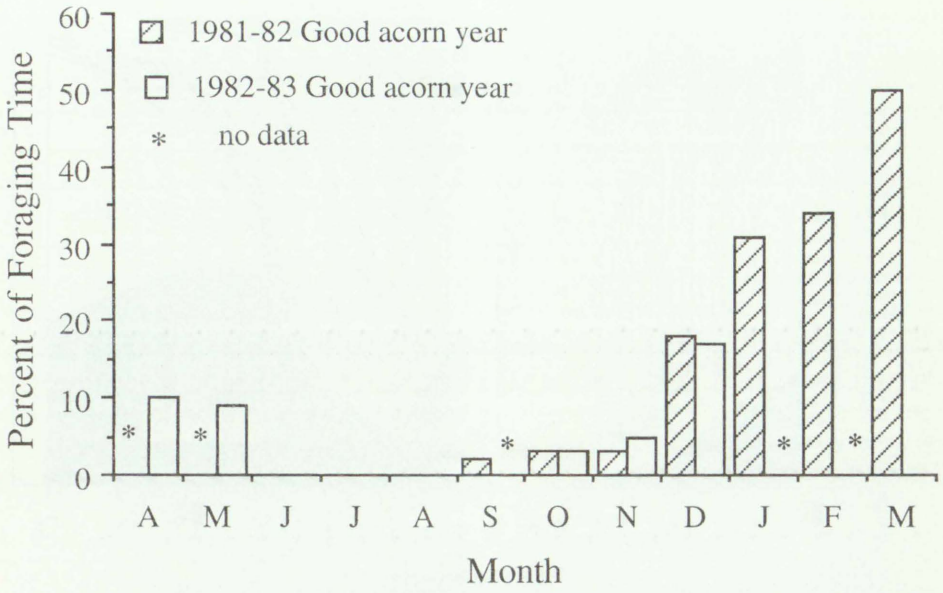

FIGURE 10. Percentage of foraging time territorial scrub-jays spent recovering and eating cached acorns and other cached food during the good acorn years (see text for explanation). Months without bars indicate no data were taken.

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

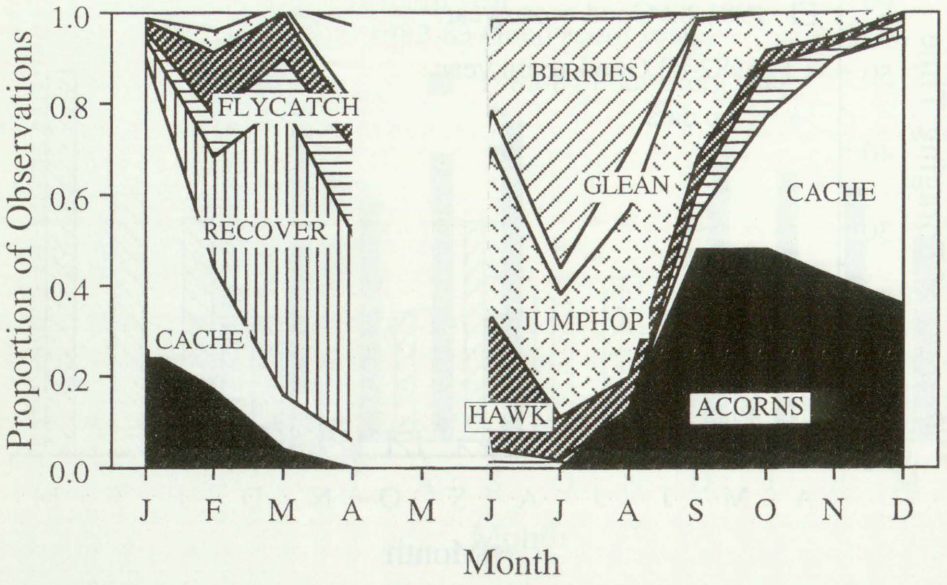

FIGURE 11. Seasonal change in foraging activities of nonbreeding floater scrub-jays, primarily first-year birds, over the year expressed as a proportion of all foraging activity (see text for explanation).

