including the Florida Scrub-Jay (Woolfenden and Fitzpatrick 1984) and the Mexican Jay (Brown 1986). In addition, because reproduction in scrub-jays is a joint effort, attributes of the pair, such as length of pair bond, may enhance breeding success (Woolfenden and Fitzpatrick 1984). Third, annual variation in environmental and ecological conditions may amplify or overwhelm these differences.

In this section, I examine reproductive success of Hastings jays and attempt to unravel the factors that influence an individual's breeding success once it has established a territory.

BREEDING CHRONOLOGY

Nest building typically begins in early March (Fig. 33), although first egg date (FED) varied significantly over the study period (Kruskal-Wallis ANOVA $\chi^2 = 50.9$, df = 4, $P < 0.001$; Table 9). Jays at Hastings fledged only one brood per year but renested up to two times if earlier nests failed. Over the study period an average of 51% of pairs losing first nests renested. Second broods (renesting after successfully fledging young) have been observed in other populations of Western Scrub-Jays (*A. californica superciliosa*, C. Van Riper, pers. comm.; *A. californica oocleptica*, F. Pitelka, pers. comm.). In Florida Scrub-Jays, 13% of pairs fledging young from first nests attempted to raise second broods (Woolfenden and Fitzpatrick 1984).

Females may begin incubation after the first egg is laid or later, and nestlings hatch synchronously or over several days. The complete nest cycle takes approximately 49

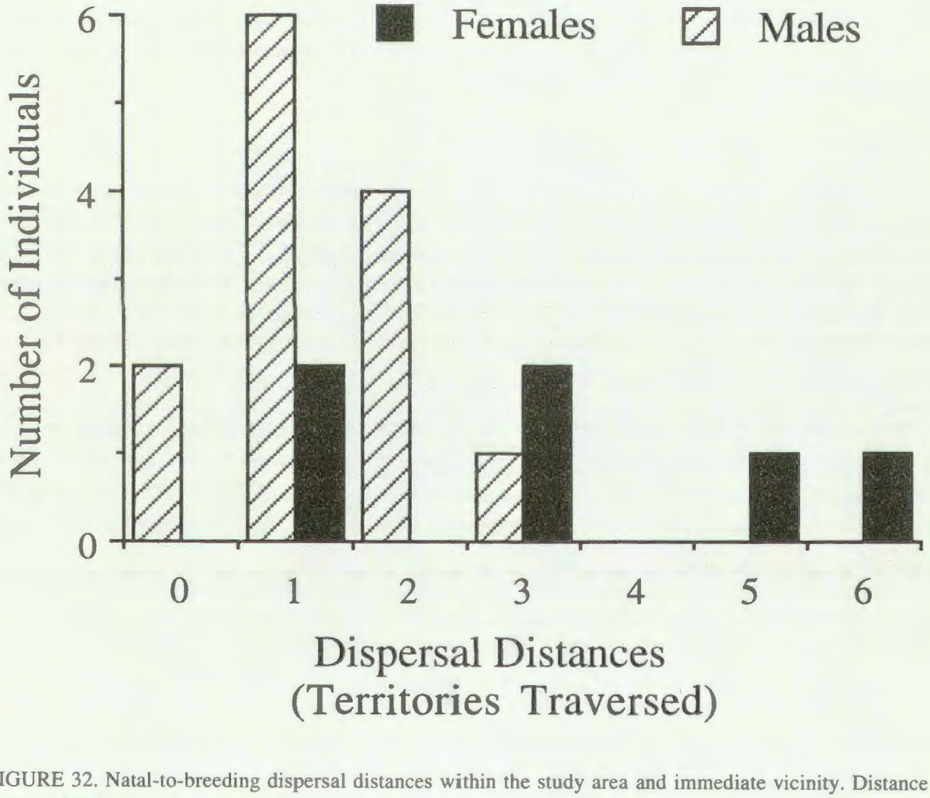

FIGURE 32. Natal-to-breeding dispersal distances within the study area and immediate vicinity. Distance is measured in territories traversed.

days: 3–5 for laying, 19–24 for incubation, and 21–24 from hatching to fledging. Most pairs have nestlings by late April and fledging peaks in late May but extends to mid-July (Fig. 33).

ANNUAL PRODUCTION OF FLEDGLINGS AND INDEPENDENT YOUNG

Tables 10 and 11 summarize the mean annual reproduction variables. Nest failure is high (51% of first nests, 60% of all nests) and renesting increases mean annual production (Table 10) by 25% (fledglings) and 21% (independent young). The proportion of pairs renesting did not vary significantly among years, but ranged from a low of 35% in 1984 (following acorn crop failure) to 58% in 1982 (Chi-square $\chi^2 = 2.3$, df = 4, $P > 0.05$; Table 9). Overall mean annual production of fledglings was 1.19/pair and varied significantly from 0.62 in 1984 to 1.56 in 1981 (Kruskal-Wallis ANOVA $\chi^2 = 17.5$, df = 4, $P = 0.001$); independent young averaged 0.88/pair and varied from 0.37 to 1.32 (Kruskal-Wallis ANOVA $\chi^2 = 25.4$, df = 4, $P < 0.001$; Table 10). Fifty-two percent of pairs monitored from clutch initiation fledged young (43% when all pairs are included; Table 11).

FACTORS INFLUENCING REPRODUCTIVE SUCCESS

Failure to lay eggs

Over five years, the proportion of territorial pairs that laid eggs varied from 96% in 1981 to 62% in 1984 (mean = 81%; Table 11). Only two of 23 first-year female:adult male pairs laid (Table 12), both in 1985. Adult females paired with first-year males laid in 4 of 10 cases. In 1984, 12 of 38 adult pairs did not lay eggs (Table 12), probably because of the poor acorn crop in fall of 1983.

Clutch size

The modal clutch size was 4 (67.9% of 140 complete clutches); three-egg clutches made up 24.3%, and 1, 2, and 5 egg clutches fewer than 8%. Clutch size did not vary among years, with a overall mean of 3.7 and annual range of 3.5 to 3.8 (Table 11). The modal clutch size was the most productive in four of five years, but three-egg clutches produced more fledglings in 1983.

