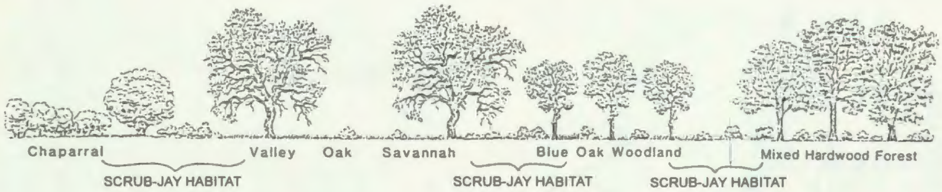

FIGURE 21. Schematic representation of habitat types and plant communities on the study area illustrating preferred, occupied scrub-jay habitat.

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.

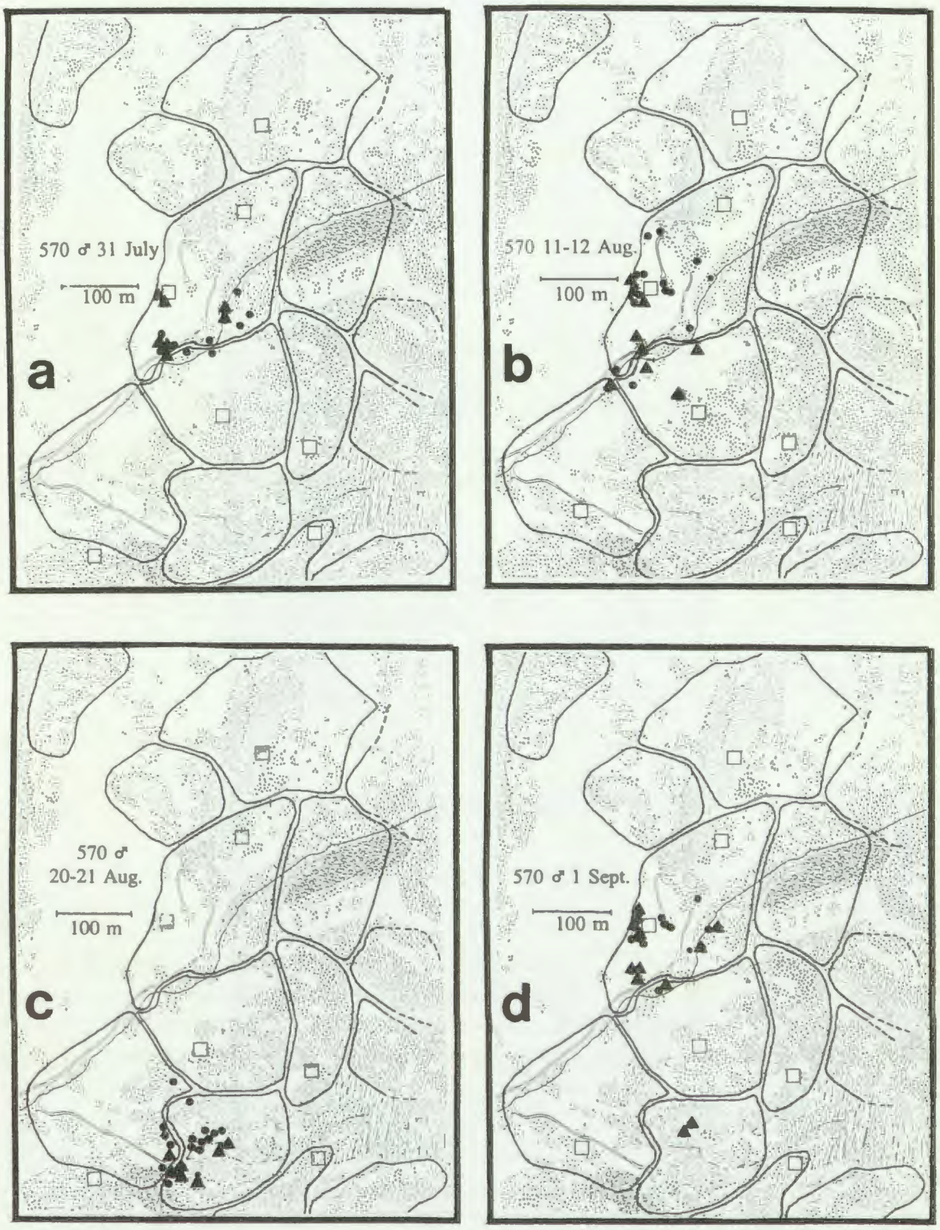

FIGURE 22. Radio-tracked dispersal of male 570 from its natal territory. Circles indicate one location, triangles ≥2 locations (N = 57 locations), open squares represent nest locations, and solid lines territory boundaries. Radio locations (a) 6 weeks (all locations on natal UB territory), (b) 7 weeks,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

