained on their natal territories (jay 570, Fig. 22a, and jay 640, Fig. 23a). Between six and eight weeks, the fledglings began wandering onto adjacent territories unaccompanied by their parents (Figs. 22b,c and Fig. 23b). After two months, juveniles either moved between their natal and other territories, remained on their natal territories (Fig 22d), or departed permanently (jay 640, Fig. 23c). When off their natal territories the three jays used other territories almost exclusively, with less than 2% of their activity in unoccupied areas (Table 6).

When on territories, the tagged jays and other floaters appeared to have free access to all areas, including former nest sites (marked by hollow squares in the figures). Breeders were dominant over floaters, including breeding females over floater males, and first-year breeders over older floaters. Floaters were not restricted to territory edges or interstitial areas.

A larger but less precise sample based on 340 resightings of 51 juveniles banded as nestlings just prior to and following dispersal indicate that both males and females may remain near or on their natal territories for extended periods. For example, females 37 and 62 fledged on BURNT and DAVIS territories, respectively, in 1981 were recorded at 47 and 36 locations between five and 24 weeks post-fledging; 27% for female 37 were on her natal territory, compared to 10% for female 62. Over 97% of all locations for these two jays were on territories. Note that all of these examples are for jays remaining on

TABLE 6. PERCENTAGE OF RADIO LOCATIONS OF THREE MALE JUVENILES ON NATAL, NON-NATAL, AND OFF TERRITORIES, JULY–SEPTEMBER 1984 (NUMBER OF LOCATIONS IN PARENTHESES)

	Sample sizes			Prior to 6 weeks post-fledging			6 weeks to 2 months post-fledging			2 to 3 months post-fledging		
Jay	hours	locations	NL[a]	natal	other[b]	off[c]	natal	other	off	natal	other	off
640	114	686	32	100%	0	0	48%	43%	9%	1%	97%	2%
				(140)			(50)	(45)	(9)	(4)	(399)	(7)
570	54	327	28	100%	0	0	88%	12%	0	59%	41%	0
				(97)			(44)	(6)		(90)	(62)	
025	72	416	33	97%	3%	0	77%	22%	1%	4%	95%	1%
				(180)	(5)		(77)	(23)	(2)	(4)	(92)	(1)

[a] Not located precisely.

[b] Non-natal territories.

[c] Unoccupied (non-territorial) areas.

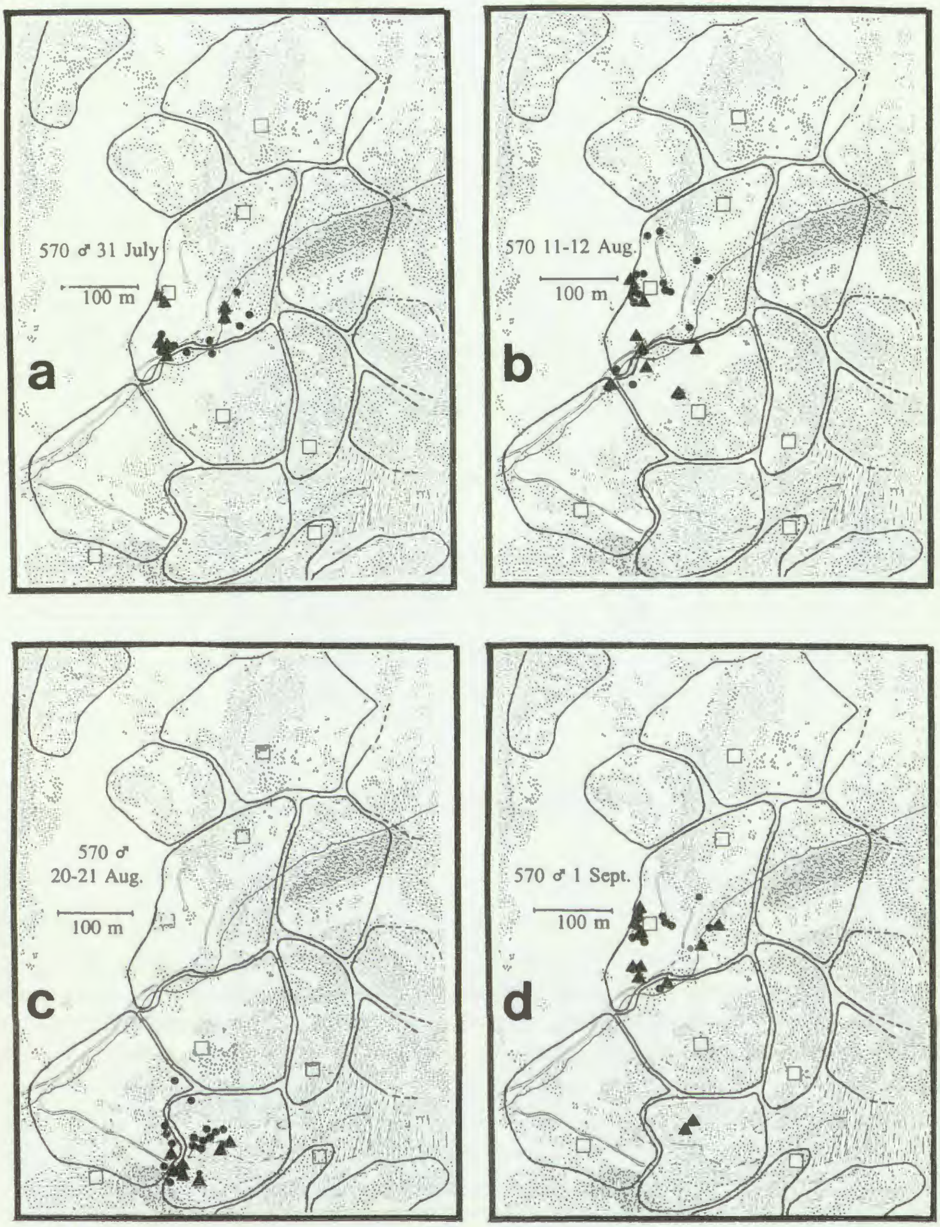

FIGURE 22. Radio-tracked dispersal of male 570 from its natal territory. Circles indicate one location, triangles ≥2 locations (N = 57 locations), open squares represent nest locations, and solid lines territory boundaries. Radio locations (a) 6 weeks (all locations on natal UB territory), (b) 7 weeks, (c) 8 weeks, and (d) 9 weeks after fledging.

the study area but that 63% of all young banded as nestlings and reaching independence were not resighted. Jays often disperse considerable distances during this initial period, as shown by the number of floaters detected and the long-distance movements recorded for three first-year birds.