Survival of eggs, nestlings, and fledglings

Data on survival (Table 13) are based on 761 eggs and 460 nestlings in 208 nests. The samples include nests where clutch size (67) and brood size (20) were not determined (see METHODS); in these cases the mean clutch size (3.7) or brood size (3.0) was assumed. Hatching success ranged from 53% in 1984 to 70% in 1985 (mean = 61%) and

TABLE 9. FIRST EGG DATE (MEAN ± SD) AND THE PERCENTAGE OF PAIRS RENESTING

Year	Number of pairs	First egg date	Range	Pairs renesting
1981	25	7 April ± 10	29 March–22 April	55% (6/11)
1982	51	7 April ± 10	20 March–27 April	58% (11/19)
1983	52	7 April ± 7	28 March–21 April	48% (14/29)
1984	42	20 April ± 11	7 April–7 May	35% (6/17)
1985	45	25 March ± 7	12 March–10 April	57% (8/14)
Overall	215	7 April ± 8	12 March–7 May	51%

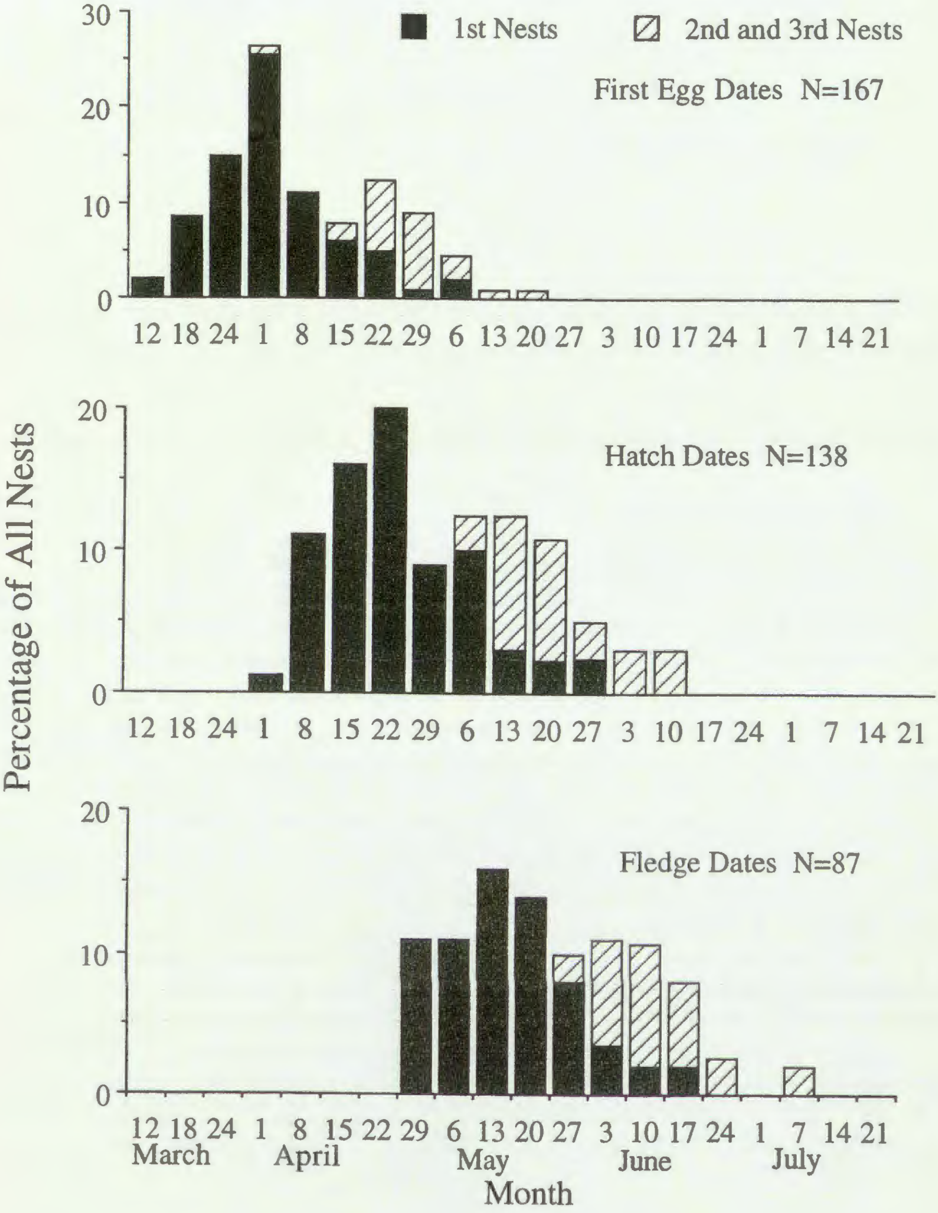

FIGURE 33. Nesting chronology of Hastings scrub-jays, 1981–1985.

fledging success from 18–40% (mean = 30%). Losses from fledging to one month post-fledging averaged 27%, and ranged from 14% to 44%. Years with low fledging success also showed the lowest fledgling survival ($R_s = 0.99$, $P < 0.05$).

Key-factor analysis

Key-factor analysis (Varley and Gradwell 1960) can be used to determine which factor

TABLE 10. Annual production (mean ± SD) of fledglings and independent young (number of pairs in parentheses)

	First nests only		All nests	
Year	Fledge	Independent[a]	Fledge	Independent
1981	1.21 ± 1.4	1.08 ± 1.2	1.52 ± 1.5	1.32 ± 1.3
	(25)	(25)	(25)	(25)
1982	1.08± 1.5	0.76 ± 1.1	1.56 ± 1.6	1.08 ± 1.3
	(51)	(51)	(50)	(50)
1983	0.58 ± 1.1	0.37 ± 0.9	0.79 ± 1.2	0.45 ± 0.9
	(52)	(52)	(52)	(51)
1984	0.50 ± 1.6	0.32 ± 0.9	0.62 ± 1.2	0.37 ± 1.0
	(42)	(41)	(42)	(41)
1985	1.16 ± 1.5	0.96 ±1.3	1.44 ± 1.5	1.18 ± 1.3
	(45)	(45)	(45)	(45)
Pooled	0.87 ± 1.4	0.66 ± 1.1	1.16 ± 1.5	0.84 ± 1.2
Means	0.91 ± 0.3	0.70 ± 0.3	1.19 ± 0.4	0.88 ± 0.4
	(215)	(214)	(214)	(212)