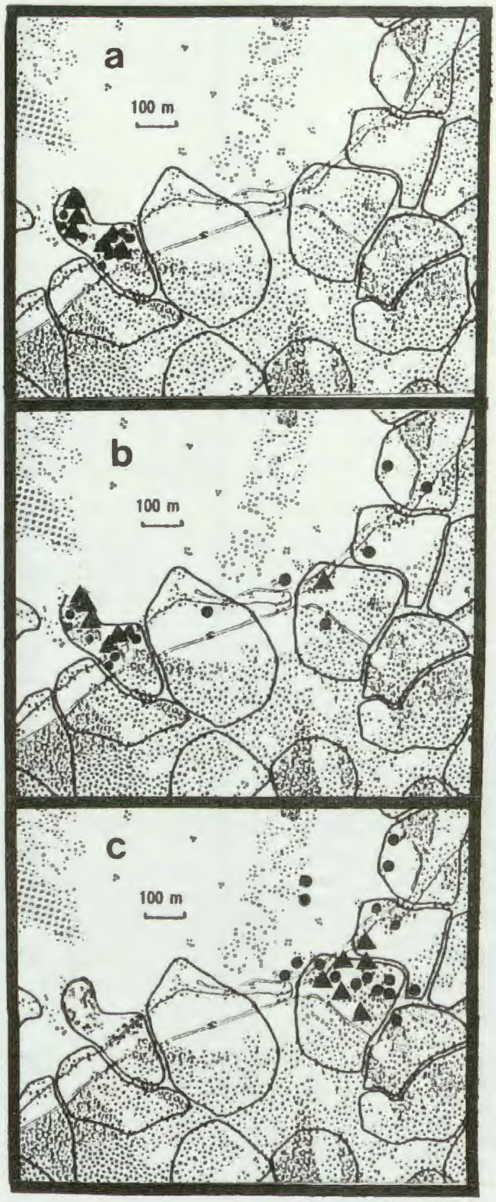

FIGURE 23. Radio-tracked dispersal of male 640 off its natal territory. Circles indicate one location, triangles ≥2 locations (N = 57 locations), and solid lines territory boundaries. Radio locations (a) 6 weeks (locations shown on map of the entire study area), (b) 7 weeks, and (c) 10 weeks after fledging.

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.