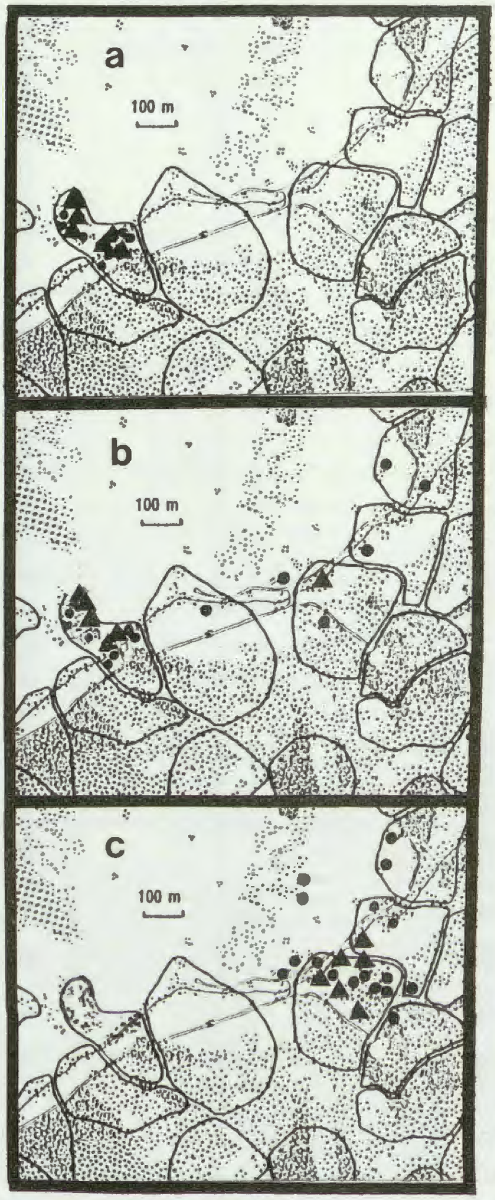

FIGURE 23. Radio-tracked dispersal of male 640 off its natal territory. Circles indicate one location, triangles ≥2 locations (N = 57 locations), and solid lines territory boundaries. Radio locations (a) 6 weeks (locations shown on map of the entire study area), (b) 7 weeks, and (c) 10 weeks after fledging.

FLOATER MOVEMENTS AND DISPERSION PATTERNS IN THE NONBREEDING SEASON

Monthly surveys from late July 1981 to early May 1982, both in areas occupied by breeders and in areas without territories, revealed an uneven distribution of floaters (Fig. 24). Floaters aggregated loosely in three distinct locations on the study area: on the MB, LF, RR territories; on the 2000R, MH, and NTN territories; and on the area circumscribed by the GOPHER, EX, and NTANK territories (see territory maps, Figs. 16–19, for specific territory locations). The mean number per aggregation over the 9-month period was 10 and ranged from 2 to 30. On surveys and during incidental field work, floaters were rarely seen in unoccupied areas, or on more than the few territories that were consistently used by them.

Floaters formed aggregations beginning in July as they reached independence and began to disperse from their natal territories. A fledgling's recruitment to a particular aggregation appeared to determine its initial dispersal distance. If aggregations formed on a fledgling's natal territory, the fledgling tended to remain in the vicinity. For example, radiotagged jays 570 and 025 fledged from UB Territory in 1984. Jay 570 joined an aggregation centered on the UB and UBCM territories, and so spent a major portion of the year on its natal territory (see Fig. 22d). On the other hand, jay 025 joined an aggregation on the EX territory, 1.0 km away, and was not detected subsequently on UB.

The same pattern of floater distribution occurred in the nonbreeding season (late July to late April) in 1982–1983 and 1984–1985. In 1983–1084, the anomalous year, all juveniles dispersed from the study area and no floaters immigrated in fall or winter; at least 33% of banded breeders also abandoned their territories in the fall and did not return until the following spring. In 1983–1984 floaters aggregated at higher elevations where acorns were abundant, as close as 4 km to the study area. No floaters were seen on the study area until March 1984, when many of the territorial breeders were returning.

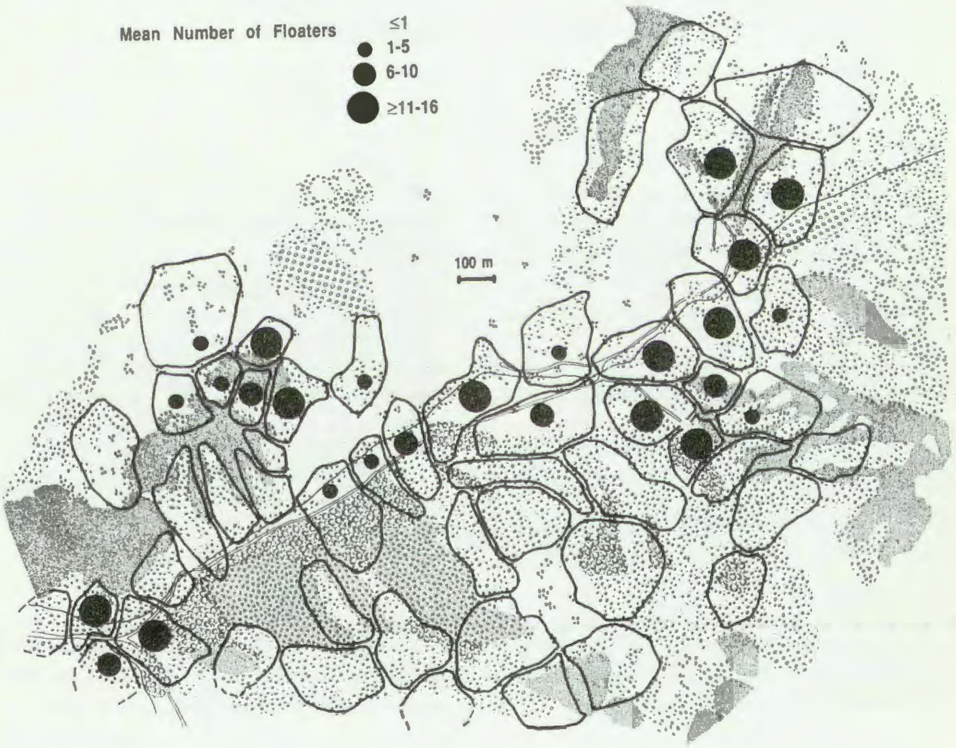

FIGURE 24. Mean numbers and distribution of floaters on the study area during the nonbreeding season 1981–1982. Data are the mean from monthly surveys of territories and unoccupied areas from August through April. Solid lines are 1982 territory boundaries; territories lacking dots indicate no floater use.

Based on periodic surveys, in three of four years the study area had the largest floater population within several kilometers, and must have attracted floaters from a wide area. Other isolated aggregations were located in the vicinity of the study area, each separated by extensive areas with no floaters. Because floaters move widely, it was difficult to estimate their numbers. For example, of 350 jays banded as floaters, 120 (32%) were never resighted, suggesting that many were merely passing through the study area. However, periodic surveys on the study area of 194 ha indicated a rough mean during the late summer to early spring period of 100 in 1981–1982, 120 in 1982–1983, <5 in 1983–1984, and 40 in 1984–1985. An estimated December population of 100 floaters on the study area in 1981 represented juveniles from about 160 territories, based upon a mean of 1.2 fledglings per pair and survivorship of 52%.

Stability of aggregations

In 1981–1982 virtually all (>90%) of the floaters in several aggregations were colorbanded. An analysis of the resightings on the BURNT and BH territories illustrates the stability of the aggregations and the localized movements of floaters. On the BURNT territory I banded 75 floaters and resighted 53 there from July 1981 to early May 1982. By mid-January a core group had formed; in eight surveys seven to 10 days apart from 1 February to 1 May, only 17 banded individuals were recorded (366 total observations). Twelve of the 17 were seen on six or more of the eight surveys, and pooling the resightings of these 17, the probability of finding one of the core group on BURNT was 0.72. During this three-month period, on 21 other occasions only four other banded individuals and four unbanded jays were seen. Prior to 1 February, 37% (63) of the 170 resightings of the 17 core-group members occurred on BURNT, compared to 71% (140) of 196 later.