[a] Young counted as independent at 4 weeks after fledging.

was primarily responsible for variation in reproductive success. First, maximum potential egg production is estimated. Then, actual egg production is measured and subsequent survivorship is followed. Thus, comparisons are between potential and actual production. This allows less tangible factors such as failure to lay eggs, failure to renest, etc., to be considered. The data are converted to logarithms, and total mortality is obtained by summing the individual mortality events ($k_1 + k_2 + \ldots + k_n = k_{total}$). Thus, k_{total} is the difference between potential and actual production. When the k values are plotted against time, the k-factor that is largest and parallels k_{total} is designated the key factor responsible for the variability. This need not always be the largest portion of annual mortality; for example, in Common Woodpigeons (*Columba palumbus*), 80% of all eggs were taken by predators, but this contributed little to the observed fluctuations in annual mortality (Murton and Westwood 1977).

TABLE 11. Annual variation in reproductive variables

				% of eggs				Breeding success	
Year	N	Percent breeding	Clutch size	Hatched	Fledged	% of hatched eggs fledged[a]	% fledged to independence	Breeding	All
1981	25	96%	3.5±1.0	64.2%	32.0%	50%	87%	67.0%	64.0%
	(6/11)	(50/78)	(25/50)	(33/38)	(16/24)	(16/25)			
1982	51	82%	3.8±0.5	59.6%	40.4%	68%	69%	61.0%	52.9%
	(11/19)	(109/183)	(74/109)	(54/78)	(27/44)	(27/51)			
1983	52	85%	3.7±0.7	56.3%	19.7%	35%	59%	36.0%	30.8%
	(14/29)	(117/208)	(41/117)	(23/39)	(16/44)	(16/52)			
1984	42	62%	3.8±0.4	53.0%	18.8%	35%	63%	27.0%	16.7%
	(6/17)	(62/117)	(22/62)	(15/24)	(7/26)	(7/42)			
1985	45	84%	3.7±0.6	69.7%	37.1%	53%	82%	66.0%	55.6%
	(8/14)	(122/175)	(65/122)	(53/65)	(24/38)	(24/45)			
Mean	216	81%	3.7	60.6%	29.6%	48%	72%	52.0%	43.2%
		$\chi^2 = 15.8$	$\chi^2 = 2.4$	$\chi^2 = 11$	$\chi^2 = 31$	$\chi^2 = 30$	$\chi^2 = 11.8$	$\chi^2 = 16.8$	$\chi^2 = 24.6$
		$P = 0.003$	$P = 0.66$	$P = 0.03$	$P < 0.001$	$P < 0.001$	$P < 0.01$	$P = 0.002$	$P < 0.001$

Note: Tests for differences among years in reproductive variables by χ^2 contingency except clutch size and mean fledged by Kruskal-Wallis ANOVA.

[a] Clutch size undetermined in 62 cases and brood size in 20; mean clutch size (3.7 eggs) and brood size (3.0 chicks) were assumed.

TABLE 12. AGE COMPOSITION OF PAIRS AND NUMBER INITIATING BREEDING

	Composition		Number of pairs		
Year	Male	Female	Total	Followed	Breeding
1981	Adult	Adult	29	24	24 (100%)
	1st yr	Adult	0	—	—
	Adult	1st yr	1	1	0
1982	Adult	Adult	40	40	40 (100%)
	1st yr	Adult	6	6	3 (50%)
	Adult	1st yr	5	5	0
1983	Adult	Adult	46	44	44 (100%)
	1st yr	Adult	2	2	0
	Adult	1st yr	6	6	0 (100%)
1984	Adult	Adult	39	38	26 (68%)
	1st yr	Adult	0	—	—
	Adult	1st yr	4	4	0
1985	Adult	Adult	35	35	35 (100%)
	1st yr	Adult	2	2	1 (50%)
	Adult	1st yr	7	7	2 (29%)
	1st yr	1st yr	1	1	0
Total	Adult	Adult	188	181	171 (94%)
	1st yr	Adult	10	10	4 (40%)
	Adult	1st yr	23	23	2 (9%)
	1st yr	1st yr	1	1	0
Grand total			223	215	177 (82%)

I considered the following variables (Table 11):

1. *Maximum potential egg production*: the modal clutch size, four, was taken as the maximum, as five egg clutches comprised only 5% of all clutches. Each year many first nests fail. I therefore added the corresponding number of eggs to potential egg production, assuming that all of these pairs could lay replacement clutches. Because only 51% of pairs renested, this overestimates potential egg production but does not effect the results of the analysis.

2. *"Mortality" events*: (a) k_1: failure to lay eggs; (b) k_2: failure to lay four eggs in clutch; (c) k_3: failure to renest; (d) k_4: egg loss; (e) k_5: nestling loss; (f) k_6: fledgling loss (to one month).

The results are plotted in Fig. 34. Nestling mortality (k_5) contributes greatest to k_{total} and parallels it most closely. However, several other factors influence k_{total}. In 1984 all factors increased except modal clutch size (k_2), and failure to lay (k_1) jumped appreciably; 1984 was the only year some adult-adult pairs failed to lay.

Causes of nest and fledgling mortality

Although losses of nestlings contributed most to annual fluctuations in reproductive output, egg and fledgling losses were also considerable. Here I assume, first, that losses of entire clutches and broods, not due to breeder death or abandonment, were due to predators; usually physical evidence confirmed this. Second, nestlings that disappeared from continuing broods were counted as having starved to death; this ignores partial brood predation (no cases detected) and also disease and parasites (probably minimal). For broods of one, no cause was assigned.