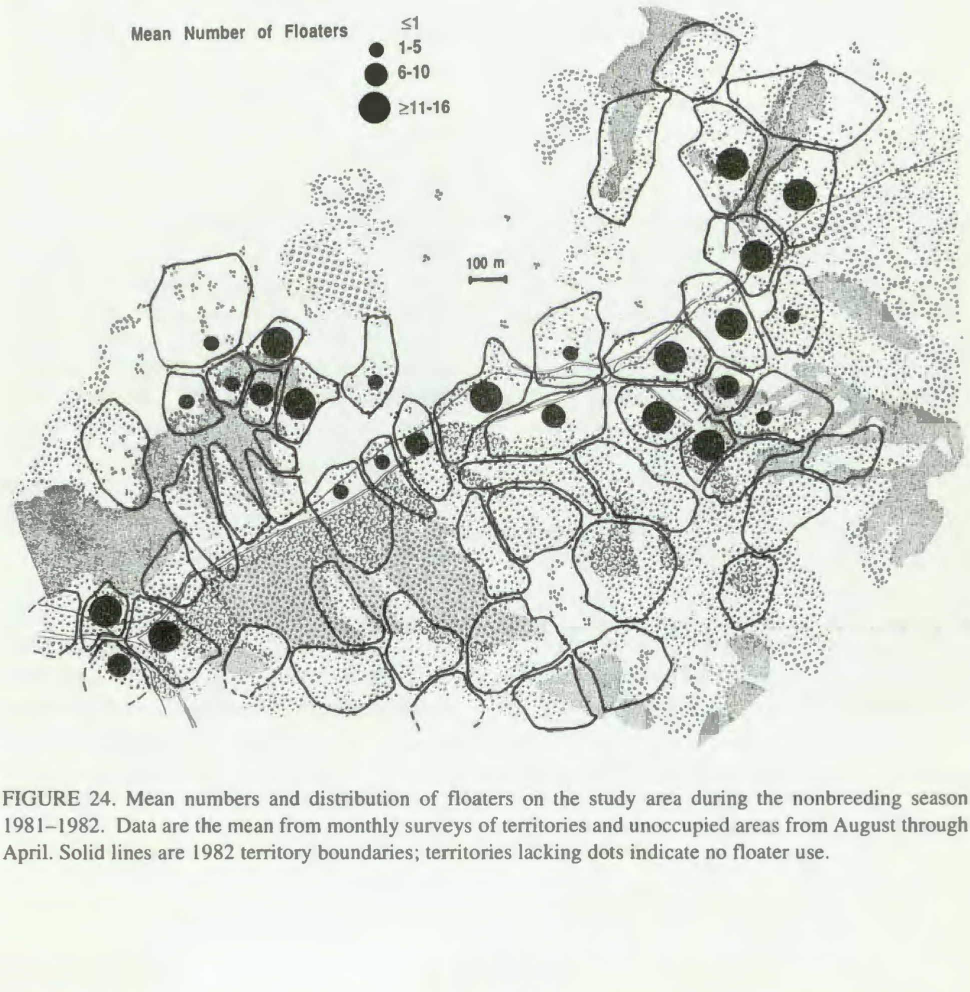

FIGURE 24. Mean numbers and distribution of floaters on the study area during the nonbreeding season 1981–1982. Data are the mean from monthly surveys of territories and unoccupied areas from August through April. Solid lines are 1982 territory boundaries; territories lacking dots indicate no floater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

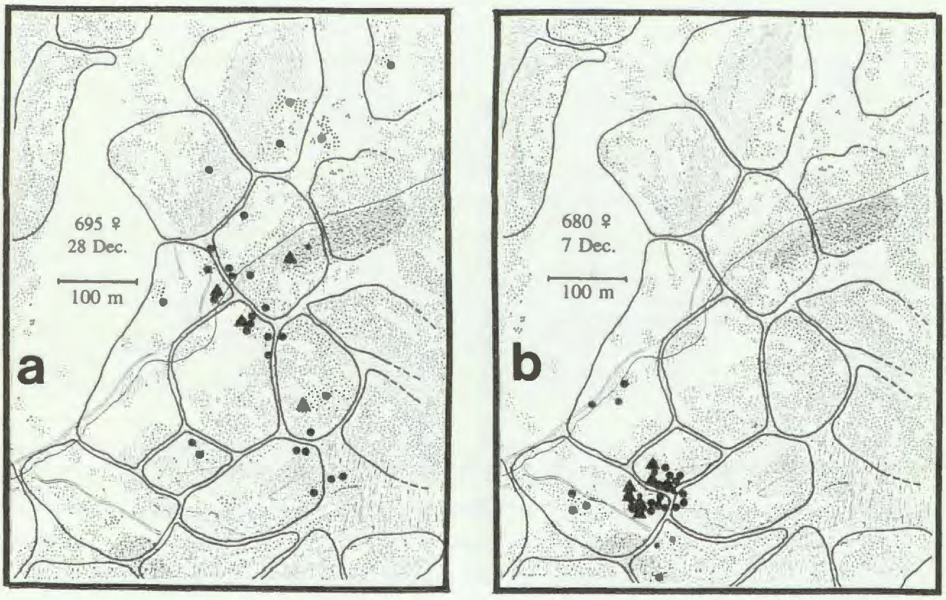

FIGURE 25. Radio-locations and winter home range use by two radio-collared first-year female floaters. Circles indicate one location, triangles ≥2 locations (N = 57 locations), and solid lines territory boundaries. (a) Female 695, and (b) Female 680.

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.