Resightings and surveys on neighboring territories, also with large numbers of floaters, revealed a similar level of stabilization in movements and indicated that transfers between the aggregations were infrequent (distances between foci of aggregations varied from 100 m to 2 km). Between July and May of 1981–1982, I recorded 604 resightings of 65 individuals on the BH and UB territories, which were one to two territories distant from BURNT, respectively. Of the 17 BURNT floaters only five were seen a total of 19 times on the BH and UB territories, with one individual seen 14 times. Floaters from BURNT were mostly resighted on adjacent territories. Occasional long-distance movements were observed when singles joined other aggregations. Most of these longer forays occurred in late autumn, and only two of the 17 core individuals at BURNT were observed after 1 February in other groups; both were in an area 1.6 km distant, where they had been originally banded in early fall. These data show a tendency of jays in localized groups to wander varying distances, and this tendency is probably a part of a continuum of seasonally varying longer distance movements.

Home range and habitat use in winter

Radio telemetry was used to acquire data on floater home range and habitat use, and to ascertain if dispersal forays are made out of the aggregations. Two females (jays 680 and 695) not hatched on the study area were radio-tracked in November and December of 1984. Locations for jay 695 covered 5 December to 11 January, with eight composite days (72 h total). Locations on 680 extended from 5 to 23 December, with four composite days (36 h total). Figure 25 illustrates typical patterns of habitat and use of local territories for each jay over one composite day (9 h, 57 location points).

Jays 680 and 695 spent 88% (N = 198 sample points) and 99% (N = 433 sample points) of the sample period on territories. Eleven locations for 695 off the study area are excluded from the percentages. Female 695 typically ranged over a far greater area and used nine territories vs. five for jay 680. Over the entire sample period, jay 680 used seven territories with a home range of 8.8 hectares; jay 695 used 11 with a home range of 26.0 hectares. However, the radio lasted longer on jay 695, and her movements were followed longer. If concurrent sample periods are compared, the differences are smaller (8.8 vs. 11.3 ha).

Floater locations indicate that they had free access to all areas and were not shunted away from nest sites or onto territory boundaries. Resightings of color-banded floaters of both sexes indicate a similar pattern of home range use and home range size and use in winter.

Home ranges of floaters in aggregations overlapped considerably, and individuals showed consistent home-range use during the winter. Floaters covered a much larger area than the average breeder's territory (mean floater home range = 21 ha, based on two radio-tagged jays and resightings of 11 jays each with over 20 locations; mean breeder territory size = 2.5 hectares, N = 194).

FLOATER MOVEMENTS AND DISPERSION PATTERNS DURING THE BREEDING SEASON

The distribution of floaters during the breeding season varied considerably. In 1981–1982 and 1982–1983 large numbers immigrated onto the study area during the fall and winter, and then abruptly disappeared by May. In 1983–1984 (year of the poor acorn crop), no floaters were seen on the study area during winter. A few returned in spring and were seen sporadically during the breeding season. In 1984–1985, floaters again immigrated into the study area, and these and many jays hatched there in 1984 remained

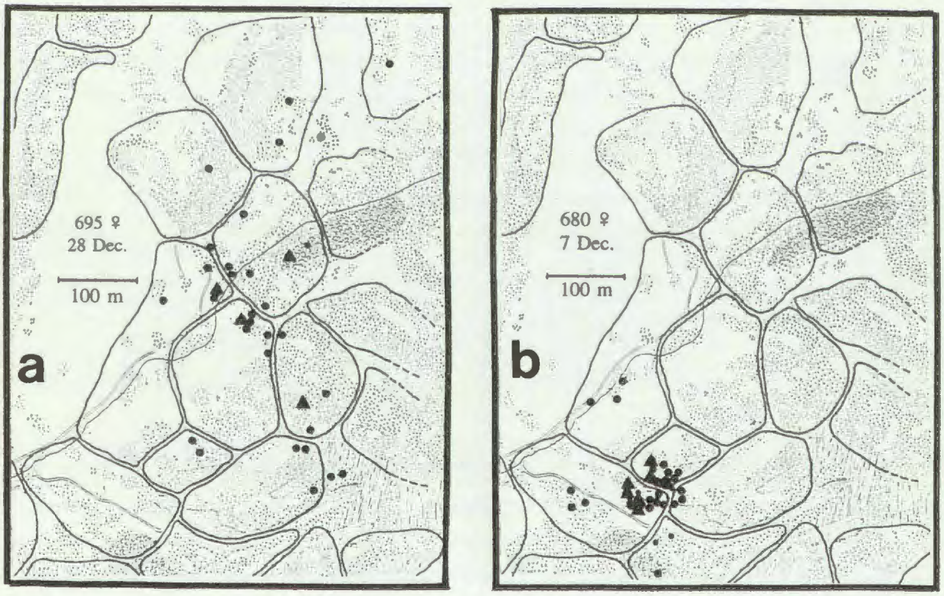

FIGURE 25. Radio-locations and winter home range use by two radio-collared first-year female floaters. Circles indicate one location, triangles ≥ 2 locations (N = 57 locations), and solid lines territory boundaries. (a) Female 695, and (b) Female 680.

throughout the breeding season. These results are given in greater detail in the following paragraphs and the sequences of dispersal are diagrammed in Figure 26.

In 1981–1982, the approximately 100 floaters on the study area were easily located during the nonbreeding season until they abruptly disappeared in late April 1982. Of 214 banded in 1981–1982, 148 were resighted 1,575 times during the fall, winter, and early spring. But between 1 May and 30 June 1982, only six were observed once each on the study area. Two were on territories in the first week of May where they had been seen frequently during the previous winter months. Three others were males who earlier had established "pseudo-territories" and had been seen in unoccupied habitat nearby. The remaining individual came to traps baited with acorns on the WSM territory. Sightings of unbanded and unidentified floaters were equally rare, despite 1,500+ field hours during the breeding season. Floaters seen during this time, both on and off territories, were silent and inconspicuous, in contrast to their behavior in other months. Indeed, those on territories were usually first observed when they were chased off by breeders.

In early July 1982, newly independent juveniles began wandering off their natal territories and joined aggregations. By late July, older floaters began reappearing in these aggregations as the breeders became tolerant of them. A total of 15 banded adult floaters (11 males, 4 females) returned to the study area out of a possible 214 pre-reproductives (nestlings and floaters) banded prior to the 1982 breeding season. Three were natal to the study area, and nine eventually bred there (three the following spring of 1983, and six in 1984 or 1985; Fig. 26).

A similar pattern was observed in 1982–1983; large numbers of floaters immigrated onto the study area in the fall of 1982 and of 71 banded, 43 were resighted a total of 275 times. In addition, of 54 jays banded as nestlings in 1982 and reaching independence, 16 were resighted as floaters. Floaters remained on territories somewhat longer in 1983, with 30 on the LF/RR territory on 5 May. Between 1 May and 30 June, 13 banded individuals were resighted 15 times. Of those, six were observed between 1–5 May on territories, and four others had established pseudo-territories and were seen in unoccupied areas nearby; of the remainder, three were seen sneaking through a territory and one was in an unoccupied area. Of the 71 floaters banded as immigrants plus 16 jays natal to the study area resighted between fall and early spring, nine (seven males and two females) returned after July. Six of the nine were natal to the study area and six eventually bred on the study area; 3 in 1984 and 3 in 1985 (Fig. 26). Thus the floaters that did return, predominantly males that fledged on the study area, had a high probability of breeding there. This suggests that philopatry, or at least persistence in a familiar area, coupled with age-related dominance, facilitates acquisition of breeding space.