Of the 208 nests, 84 (40.4%) fledged young (Table 13). Predation accounted for most

TABLE 13. FATE OF EGGS, FLEDGLINGS, AND NESTS

	Individuals			Nests		
	N	% individuals	% loss	N	% nests	% loss
Eggs and nests	761	100%		208	100%	
losses due to:						
Hatching failure	39	5.1%	12.0%	0		
Desertion	3	0.4%	1.0%	1	0.5%	1.4%
Breeder death	20	2.6%	6.7%	6	2.9%	8.2%
Predation	239	31.4%	79.4%	66	31.7%	90.4%
Total lost before hatching	301	39.5%	100%	73	35.1%	100%
Nestlings and nests	460	100%		135	100%	
losses due to:						
Breeder death	15	3.3%	6.4%	4	3.0%	7.8%
Starvation	79	17.2%	33.9%	—[a]	—[a]	—[a]
Predation	132	28.7%	56.7%	41	30.4%	80.4%
Ambiguous	7	1.5%	3.0%	6	4.4%	11.8%
Total lost after hatching	233	50.7%	100%	51	37.8%	100%
Survivorship	227	29.8%	(eggs)	84	40.4%	
		49.3%	(nestlings)		62.2%	

[a] All losses of entire broods assumed to be caused by predation.

losses during the egg and nestling stages, abandonment and breeder death less than 10%, and starvation 17.2%.

Yearly variation in predation and starvation

Predation on eggs averaged 31.7% but varied significantly over the five years, as did predation on nestlings (mean = 30.6%; Table 14). The mean percentage of nestlings starving (16.3%) was not statistically different among years.

ECOLOGICAL AND ENVIRONMENTAL EFFECTS

Weather

For scrub-jays at Hastings, I found no significant correlations between weather variables (mean annual, winter, and spring rainfall; mean, mean minimum, and mean maximum winter and spring temperatures) and reproductive variables (including FED and overall mean annual reproductive success). Nor did I find any significant correlations between weather and the annual relative abundance of the diet fed to nestlings (e.g., flying insects from the yellow-pan samples or ground-dwelling insects from the grassland sweep samples) or acorn crops (from surveys of 250 oaks; Carmen et al. 1987).

Food and reproduction

Correlations among four reproductive variables and the relative abundance of several food types are presented in Table 15. Total flying insect abundance was positively correlated with FED (i.e., higher insect abundance coincided with later FED). This is surprising and counterintuitive because jays usually initiate breeding before adult insects become abundant, and early onset of breeding is expected to be correlated with higher insect abundance. I was unable to measure the relative abundance of lepidopteran larvae on oak leaves, which are the main prey of jays early in the spring and more likely to influences reproductive activity.

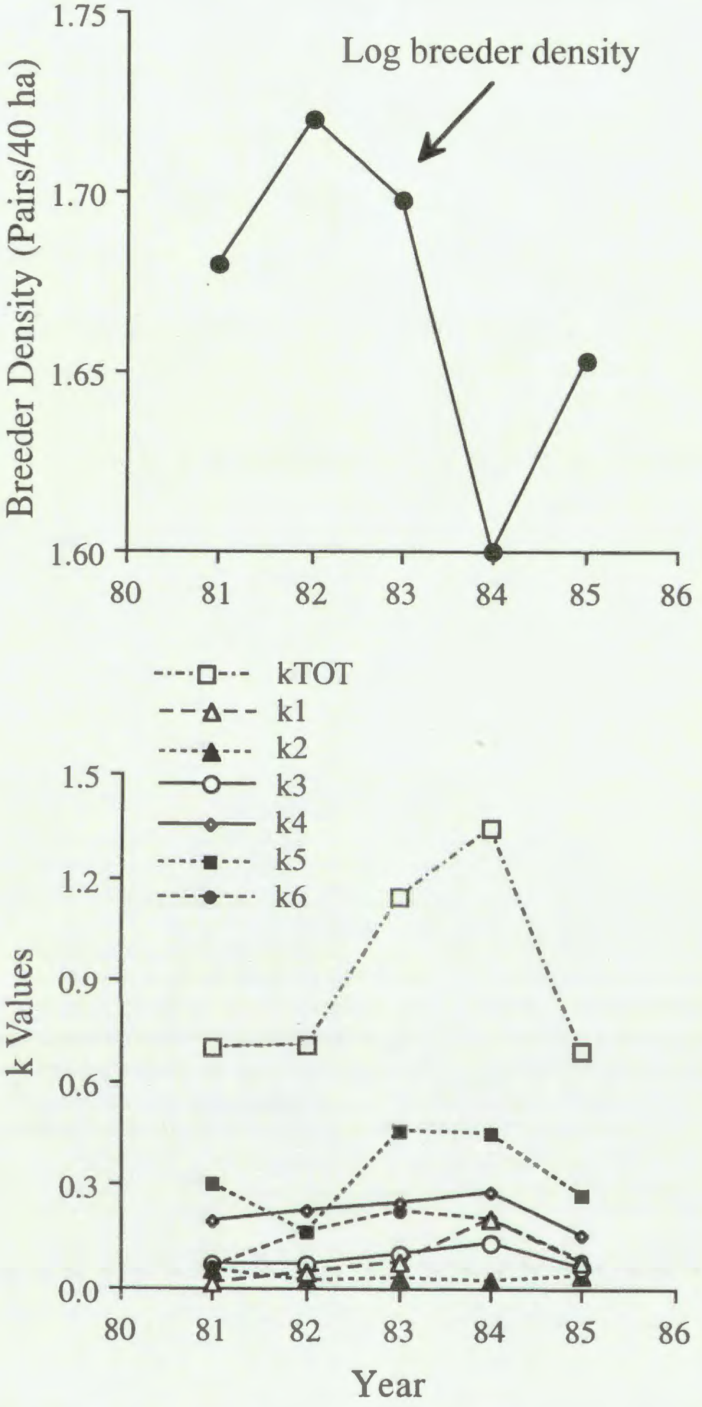

FIGURE 34. Log of breeder density (pairs/40 ha) and k-values 1981–1985 (see text for explanation of key-factor analysis). k1: failure to lay eggs; k2: failure to lay four eggs in clutch; k3: failure to renest; k4: egg loss; k5: nestling loss; k6: fledgling loss.