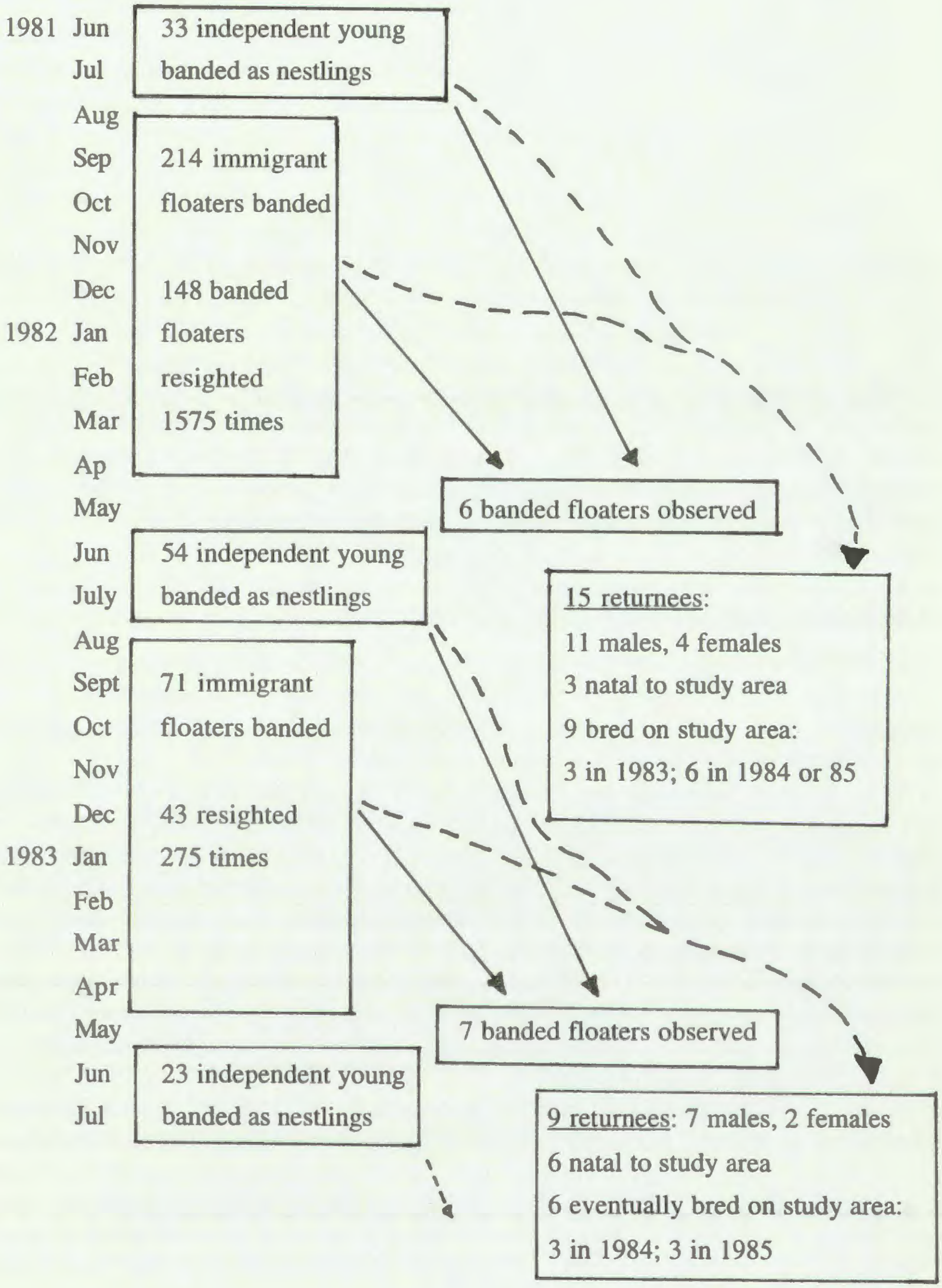

FIGURE 26. Chronology of dispersal and floating showing build-up of floaters during the winter, their disappearance in May, and the number and eventual fate of those that returned in late summer and fall.

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.