Breeder aggression towards floaters increased during nest building and egg laying, and coincided with the disappearance of floaters. However, floaters also left areas in which they were not disturbed. Two cases are illustrative.

Part of BURNT territory, along Big Creek, was occupied by a stable group of 17 floaters from January through April 1982. The breeders laid their first egg on 2 April and nested 75 m from the activity area of the floaters. The floaters were excluded from the nest area, but in 23 h of observation the breeders had only 6 interactions with the floaters away from the nest. Nevertheless, the floaters moved elsewhere, and the number dropped from 15 on 18 April to none on 1 May.

The NET area was occupied by territorial adults in three of five breeding seasons (see Figs. 16–19). In 1983, when it was unoccupied, approximately 22 floaters used it in April and all disappeared by 5 May.

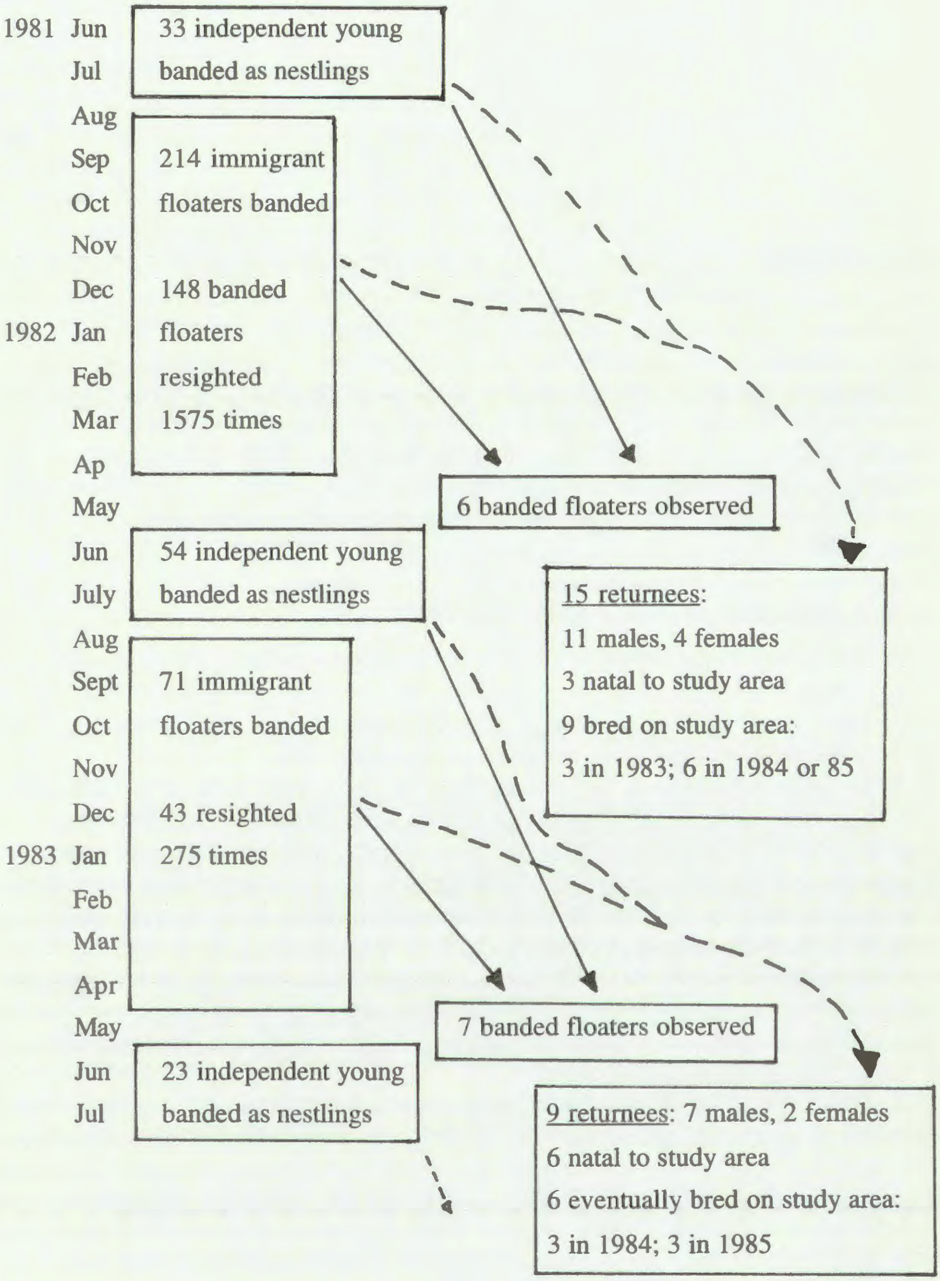

FIGURE 26. Chronology of dispersal and floating showing build-up of floaters during the winter, their disappearance in May, and the number and eventual fate of those that returned in late summer and fall.

The few sightings of floaters during the breeding season, and two contrasting observations described below, make it difficult to generalize about their movement patterns. First, the few floaters seen in May–June 1982 and 1983 were either solitary or in pairs, and used territories as well as the unoccupied interstitial space between territories. This suggests that when the large aggregations broke up, floaters wandered singly or in pairs. Second, seven large flocks (40–50 birds) were observed on the study area between 4–9 May in 1983. In contrast to the loose aggregations during the nonbreeding season, these were cohesive groups and appeared to be traveling long distances. All of the flocks were moving east from hilltop to hilltop. Only one individual in one of these flocks was identified, a floater resighted frequently on the study area. All appeared to be first-year birds. While the timing of flock appearances coincided with the decline in floaters on the study area in general, I observed such large flocks only in 1983. Although purely speculative, these flock movements may result from high breeding success closer to the coast, where habitat is broadly more favorable, including a higher abundance of coast live oak.

Following the 1983 acorn failure, floaters began to arrive on the study area in mid-April 1984, at the same time that many of the breeders returned. Some of these returning breeders became floaters after they failed to regain their territories. In addition, three returning females evicted replacement females on their territories, which then became floaters. By the end of May, most of these floaters had disappeared. Only seven banded floaters were resighted 16 times during this period.

Movements and habitat use during the 1985 breeding season

In fall and winter of 1984, natal juveniles remained on the study area and floaters again immigrated, although in fewer numbers (approximately 40) than in 1981–1982 and 1982–1983. Their unexpected persistence in the spring of 1985 provided an opportunity to acquire data on their behavior during the breeding season.

In the last week in March and the first week of April 1985, 11 floaters were affixed with radio backpacks: three known males, two known females, and three males and three females sexed by discriminant function analysis. All but one were first-year jays. Between 28 March and 12 June, I recorded 270 h of focal animal sampling and radio tracking locations. In addition, 35 "simultaneous" positions of all the tagged jays were taken to examine group movements.

I had expected that by May the jays would move elsewhere, as in previous years. However, only one tagged female disappeared and could not be relocated. Two jays (one male and one female) moved 2 km up Big Creek, off the study area, but remained on local areas throughout May and June.

The other eight tagged jays, and numerous banded and unbanded floaters, remained on the study area. Data on their movements are divided into March–April, when floaters were tolerated by breeders, and the May–June period, when they were not. In March and April, 90% (399 of 445) of all positions for 10 of 11 floaters were on territories (with individual use ranging from 75% to 100%). Despite the early onset of breeding (mean first-egg date was 25 March) and the presence of eggs in nests, floaters still used territories extensively without breeder aggression except near nests.