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

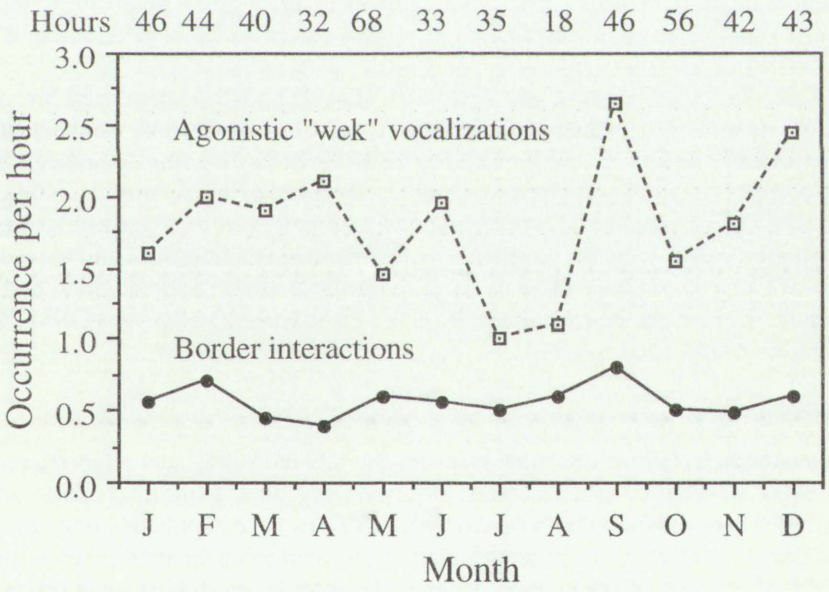

FIGURE 12. Rate of border interactions and aggressive "*wek*" vocalizations territorial scrub-jays directed towards territory neighbors. Numbers at top of figure are hours of observation of territorial scrub-jays.

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.

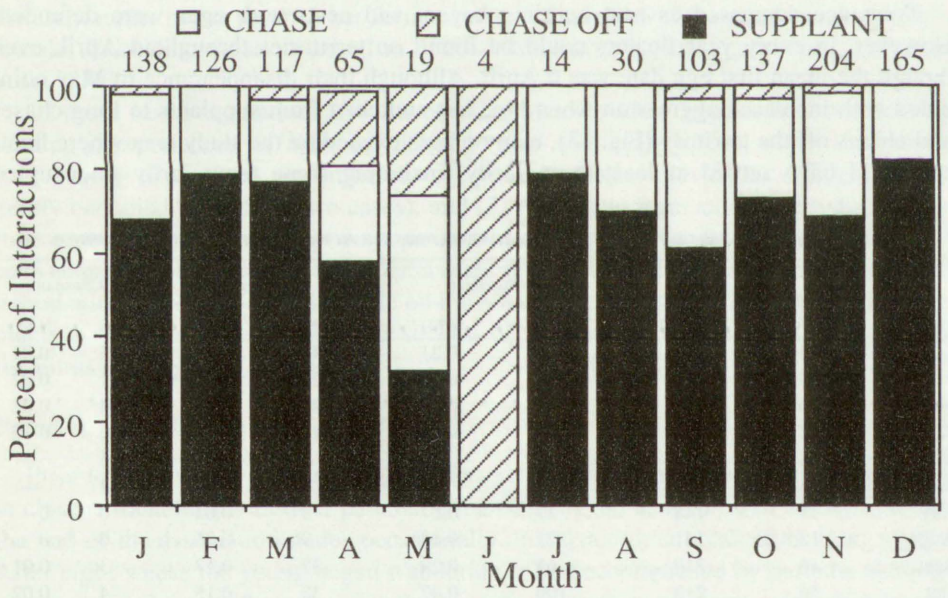

FIGURE 13. Seasonal change in aggressive behaviors breeders directed at floaters. Numbers above bars are total number of interactions recorded in each month.

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).