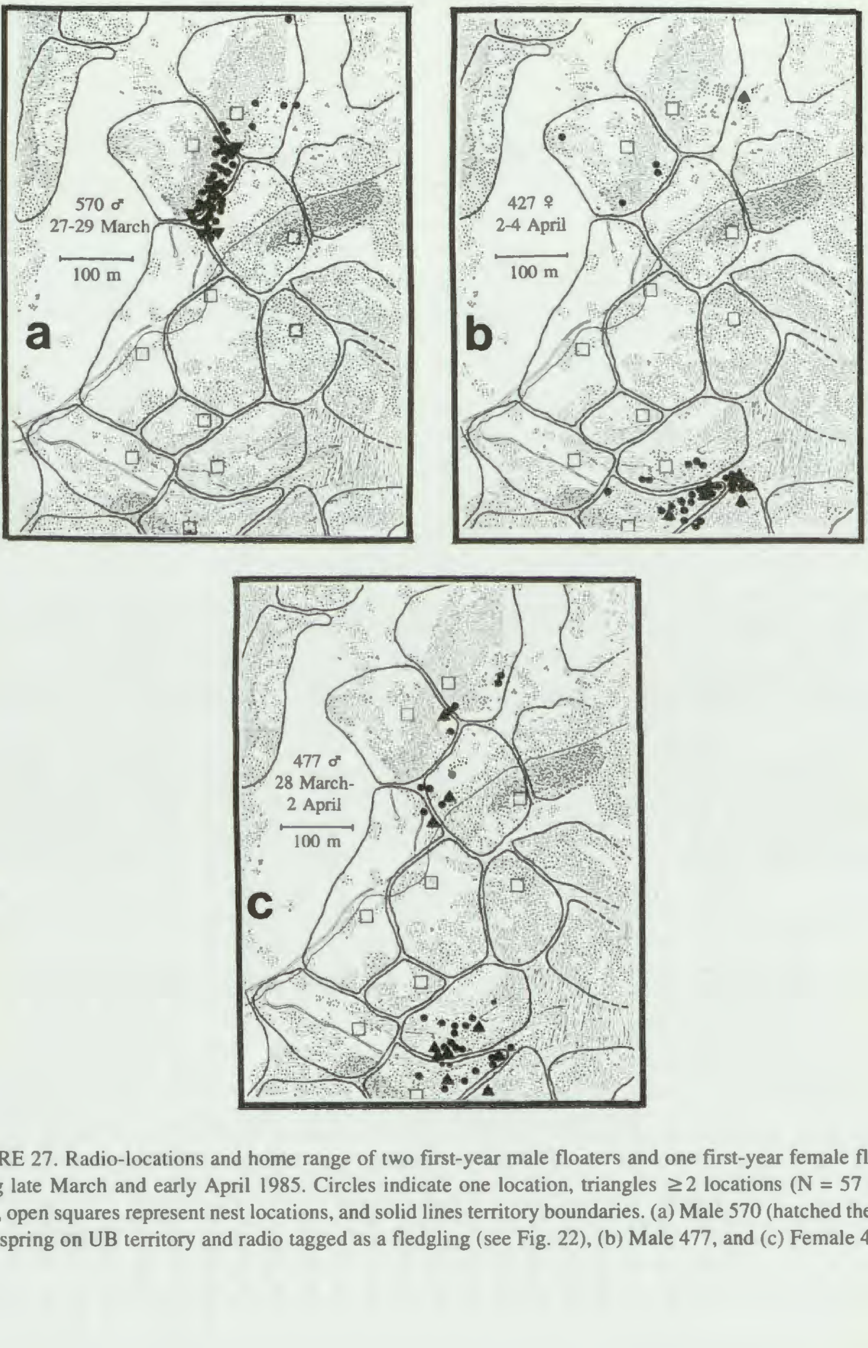

FIGURE 27. Radio-locations and home range of two first-year male floaters and one first-year female floater during late March and early April 1985. Circles indicate one location, triangles ≥2 locations (N = 57 locations), open squares represent nest locations, and solid lines territory boundaries. (a) 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 on territory	Percentage off territory	Out of sight	Off area
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: Days	N of composite sample: Hours	Dates	Home range: Size (ha)	Home range: 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).