Figure 27 illustrates composite days (9 sample hours, 57 location points) for three tagged jays (two males and one female) during March and early April 1985. Male (570) was fledged from territory UB in 1984 and tagged and followed in July through September; the other two were immigrants. The tagged jays and other floaters used two main areas, the

BCM/NTANK territories and the EX/LTR territories, with aggregations of approximately 20 and 10 floaters, respectively. It does not appear that breeders confined the floaters to the edges of territories, but they did exclude floaters from nest sites (Fig. 27).

A change in territory LBCM (Fig. 28) had important repercussions for local floater distribution. The LBCM pair consisted of a first-year female and a three-year-old male breeding for the first time. A nest was built, but no eggs were laid. Approximately 15 floaters used the territory extensively. In the first week of May, the pair broke up; the female joined the floaters and the male paired with the COOPERS female, who separated from her new mate. The LBCM territory was abandoned at this time. The vacated LBCM territory became the major center of floater activity in May and June. Other areas with high use included EX/UTR and COOPERS/BUCKM.

In mid-May, seven of the radio-tagged floaters were still on the study area. Three others were 2 km upstream along the same drainage and used the study area occasionally; one was unaccounted for. The telemetry data indicate that even in mid-May, floaters used territories extensively with 45% (412 of 914) positions on occupied territories. If the LBCM territory (occupied by a breeding pair until 5 May) is included as a territorial area, 93% of the positions in May and June were on territories. If LBCM is considered unoccupied, individual floater use of occupied territories varied from 29% to 80%.

Figure 28 shows composite days for four jays (two males and two females) in mid-May. In contrast to winter and early spring locations, floaters used territory boundaries, interstitial areas, and the newly vacated LBCM territory. Yet on several occasions I observed floaters approaching nests with nestlings as close as 20 m, with no response from the breeders. June positions for the 10 radio-tagged jays were similar and by the middle of July the tagged jays were once again tolerated by breeders.

Jay 570, a male fledged on the UB territory the previous spring and radio-tracked the previous July through September (see Fig. 22), remained on or near its natal territory from March through June (Figs. 27a, 28a). Using the boundaries of the 1984 UB territory, 51% of 62 locations in March–April were on its natal territory, but only 10% if the 1985 territory boundaries are used. In May–June, 40% and 3% of the locations were on the 1984 and 1985 territories, respectively. In interactions with its parents, 570 was treated like any other floater, largely ignored on the margin of the territory and rebuffed when near the nest or the breeders. The other UB nestling (also radio-tracked in August and September of 1984, but not in March-June) remained on the EX territory, one km from the UB territory, where it was found throughout April, May, and June of 1985. This jay had no interactions with its parents since the previous spring when, as a juvenile, it left its natal territory.

These data demonstrate that floaters did not use unoccupied habitat, but concentrated their activity on territories. Territory use (Table 7) ranged from an average 98% in August–September, 90% in December–January, 89% in March and April, and 44% in May and June (94% if territory LBCM, deserted in May, is counted as a territory).

Home range of floaters during the 1985 breeding season

Home range estimates are based upon the composite one- or two-day samples from 13–17 May 1985 (five males, two females; Table 8, Fig. 29a), which is the height of the breeding season and, usually, of breeder aggression toward floaters. Individuals used from 3 territories and 2.85 ha (male 447), to portions of 8 territories and 9.73 ha (male 487), with an overall mean of 4.3 territories and 4.9 ha (Table 8). Area use by males and females did not differ. Home range estimates based on radio positions from late April through June are slightly larger (average increase 37%) than those from the one-day samples (Table 8). Thus, during the 1985 breeding season, floater home range was larger than average breeder territory size.

Habitat use by floaters

In four of five breeding seasons, breeders did not tolerate floaters on their territories.

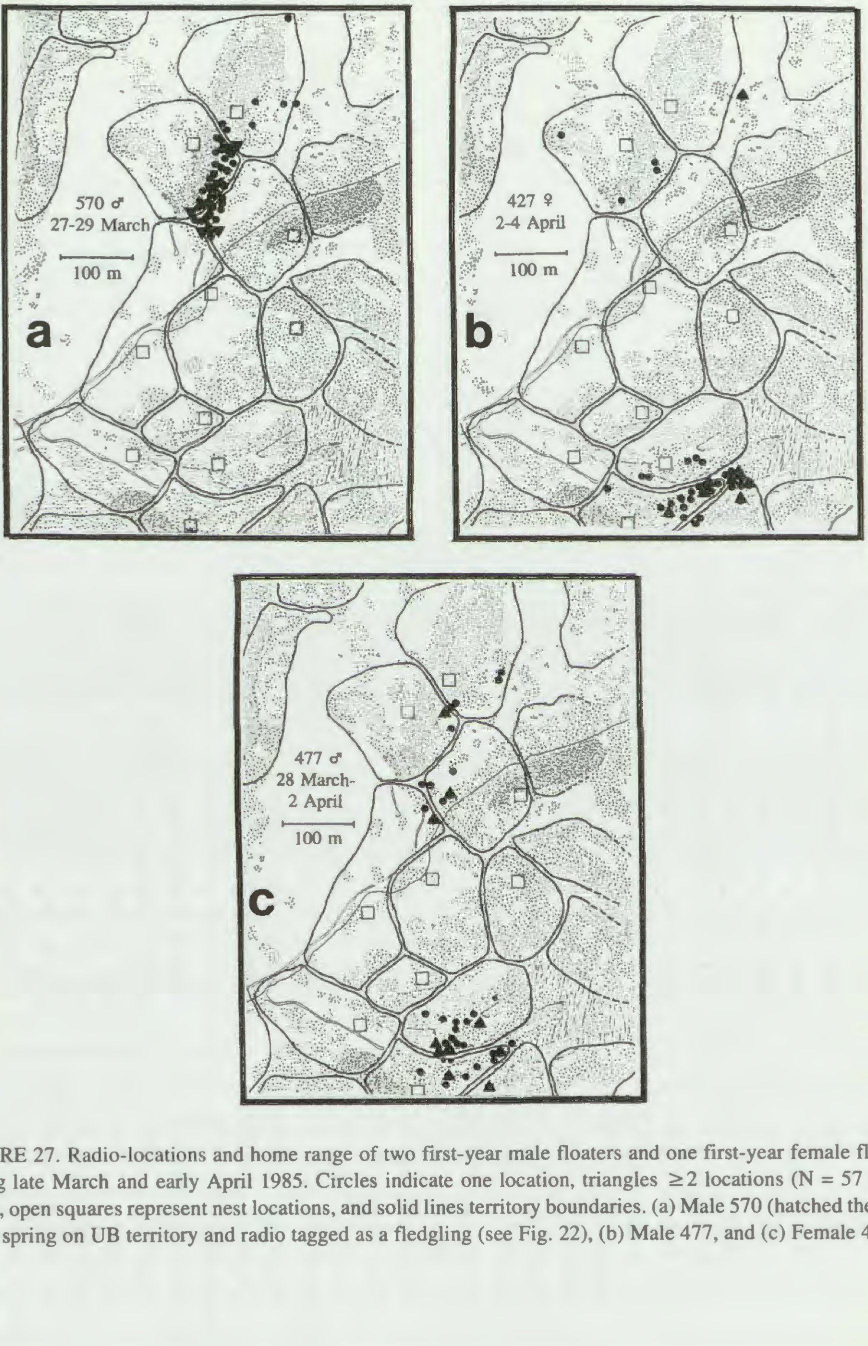

FIGURE 27. Radio-locations and home range of two first-year male floaters and one first-year female floater during late March and early April 1985. Circles indicate one location, triangles ≥2 locations (N = 57 locations), open squares represent nest locations, and solid lines territory boundaries. (a) Male 570 (hatched the previous spring on UB territory and radio tagged as a fledgling (see Fig. 22), (b) Male 477, and (c) Female 427.