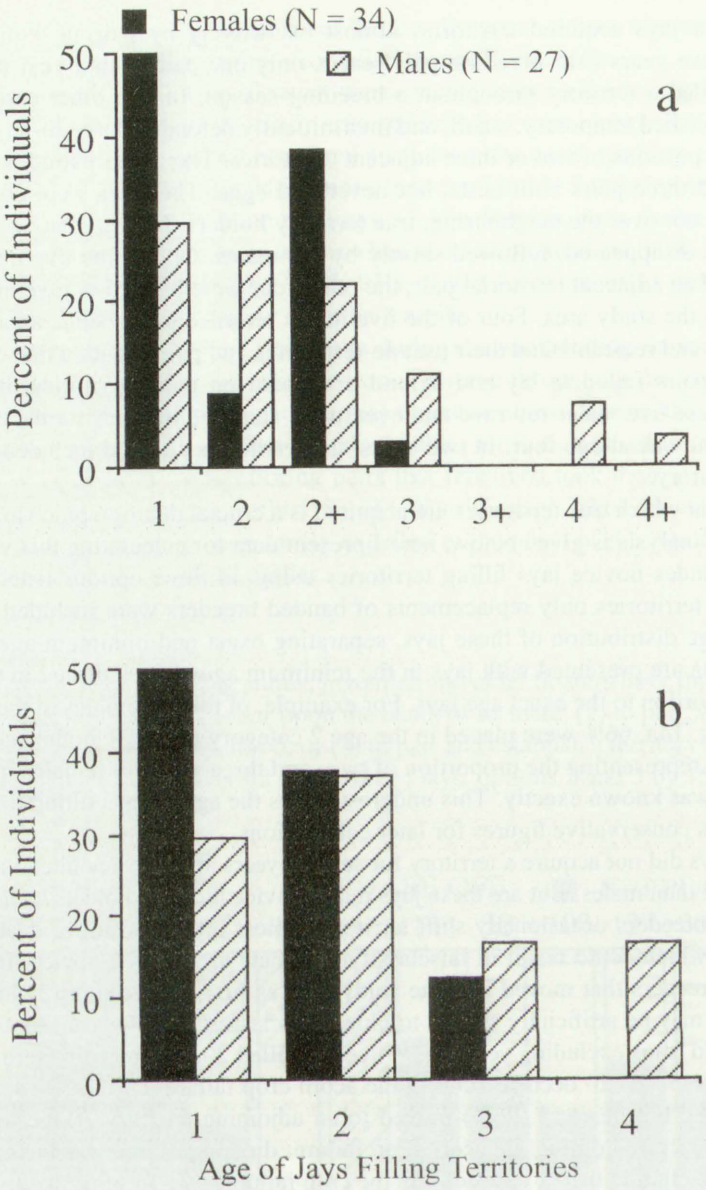

FIGURE 14. Age distribution of first-time breeders filling territory vacancies: a) age distribution includes exact and minimum ages; b) age distribution with minimum age scrub-jays included in age categories in proportion to the distribution of exact age scrub-jays filling territories.

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 hatched	Number independent	Number acquiring breeding status in 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.

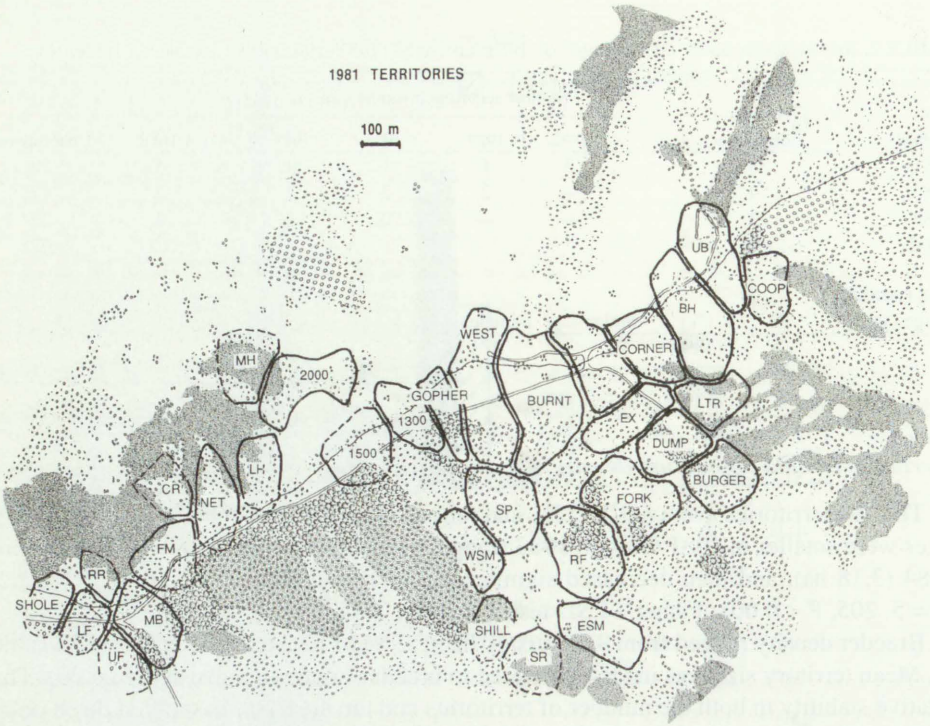

FIGURE 15. Location of scrub-jay territories in 1981. Vegetation key as in Figure 2.