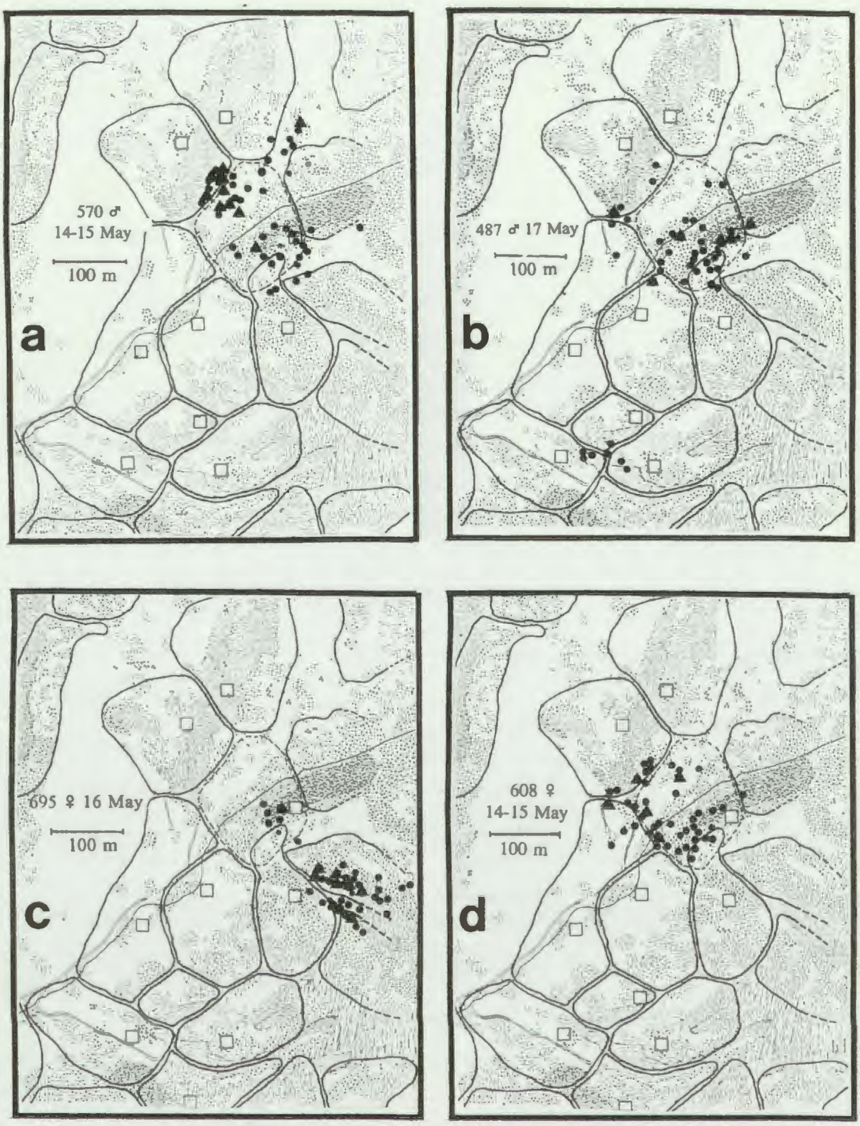

FIGURE 28. Radio-locations and home range of two first-year male floaters and two first-year female floaters during mid-May 1985. Circles indicate one location, triangles ≥2 locations (N = 57 locations), open squares represent nest locations, and solid lines territory boundaries. The stippled line indicates 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.