TABLE 7. RADIO LOCATION SUMMARIES FROM JULY 1984 THROUGH JUNE 1985

Period	Number of jays	Active locations[a]	Percentage		Out of sight	Off area
			on territory	off territory		
1984						
July	3	422	100%	0%	31	0
August	3	551	98%	2%	45	0
September	2	363	98%	2%	17	0
December	2	430	93%	7%	37	2
1985						
January	1	150	87%	13%	3	9
March	2	93	90%	10%	0	0
April	10	357	88%	12%	12	27
May	9	653	48%	52%	31	89
			(91%)[b]	(9%)		
June	6	257	39%	61%	4	21
			(99%)	(1%)		

[a] Active points exclude those off study area and unknown locations (jay out of sight). Data points are locations recorded every 10 minutes during 3-hour focal animal samples.

[b] Percentages in parentheses include territory LBCM that was abandoned by the breeders on 5 May.

In 1985, increased tolerance allowed floaters access to occupied territorial space, but mostly near territory edges and away from nest sites. In May and June of 1985 floaters also used the LBCM territory (abandoned in early May) and the margin of the NTANK territory (Figures 27, 28, and 29a); other areas with floaters continued to be occupied by territorial jays.

To assess the quality of the habitat used by floaters, I examined how territorial jays used the area over a several year period. From 1981 through 1985 the reoccurrence of nests on the LBCM and neighboring territories, the contiguous territory boundaries, lack of unoccupied habitat, and the constant occupation of these territories (Fig. 29b) demonstrate that this area, heavily used by floaters in May and June (Fig. 29a), is prime habitat.

Because breeders still could be limiting floaters' access to favorable areas, I collected data on microhabitat use and foraging behavior of floaters and breeders in May–June.

TABLE 8. HOME RANGES OF SEVEN FLOATERS (5 MALES AND 2 FEMALES) DURING MID-MAY 1985 AND THE ENTIRE SAMPLE PERIOD DURING THE BREEDING SEASON

Jay	N of composite sample		Dates	Home range	
	Days	Hours		Size (ha)	Territories overlapped
695♀	1	9	16 May	3.07	3
	3	21	8 April–31 May	5.21	4
618♂[a]	1	9	13–14 May	3.56	3
	5	45	10 April–14 May	4.55	4
608♀	1	9	14–15 May	4.43	4
	4	33	11 April–11 June	4.92	4
487♂	1	9	17 May	9.73	8
	3	30	19 April–7 June	14.56	11
570♂[a]	1	9	14–15 May	5.53	5
	5	45	27 March–11 June	8.41	6
287♂	1	9	15 May	5.38	4
	3	27	15 April–12 June	9.17	6
447♂	1	9	15 May	2.85	3
	2	21	28 March–2 June	3.10	4

[a] Sexed by discriminant function analysis (see METHODS).

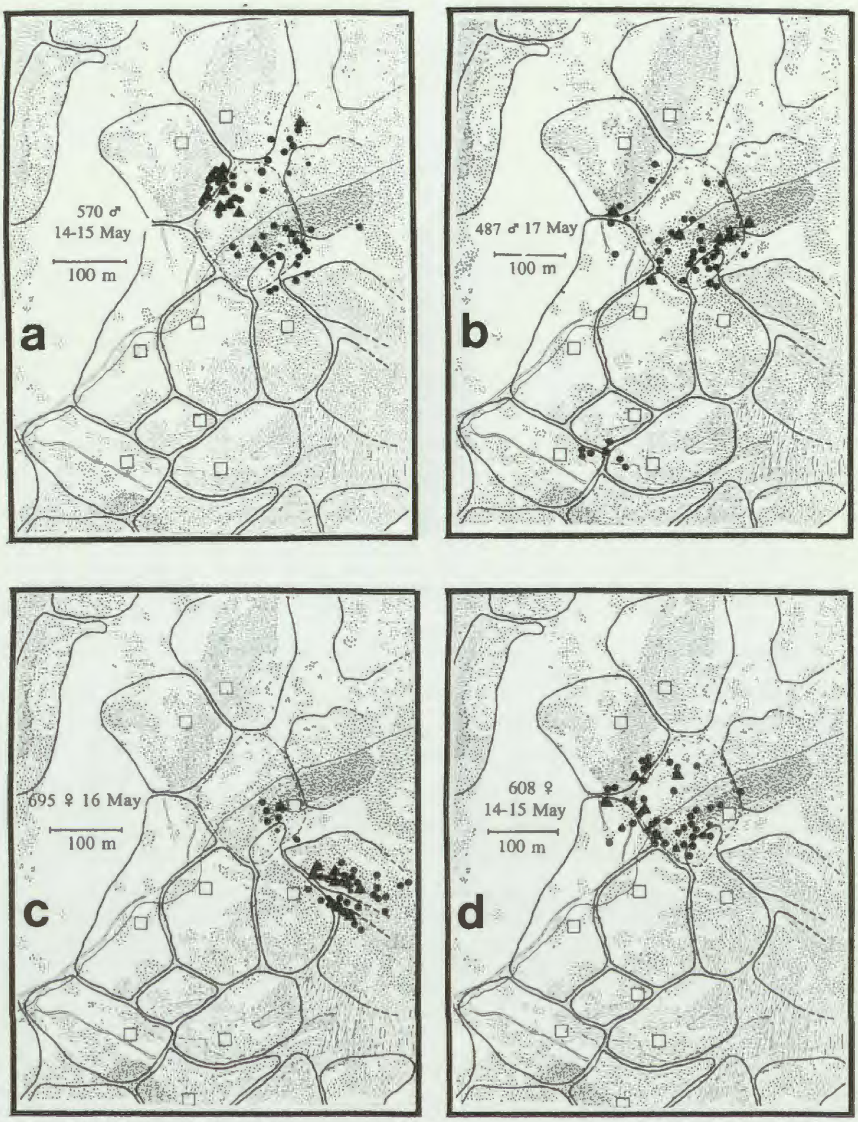

FIGURE 28. Radio-locations and home range of two first-year male floaters and two first-year female floaters during mid-May 1985. Circles indicate one location, triangles ≥2 locations (N = 57 locations), open squares represent nest locations, and solid lines territory boundaries. The stippled line indicates the boundary of the LBCM territory that was abandoned on 1 May. (a) Male 570 (hatched the previous spring on UB territory and radio-tagged; see Figs. 22 and 27), (b) Male 487, (c) Female 695, and (d) Female 608.

Data on floaters comes from five radio-tagged individuals that used the LBCM and BUCKM/COOPERS territories; data on breeders comes from the time-budget data collected on four pairs, primarily LBCM, in May 1983. In both samples microhabitat use and foraging style were recorded every 10 min during 3-h focal animal observations. Microhabitat was divided into four categories and foraging method into 10 categories (Fig. 30); no difference existed between breeders and floaters in either case.