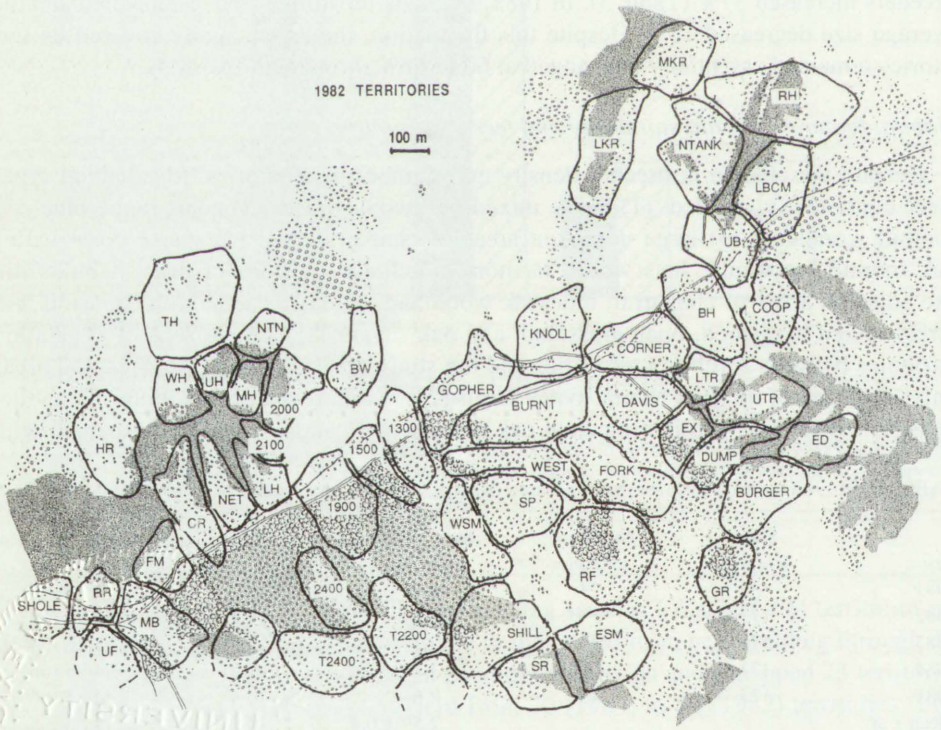

FIGURE 16. Location of scrub-jay territories in 1982. Vegetation key as in Figure 2.