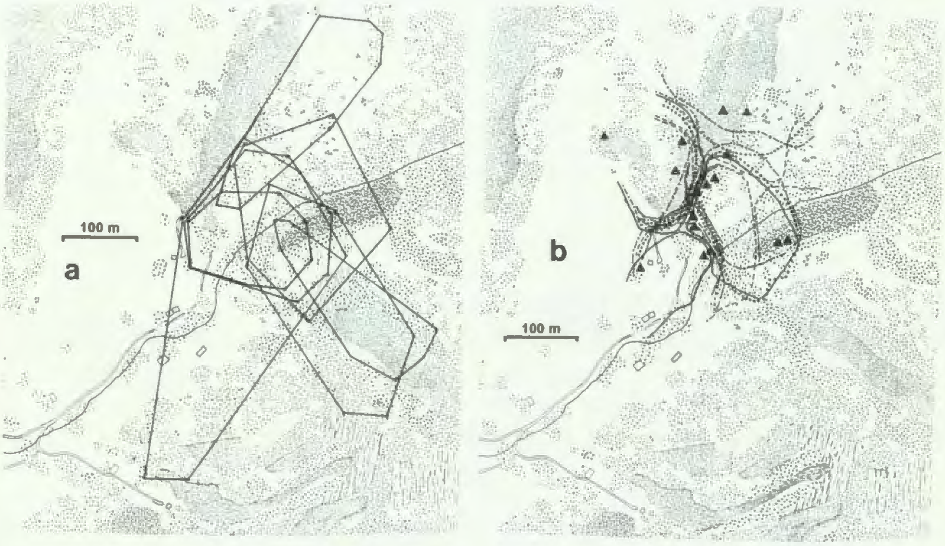

FIGURE 29. Home range of floaters in relation to territories and nest locations. (a) Home range of seven floaters (5 males, two females) in mid-May 1985. Lines represent minimum convex polygons encompassing 57 radio locations on each individual taken during three 3-h watches over a 1- or 2-day period. (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.

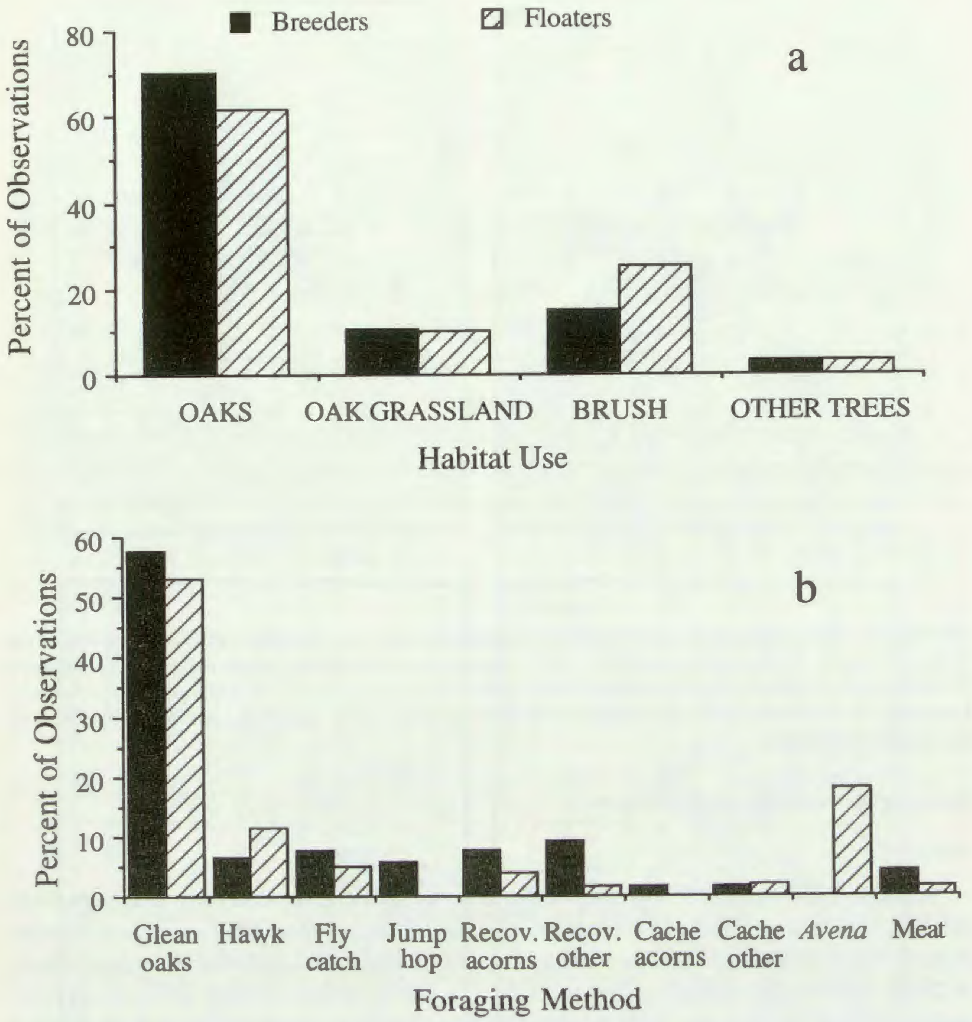

FIGURE 30. Comparison of breeders and floaters in (a) habitat use ($\chi^2 = 0.24$, df = 3, $P > 0.90$; N = 189 breeders, 224 floaters) and (b) foraging behavior ($\chi^2 = 17.1$, df = 18, $P > 0.90$; N = 120 breeders, 139 floaters) during the breeding season (5 May–20 May).