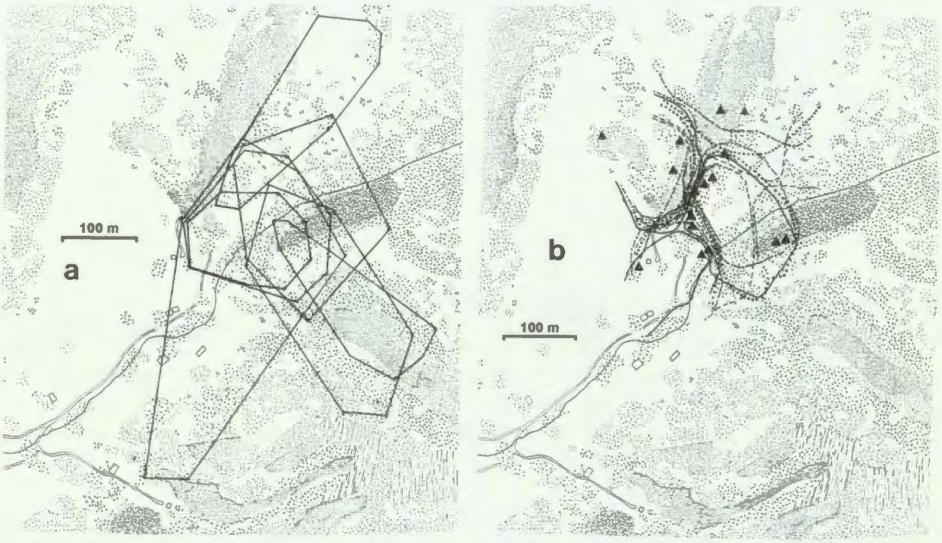

FIGURE 29. Home range of floaters in relation to territories and nest locations. (a) Home range of seven floaters (5 males, two females) in mid-May 1985. Lines represent minimum convex polygons encompassing 57 radio locations on each individual taken during three 3-h watches over a 1- or 2-day period. (b) Territory boundaries in 1981–1985 (each year marked with different line pattern) and nests 1981–1985 (marked with stars) in the LBCM area.

Social Organization of Floaters

Age ratios

In 1981–1982 and 1982–1983, most floaters captured and banded were first-year birds (86.5%, N = 233, and 94%, N = 71, respectively). Estimates from field surveys of floaters in these same years also indicate a ratio of approximately 10:1 in favor of first-year jays; in 1983–1984 no jays floated on the study area. A survey in fall of 1985 revealed approximately 40% of the floaters were adults. Patterns of floater immigration and emigration result in an uneven mixing of the age classes for two reasons. First, a variable but large number of first-year jays immigrated into the study area each year except 1983–1984 when no immigration occurred. Second, nearly all floaters left the study area at the onset of the breeding season and few returned later; 1985 was an exception because of the persistence of floaters through the breeding season. These differing patterns of floater movements may lead to a highly variable age structure of floaters in local areas.

Sex ratio

Twenty-two floaters were sexed as females by their "rattle" calls and the remainder by a discriminant function analysis. In the sample of floaters captured over the entire study period and sexed statistically, 126 of 300 (42%) were classified as males and 174 (58%) as females. Within the aggregation of 17 floaters on the BURNT territory, eight were male, seven female, and two of unknown sex. The sex ratio of floaters at the onset of the breeding season appeared to favor females; of 31 caught in March and April 1982, 11 were male and 20 female; of 54 caught in March and April 1983, 19 were male and 34 female.

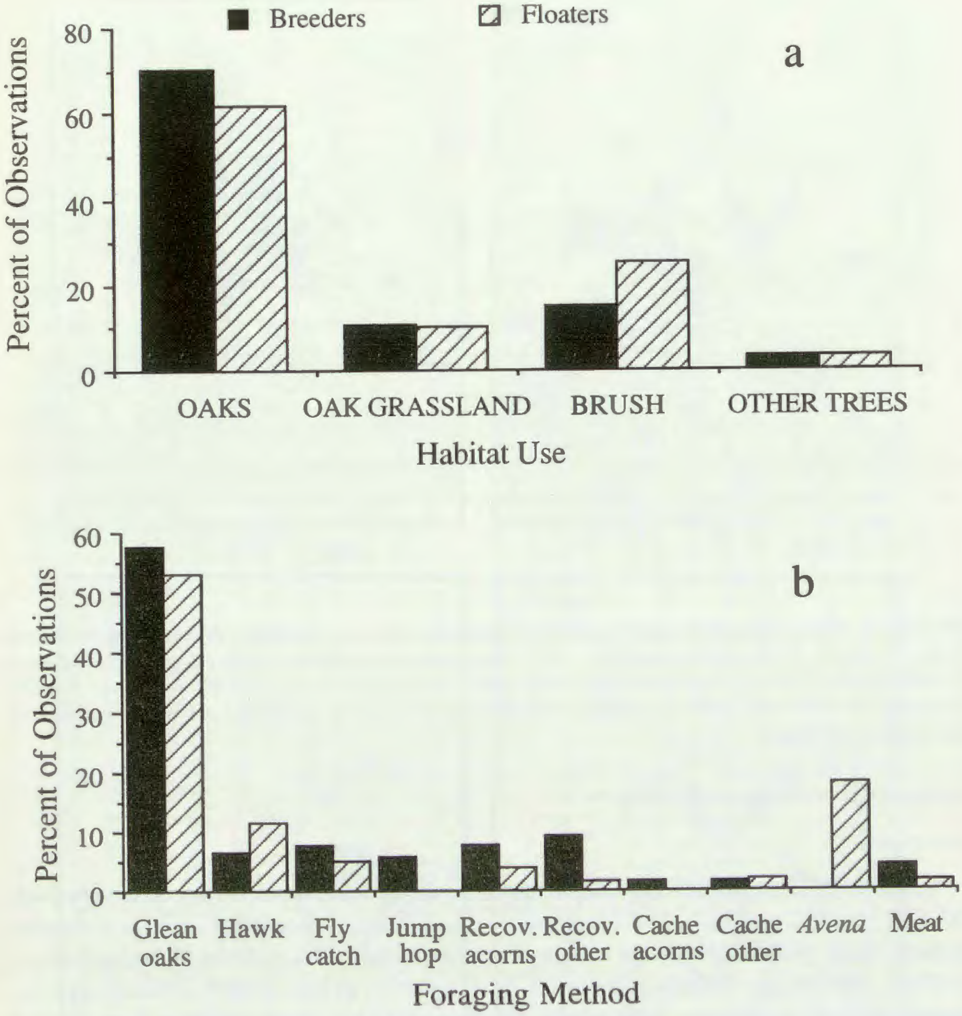

FIGURE 30. Comparison of breeders and floaters in (a) habitat use ($\chi^2 = 0.24$, df = 3, $P > 0.90$; N = 189 breeders, 224 floaters) and (b) foraging behavior ($\chi^2 = 17.1$, df = 18, $P > 0.90$; N = 120 breeders, 139 floaters) during the breeding season (5 May–20 May).

Aggregations vs. flocks

I refer to groups of floaters as aggregations rather than flocks, because individuals moved independently of one another. The locations of the radio-tagged floaters in the LBCM area in April and May illustrate the independent movement of individuals. Eight simultaneous locations, taken one hour apart from 0600 to 2000 hours on 7 May, are plotted in Fig. 31. All were located at least once on the LBCM territory (at the center of Fig. 31). Groupings of like symbols would indicate cohesive group movement, but the results show otherwise. Aggregations appeared to form primarily as a result of overlapping home ranges, and thus site serves as a better predictor of a given floater's location than does the presence or absence of other individuals.