TABLE 14. ANNUAL PREDATION AND STARVATION RATES OF EGGS, NESTLINGS, AND NESTS

	Predation on				
Year	Eggs	Nestlings	E+N combined	Nests	Starvation of nestlings
1981	29.6%	38.0%	51%	50%	12.0%
	(21/78)	(19/50)	(40/78)	(12/24)	(6/50)
1982	32.8%	10.1%	39%	39%	16.5%
	(60/183)	(11/109)	(71/183)	(20/51)	(18/109)
1983	37.0%	35.9%	57%	64%	20.5%
	(77/208)	(42/117)	(119/208)	(36/56)	(24/117)
1984	38.5%	40.3%	60%	63%	14.5%
	(45/117)	(25/62)	(70/117)	(19/30)	(9/62)
1985	20.6%	28.7%	41%	42%	18.0%
	(36/175)	(35/122)	(71/175)	(20/47)	(22/122)
Mean	31.7%	30.6%	50%	52%	16.3%
	$\chi^2 = 16$	$\chi^2 = 27$	$\chi^2 = 24$	$\chi^2 = 10$	$\chi^2 = 2.3$
	$P = 0.003$	$P = 0.001$	$P < 0.001$	$P = 0.03$	$P > 0.05$

Note: Statistical tests of differences in predation and starvation losses among years by chi-square contingency.

Both total acorn abundance and the abundance of *Q. agrifolia* acorns were correlated with standardized FED and overall breeding success (Table 15). When acorns, particularly those of *Q. agrifolia*, were abundant, scrub-jays bred earlier and were more successful.

To test whether acorn availability enhances reproductive success, I supplied four pairs of jays with acorns during the crop failure of 1983–1984. Each week, from late December through March, I placed 200 acorns on an elevated feeding platform at the center of each territory. The jays in all cases responded quickly and stored the acorns within 30 min. The fed pairs all laid eggs (compared to 22 of 34 unfed pairs) and laid an average of 15 days earlier than the average for the unfed pairs (see discussion of effect of acorn supplementation on time-budgets of jays). Schoech (1996) found that Florida Scrub-Jays fed supplemental dog food from January to clutch completion laid their clutches an average 16 days earlier than nonsupplemented groups.

Timing

At Hastings, while neither clutch size nor production from first nests alone is correlated with standardized FED, the number of independent young from first nests, and total fledged and independent young from all nest attempts, was greater for early nesting pairs

TABLE 15. SPEARMAN RANK CORRELATIONS OF MEAN ANNUAL REPRODUCTION VARIABLES WITH ANNUAL ACORN AND INSECT ABUNDANCE (N = 5 YEARS)

Mean	Yellow-pan insects	Sweep-net insects	Total acorns	*Q. agrifolia* acorns only
FED[a]	0.94**	0.20	–0.76*	–1.00***
Fledged	–0.21	–0.16	0.60	0.52
Independent	–0.32	0.34	0.17	0.45
Percent successful	–0.54	0.45	0.75*	0.85**

[a] First egg date, standardized so that the earliest egg each year falls on the same date.

*0.1 > P > 0.05

**0.05 > P > 0.01

***0.01 > P > 0.001

(Spearman rank test, all $P < 0.01$). To examine what factors contribute to higher success of jays initiating breeding early in the spring, unstandardized FED was divided into three categories: early (prior to 1 April), middle (1 April to 12 April), and late (past 12 April). The middle category's midpoint is 6 April, the overall mean FED for the population. The results of this analysis indicate that the benefits of early nesting occur in two ways. First, early nesters had a higher probability of renesting; 60%, 53% and 6% for early-, middle-, and late-nesters, respectively (R×C test, $P < 0.001$). Second, early nesters experienced lower fledgling losses; 14%, 37%, and 33% for early-, middle-, and late-nesters, respectively (R×C test, $P < 0.001$).

The benefits of early nesting are not likely to end at independence. In several studies, early-fledging individuals have greater competitive ability or higher status leading to an improved probability of obtaining a territory and breeding (e.g. Eurasian Magpies [Eden 1987]; Black-capped Chickadees, *Poecile atricapillus* [Glase 1973]; Eurasian Nuthatches, *Sitta europaea* [Matthysen 1987]; and Song Sparrows [Arcese and Smith 1985]).

Breeder density

Breeder density varied from 9.2–12.2 pairs/40 ha (Table 3); the correlation with annual fledgling production was not significant. Highest fledgling production came in 1982, the year of highest breeder density, and the lowest in 1984 with the lowest breeder density.

Territory quality

No discernable relationship existed between territory quality and mean annual fledgling production; 1.3, 1.1, and 0.9 fledglings per territory for Types 1 through Type 3, respectively (Kruskal-Wallis ANOVA $\chi^2 = 1.3$, df = 2, $P = 0.37$). Although the trend is in the expected direction, factors such as high rates of nest loss and differences in parental quality, particularly those associated with age effects, may obscure the effect of territory quality on measured reproductive success.

EFFECTS OF AGE AND EXPERIENCE

Age of breeders

Age is the most important influence on reproductive success (Table 16). Adult pairs comprised the vast majority of all pairs and were responsible for nearly all successful reproduction (98% of 253 fledglings). Of 23 adult male:first-year female pairs on true territories, only two pairs laid and hatched young and only one fledged young. All 23 adult male:first-year female pairs successfully defended territories, built nests, and in all other respects appeared to be stable, bonded pairs. An additional four adult male:first-year female pairs defended pseudo-territories. Of 10 first-year male:adult-female pairs, four laid eggs, two hatched young, but none fledged young. Also, none of these pairs established pseudo-territories. Only one first-year pair defended a territory throughout the breeding season; no eggs were laid.

To determine whether age beyond the first year affects reproduction, I compared the reproductive output of jays of one sex from 2 to ≥5 year-old paired with jays of the other sex two years or older; hence, the age of the mate of a jay of a given age could vary from two years to the potential longevity in the population (the oldest known breeder, a male, was 11 years old in 1987). Although the age of both members of a pair is important, there were few pairs where the exact age of both individuals was known.