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.

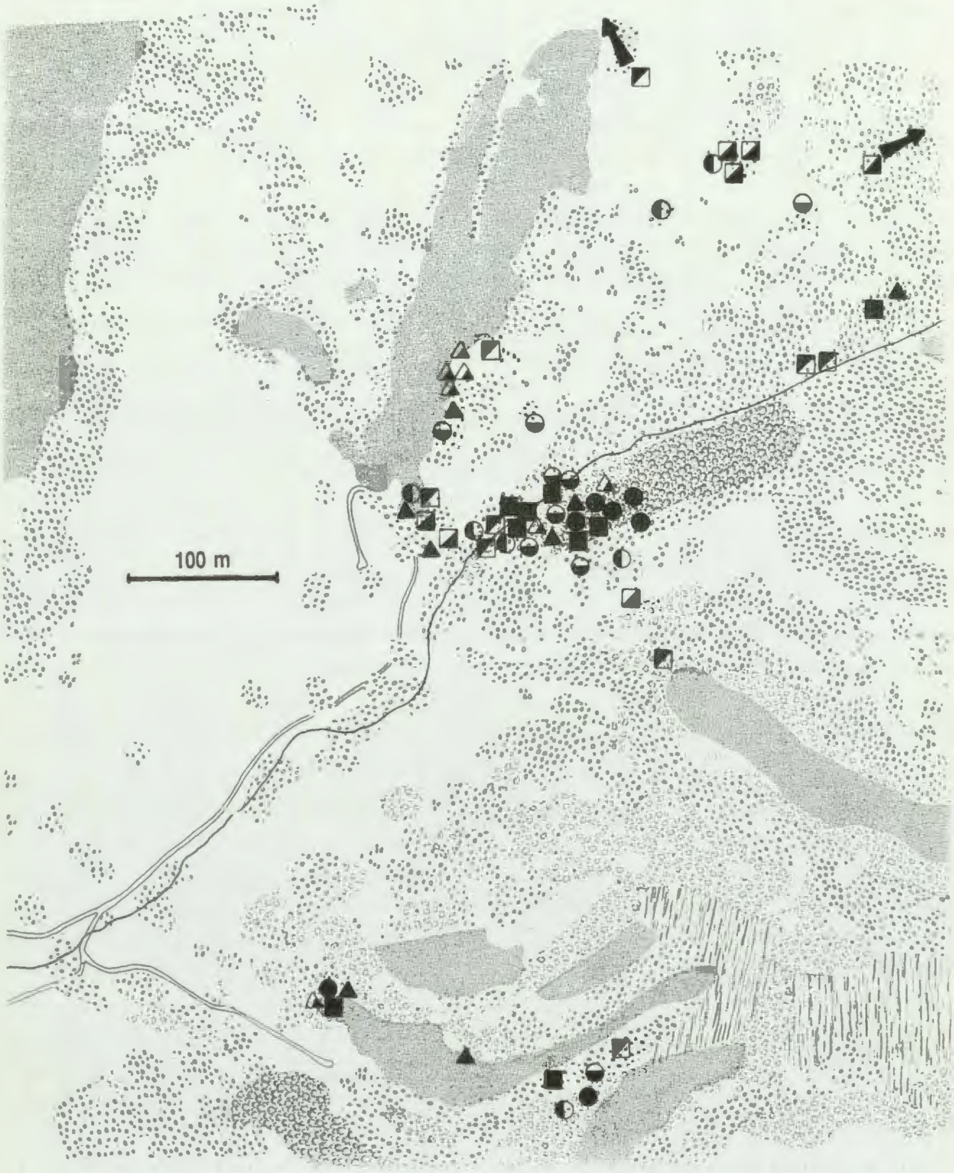

FIGURE 31. Floater association and movements of seven individuals during the breeding season. Eight simultaneous radio-locations were taken one hour apart from 0600 to 2000 hours on 7 May, 1985. The eight different geometric shapes represent the eight simultaneous locations of seven individuals.

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),