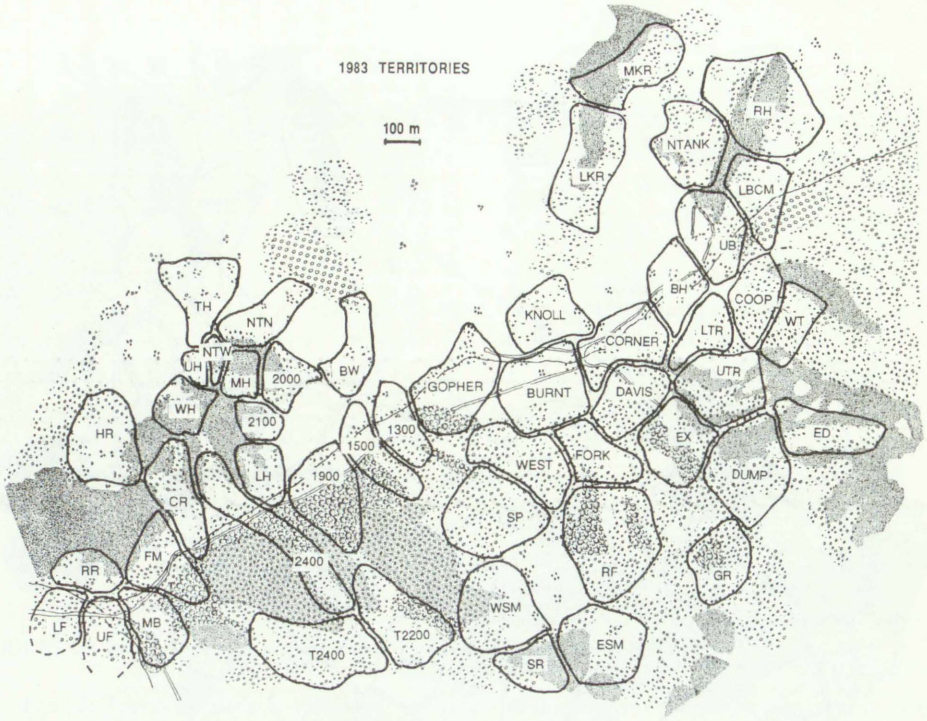

FIGURE 17. Location of scrub-jay territories in 1983. Vegetation key as in Figure 2.

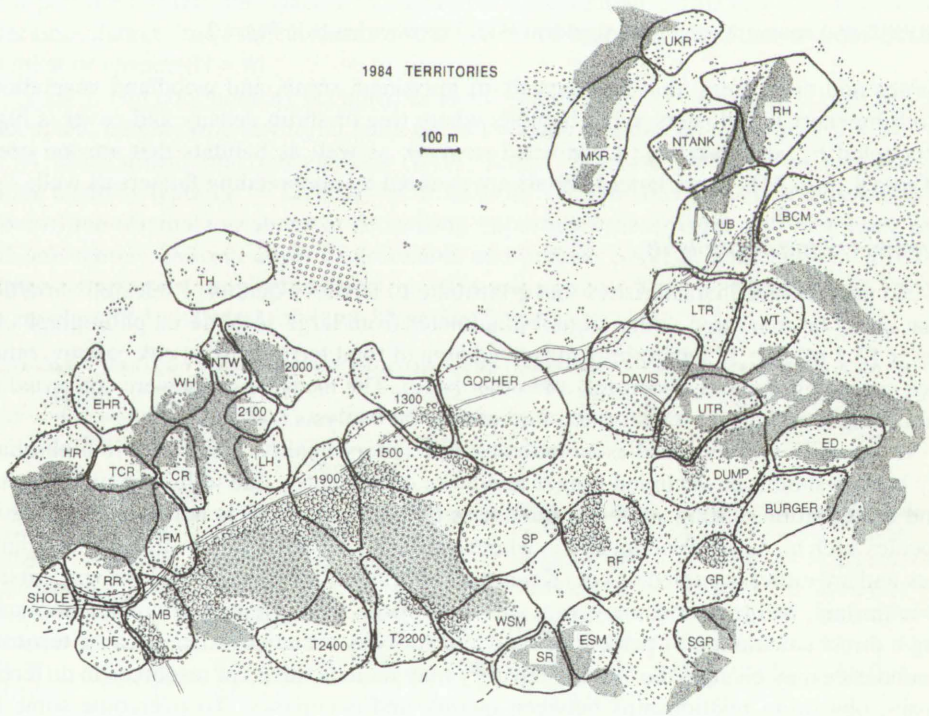

FIGURE 18. Location of scrub-jay territories in 1984. Vegetation key as in Figure 2.

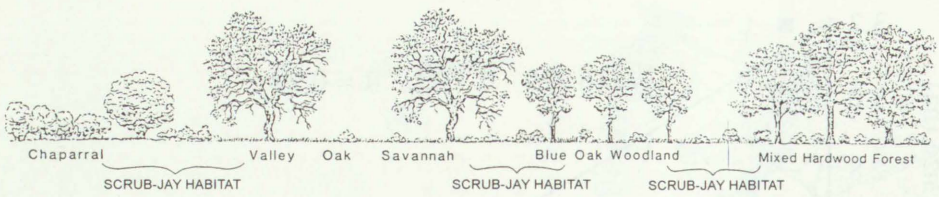

FIGURE 21. Schematic representation of habitat types and plant communities on the study area illustrating preferred, occupied scrub-jay habitat.

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.