Female age was significantly correlated with standardized FED, clutch size, total fledged, and total independent young (Table 17). This was true also of FED with age of male, and approaches significance with total fledged ($P = 0.06$) and independent young ($P = 0.08$; Table 17). These relationships are broken down by age class in Table 18 and Figure 35, and reveal a significant decrease in FED and a significant increase in fledglings and independent young per pair for females and males through age four (when first-year birds are included, all variables show a significant increase with age). Most of these variables varied significantly among years, but the relationships between age and reproduction also hold within a single year (1985), the year with the most complete data (Fig. 35). However, because most of the data for the older age classes are from 1985 (a good production year), the values may slightly overestimate average reproductive output for the older age classes.

Duration of pair bond

FED and years together as a pair shows a significant negative correlation ($R_s = -0.36$, $P < 0.01$; Table 17); the longer the pair remained intact, the earlier it nested. Jays with enduring pair bonds nested an average 10 days earlier than recently paired jays.

Prior breeding experience

In comparisons between novice and experienced pairs older than one year, neither FED, number fledged, and number independent were statistically significant, despite nearly twice the fledgling output of experienced pairs (Table 19).

SURVIVORSHIP

Patterns of age- and sex-specific survival affect population structure (Caughley 1977), mating systems (Murray 1984), social organization (Woolfenden and Fitzpatrick 1984), and overall fitness, through their influence on life-time reproductive success (Koenig and Mumme 1987, van Balen et al. 1987, Fitzpatrick and Woolfenden 1988, Fitzpatrick et al. 1989). Newly independent young in most cooperatively breeding species face the options of independent breeding or delayed dispersal (and helping); in noncooperative species, the options are independent breeding or floating. Survivorship plays a key role in determining the relative benefits of these options. Increased survivorship of helpers on their natal territories and their assisted parents are hypothesized to be important factors favoring delayed dispersal and cooperative breeding (Brown 1974, Emlen 1982, Koenig and Pitelka 1981, Woolfenden and Fitzpatrick 1984; Arnold and Owens 1998, 1999). In

TABLE 16. PERCENTAGE OF TERRITORIAL PAIRS BY AGE COMPOSITION THAT LAID EGGS, BREEDING SUCCESS, AND MEAN NUMBER FLEDGED

Age composition	Number of pairs	% breeding	% breeding success	Mean number fledged	Total number fledged
Both first-year	1	0%	0%	0	0
Adult ♂: first-year ♀	23	8.7%	4.3%	0.1	2
First-year ♂: adult ♀	10	40.0%	10.0%	0.3	3
Both adult	181	94.0%	60.0%	1.4	248

TABLE 17. Spearman rank correlations of four reproductive variables with age of male (2 to 5+ years), age of female (2 to 5+ years), and years together as a pair (0 to 2) (N in parentheses)

	Age of male	Age of female	Years together
FED[a]	–0.45	–0.48	–0.36
	(44)	(32)	(58)
	P = 0.009	P = 0.002	P = 0.01
Clutch	0.21	0.44	0.04
	(33)	(26)	(48)
	NS[b]	P = 0.02	NS
Fledge	0.24	0.41	0.12
	(60)	(46)	(83)
	P = 0.06	P = 0.005	NS
Independent young	0.23	0.32	0.13
	(60)	(46)	(83)
	P = 0.08	P = 0.03	NS

[a] First egg date standardized so that the first egg each year falls on the same date.

[b] $P > 0.10$.

addition, survivorship of breeders may largely determine how many breeding vacancies open, and the survivorship of floaters (and helpers) determines the intensity of competition for these vacancies.

Here I examine survivorship of both territorial breeders and nonterritorial floaters and calculate sex- and age-specific survival rates based on population averages over a five-year study period. The resulting life table allows calculation of other key demographic parameters that are important in evaluating the costs and benefits of early dispersal and floating.

TABLE 18. Effects of breeder age on reproduction (mean ± sd) (N in parentheses)

	Age (yr)					
	1	2	3	4	5+	P[a]
FED[b]						
Female	–	7 Ap ± 14	12 Ap ± 17	21 Mr ± 7	24 Mr ± 7	$\chi^2 = 11.4$
	(0)	(8)	(7)	(6)	(11)	P = 0.001
Male	8 Ap ± 13	20 Ap ± 15	10 Ap ± 14	28 Mr ± 10	1 Ap ± 13	$X^2 = 7.64$
	(2)	(4)	(8)	(4)	(28)	P = 0.05
Clutch size						
Female	–	3.1 ± 1.1	3.6 ± 0.5	3.5 ± 0.6	4.0 ± 0.5	$\chi^2 = 4.23$
	(8)	(7)	(6)	(11)	NS	
Male	3.0 ± 0	2.5 ± 2.1	3.7 ± 0.5	3.5 ± 0.6	3.7 ± 0.8	$\chi^2 = 5.01$
	(2)	(2)	(7)	(4)	(21)	NS
Fledglings						
Female	0.08 ± 0.4	0.7 ± 1.3	1.1 ± 1.5	2.4 ± 1.1	2.2 ± 1.8	$\chi^2 = 8.7$
	(24)	(15)	(9)	(8)	(14)	P = 0.03
Male	0.3 ± 1.0	0.6 ± 1.5	0.8 ± 1.2	1.7 ± 1.3	1.6 ± 1.6	$\chi^2 = 3.1$
	(9)	(7)	(10)	(7)	(36)	NS
Independent young						
Female	0.04 ± 0.2	0.6 ± 1.1	1.1 ± 1.5	2.0 ± 1.1	1.7 ± 1.6	$\chi^2 = 6.7$
	(24)	(15)	(9)	(8)	(14)	P = 0.08
Male	0.3 ± 1.0	0.4 ± 1.1	0.3 ± 0.5	1.1 ± 1.1	1.2 ± 1.4	$\chi^2 = 2.2$
	(9)	(7)	(10)	(7)	(36)	NS

[a] Kruskal-Wallis tests of differences among ages classes 2–5; if age class 1 is included all comparisons are significant. NS denotes $P > 0.10$.

[b] FED = first egg date. Ap=April, Mr=March.