Dominance interactions

Linear dominance hierarchies are common in flocks in many birds (Sabine 1959, Fretwell 1969, Smith 1984) including in Florida Scrub-Jay families (Woolfenden and Fitzpatrick 1977). Dominant individuals in flocks may derive at least three advantages compared to less dominant birds: (1) dominants have first access to food (Pulliam 1976); (2) dominants spend more time foraging through decreased time scanning or maintaining alertness for predators (Powell 1974; Caraco 1979a,b; Goldman 1980); and (3) dominants have a greater probability of acquiring a territory or mate in the flock home range (Fretwell 1969, Eden 1987; Smith 1978, 1984). It was therefore surprising that interactions among floaters within aggregations were largely nonaggressive. While interactions were fairly common, most involved supplanting others by moving towards them; chases and aggressive vocalizations, common in breeder-breeder and breeder-floater interactions, were extremely rare. For this reason, data are too limited to determine whether the floaters establish a constant dominance hierarchy. For example, within the BH/DAVIS aggregation, between November 1981 and April 1982, I observed 51 interactions (supplants) between 32 individual floaters where both were identified. Only five jays were seen supplanting more than one other jay, accounting for 22% of the 51 interactions. No reversals were seen, but there were only three cases where the same individuals interacted aggressively on different occasions. However, certain male floaters were clearly more aggressive than others; some of these jays established pseudo-territories in their area of dominance over other floaters.

Floater–floater pairing

By December of most years, <5% of floaters appeared to form pairs as evidenced by courtship feeding and associating closely. Even fewer defended pseudo-territories in April through mid-May. But in 1985, when floaters remained throughout the breeding season, three of 11 radio-tracked floaters formed pairs with untagged birds. None of these pairs built nests and only one pair attempted to defend a territory; the pair was dominant over, but did not exclude, other floaters, but was not dominant over territorial neighbors.

Virtually all breeding vacancies were filled by single jays replacing the mate of a widowed territory holder. Rarely did a floater establish a territory in previously unoccupied areas; in five cases (four by males and one by a female), a jay settled on the new territory and then acquired a mate. Thus, pairing by floaters does not precede or lead directly to territory acquisition.

DISPERSAL DISTANCES

Data from radio-tagged jays and resightings of floaters banded as nestlings indicate that initial dispersal for both sexes can be localized. Natal-to-breeding dispersal distances for 13 males and 6 females that acquired a territory and breeding status on or very near the study area are shown in Fig. 32; females traversed more territories than males (3.2 vs. 1.3). Because these data represent only a small proportion of the jays hatched on the study area that presumably acquired a territory elsewhere, they underestimate average dispersal distances. For example, three individuals banded as first-year floaters in winter were later recorded 32–40 km to the northwest from 5–9 months after banding.

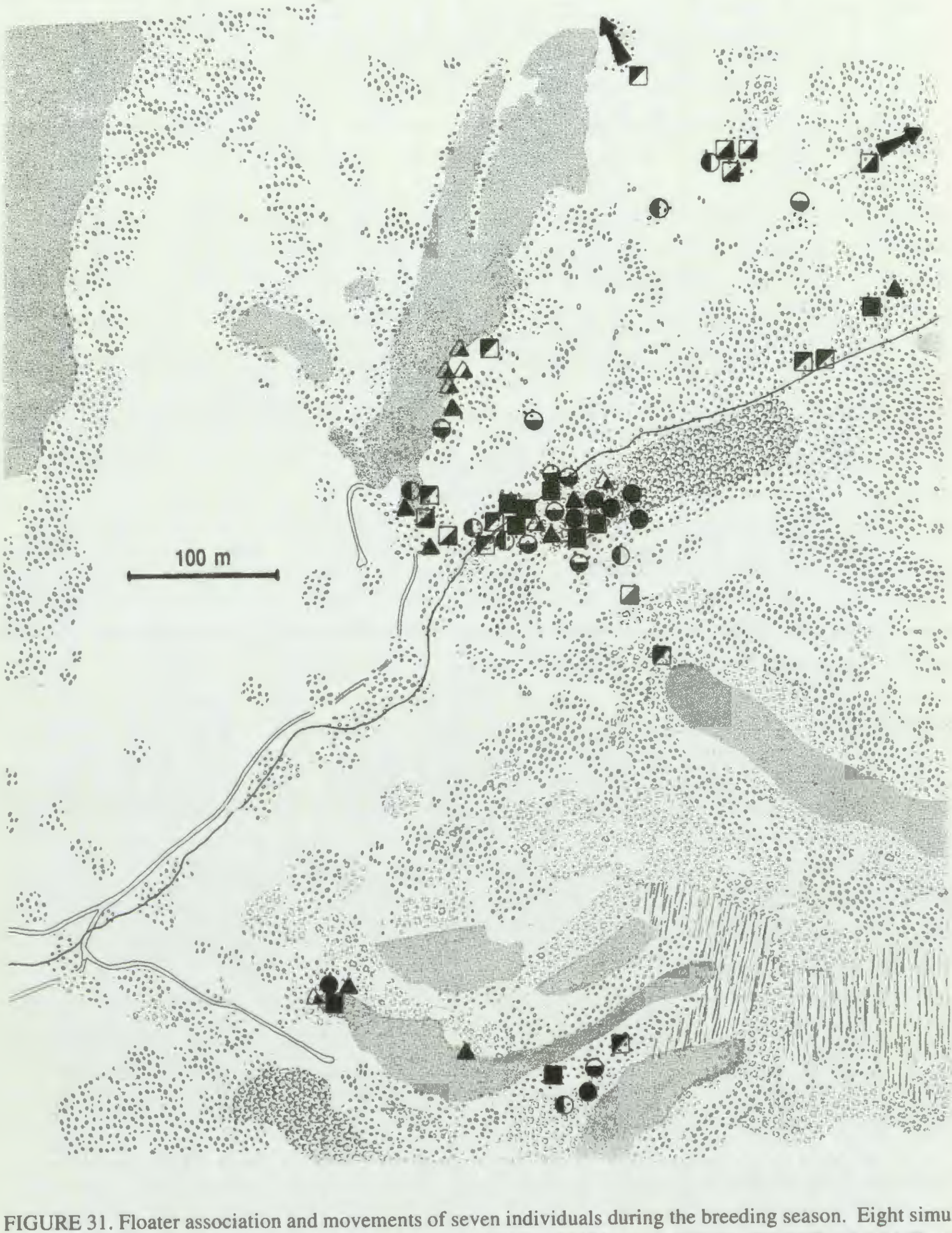

FIGURE 31. Floater association and movements of seven individuals during the breeding season. Eight simultaneous radio-locations were taken one hour apart from 0600 to 2000 hours on 7 May, 1985. The eight different geometric shapes represent the eight simultaneous locations of seven individuals.

REPRODUCTION

Reproductive success depends on many factors. First, a jay must acquire a territory and a mate. Both territory size and quality may influence clutch size (review by Klomp 1970, Högstedt 1980), time of nest initiation (Perrins 1970), and overall reproductive success. Second, fecundity and reproductive success increase with age and past breeding experience in most avian species studied (Klomp 1970, Harvey et al. 1979, Sæther 1990),