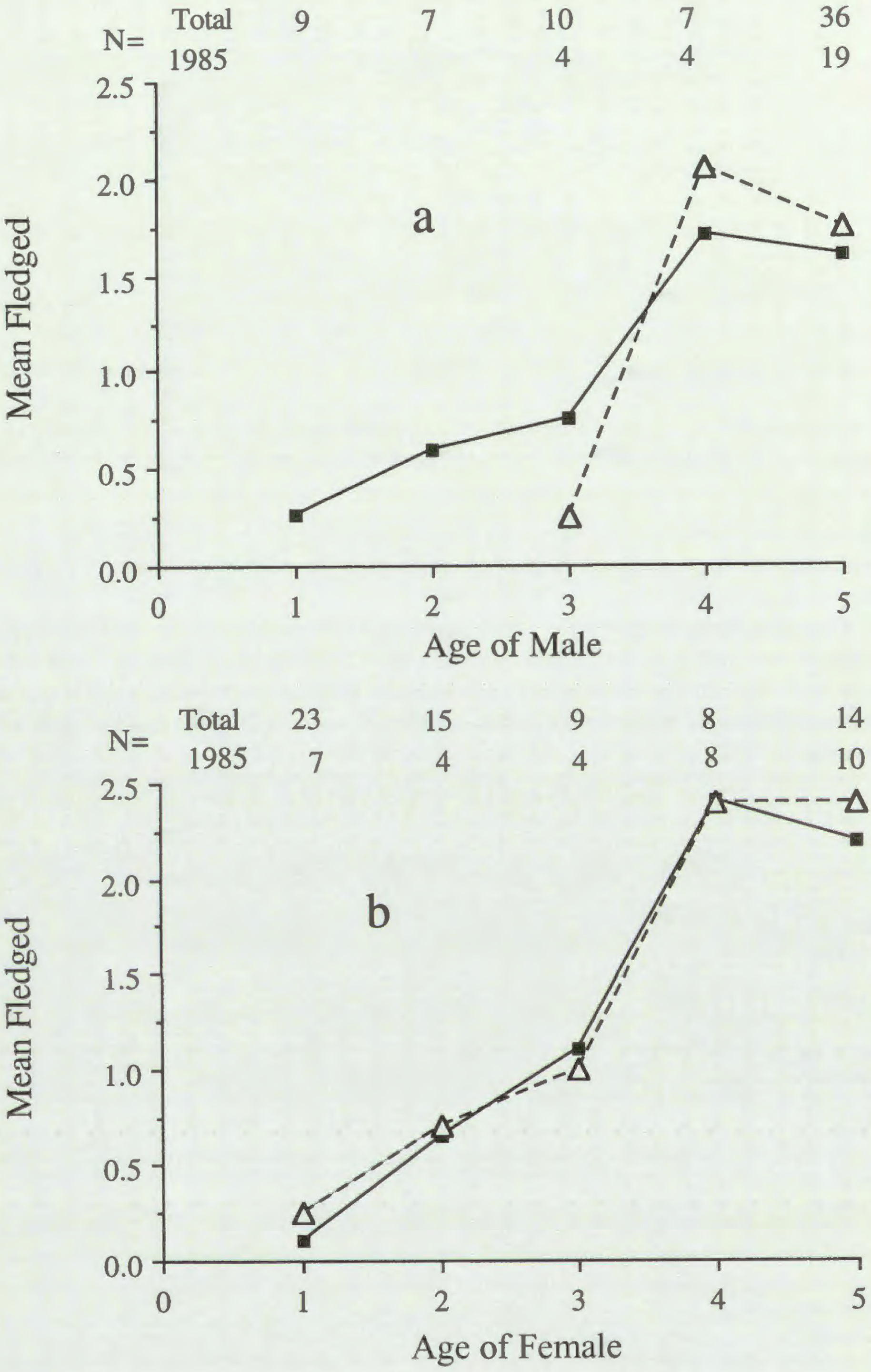

FIGURE 35. Age-specific fledgling production of breeding males (a) and females (b). Pooled data from all years, and for 1985 only, are plotted. Sample sizes for each year are plotted across the top.

TABLE 19. EFFECT OF PAST BREEDING EXPERIENCE ON REPRODUCTION (PAIRS THAT INCLUDED A FIRST-YEAR JAY ARE EXCLUDED) (NUMBER OF NESTS IN PARENTHESES)

	No prior experience	Experienced	P[a]
First egg date	9 April ± 12	3 April ± 12	Z = 1.25
	(6)	(52)	P = 0.21
Young fledged	0.73 ± 1.1	1.39 ± 1.6	Z = −1.13
	(11)	(70)	P = 0.26
Independent young	0.6 ± 0.9	1.01 ± 1.3	Z = −0.82
	(10)	(70)	P = 0.41

[a] Mann-Whitney U-tests for differences in variables between experienced and inexperienced breeders.

SURVIVORSHIP OF BREEDERS

Assumptions

Once a scrub-jay acquires a territory and breeding status, it typically retains both until death. Although it is usually not possible to separate deaths from emigration, several lines of evidence indicate that death was responsible for virtually all breeder disappearance on the study area.

Scrub-jays at Hastings rarely leave their territories. As no floater was ever seen to dominate a breeder, it is unlikely that breeders were ever evicted by floaters. Excluding 1983–1984 (the year of the acorn crop failure), only one individual assumed dead later returned to its territory. In that case, neither the male nor female was seen on their territory between October and February, when the male returned with a first-year female. In contrast, between August 1983 and February 1984, 59 of 103 banded breeders disappeared; 38 returned later, most in March and April.

Typically, jays that lost a mate remained on their own territory and acquired a new mate from the pool of floaters. However, in several instances, a known breeder paired with the resident on a different territory. This presents two lines of possible error in calculating survivorship rates. First, it was not always clear whether these jays separated from their mates or their mates had died. I classified them as separations if the bird was later seen as a floater (i.e., adults with breeding experience can become floaters); however, the probability of observing such individuals is low and the calculations of survivorship may be artificially low. However, separations were relatively rare.

Second, individuals that move away from the study area may be undetected. However, data on breeder movements on the study area indicate that they are of very limited distance. On surveys surrounding the study area, only one former breeder was found—a male that had disappeared during the acorn crop failure. I therefore conclude that I detected nearly all permanent moves of breeders off their original territories.

ANNUAL SURVIVORSHIP

Annual survivorship was calculated from 1 April to 31 March each year, and data from 74 banded males and 72 banded females (292 breeder-years) were analyzed. Survival was calculated by comparing the number of jays at risk during the period to the number alive at the end of the period. I include two samples derived slightly differently: (1) an entire year sample that includes only those individuals already banded at the beginning of the period (1 April); and (2) a "partial" year sample that includes the above jays plus those banded after 1 April of a given year. In the latter sample, if the jays banded after 1

April survived, the fraction of the year as a banded breeder is added to the calculation of survivorship. Using the partial year sample increases the sample sizes, especially for the early years of the study when comparatively few breeders were color-banded.

Annual variation in survivorship of breeders (all ages pooled) is presented in Table 20. Overall male survivorship (partial year sample) ranged between 71.5% and 89.7% with a four-year mean of 83.4%. Female survivorship was lower in every year, but not statistically different from that of males, ranging from 62.7% to 84.5% and averaging 77.9%.

Male and female survivorships were correlated ($R_s = 0.96$, $N = 5$) and were not statistically different among years. Survivorship was similar in all years except 1983–1984, and territorial jays that disappeared after August 1983 and had not returned by late April 1984 were considered dead as a result of the crop failure. In all, an estimated 30 out of 103 banded jays (the fall 1983 study population) died in this year, 45% of deaths during the 5-year study. The crop failure affected males and females equally, with 16 female and 14 male deaths, constituting 33% and 29% of the banded territorial jays in fall 1983.

Seasonal patterns

To analyze seasonal patterns of breeder mortality, I divided the year into the breeding season (March–June), late summer dry period and molt (July–October), and winter (November–February). Mortality did not vary significantly by season either for males (N = 32) or females (N = 35; Fig. 36a) or for both sexes combined. Although the proportion of females dying during the breeding season is twice that of males, the differences are not statistically significant, in my view because of small sample sizes. Excluding deaths attributable to the acorn crop failure results in similar distributions of seasonal and gender mortality (Fig. 36b).

TABLE 20. ANNUAL SURVIVORSHIP OF BREEDERS

Year		Males	Females
1981–1982			
	Entire years[a]	85.7% (14)[c]	84.0% (11)
	Partial years[b]	89.7% (25)	84.5% (18)
1982–1983			
	Entire years	88.4% (43)	79.4% (34)
	Partial years	89.7% (52)	83.3% (47)
1983–1984			
	Entire years	70.4% (54)	61.4% (44)
	Partial years	71.5% (59)	62.7% (51)
1984–1985			
	Entire years	82.4% (51)	81.0% (42)
	Partial years	82.6% (53)	81.3% (44)
Overall (mean of annual values)			
	Entire years	81.7% (162)	76.5% (131)
	Partial years	83.4% (189)	77.9% (160)

Year % mortality: $G = 10.3$, df = 3, $0.025 > P > 0.01$
Sex % mortality: $G = 2.0$, df = 3, $P > 0.10$

[a] Entire years include only scrub-jays banded by 1 April.

[b] Partial years include scrub-jays banded by 1 April and those banded before the next 1 April. For scrub-jays banded after 1 April, if the scrub-jay died during the year it was counted as dead; if it lived, the proportion of the year since banding was added into the calculation of survivorship.

[c] Total number of scrub-jays at risk during the year.

Age-specific survivorship of breeders

Survivorship calculated on a yearly basis as above, where all individuals are lumped, ignores differences in age-specific survivorship. On the other hand, lumping all years to calculate age-specific mortality ignores the effects of annual variation. Ideally, age-specific mortality should be compared within years among cohorts (e.g., Sherman and Morton 1984, Gibbs and Grant 1987), but this requires large sample sizes. I therefore calculated age-specific survivorship as averages for same-age jays from different cohorts.

Age-specific survivorship schedules for breeders (Table 21) suggested that survivorship was not greatly affected by age of adults. One complication is the relatively few sample years and the large drop in survivorship during the acorn crop failure, which appeared to affect breeders irrespective of age. Adult mortality rate in birds is often assumed to be age-constant (but see Caughley 1977) and some long-term studies support the concept (e.g., Island Scrub-Jays [Atwood et al. 1990], Acorn Woodpeckers [Koenig and Mumme 1987]); others do not (Loery et al. 1987). In the Florida Scrub-Jay, Fitzpatrick and Woolfenden (1988) found constant survivorship of breeders through age 11 followed by a sharp decrease, suggesting senescent mortality.

Woolfenden and Fitzpatrick (1984) and Koenig and Mumme (1987) examined senescent mortality by comparing survivorship of known vs. unknown aged breeders. In this study, for a breeder's age to be known I had to band it when no more than 15 months old at which time it enters the first complete molt. Because the study includes only four years of survivorship, the known-age sample excludes jays older than five. If survivorship decreases with age, the known-age sample (N = 44) should show higher survivorship than the unknown age sample (N = 102); however, no difference was found (Lee-Desu survivorship statistic D = 0.03, P = 0.8).

I also compared the survivorship of jays that began breeding as first-year birds (N = 31) with those waiting until two or older (N = 27). Survivorship over one year (e.g., from one to two for first-year birds and from two to three for a two-year old) is not statistically different for the two groups ($\chi^2 = 2.0$, P = 0.15), although older first-time breeder survivorship averaged 89% vs. 74% for first-year breeders. Calculated over a several-year period, jays that bred as yearlings experienced higher mortality (annual average = 18.9%) than jays waiting until two or three (annual average 11.2%; Lee-Desu survivorship statistic, D = 3.6, P = 0.058). Of course, this may be due to lower survivorship of first-year birds rather than any effect from a delay in breeding. The definitive comparison, which I am unable to make, would be between first-year territorial jays and first-year nonbreeding floaters, an important but elusive parameter in weighing the costs and benefits of delayed vs. early dispersal.

TABLE 21. AGE SPECIFIC SURVIVORSHIP OF KNOWN AGE MALE AND FEMALE BREEDERS FROM AGE 1 TO ≥5 YR

	Males				Females		
Age	Number at risk	Number survived	% survival	Age	Number at risk	Number survived	% survival
1	9	8	89	1	18	15	83
2	14	11	79	2	13	10	77
3	9	8	89	3	8	7	87
4	4	3	75	4	—	—	—
≥5	50	40	80	≥5	28	20	72

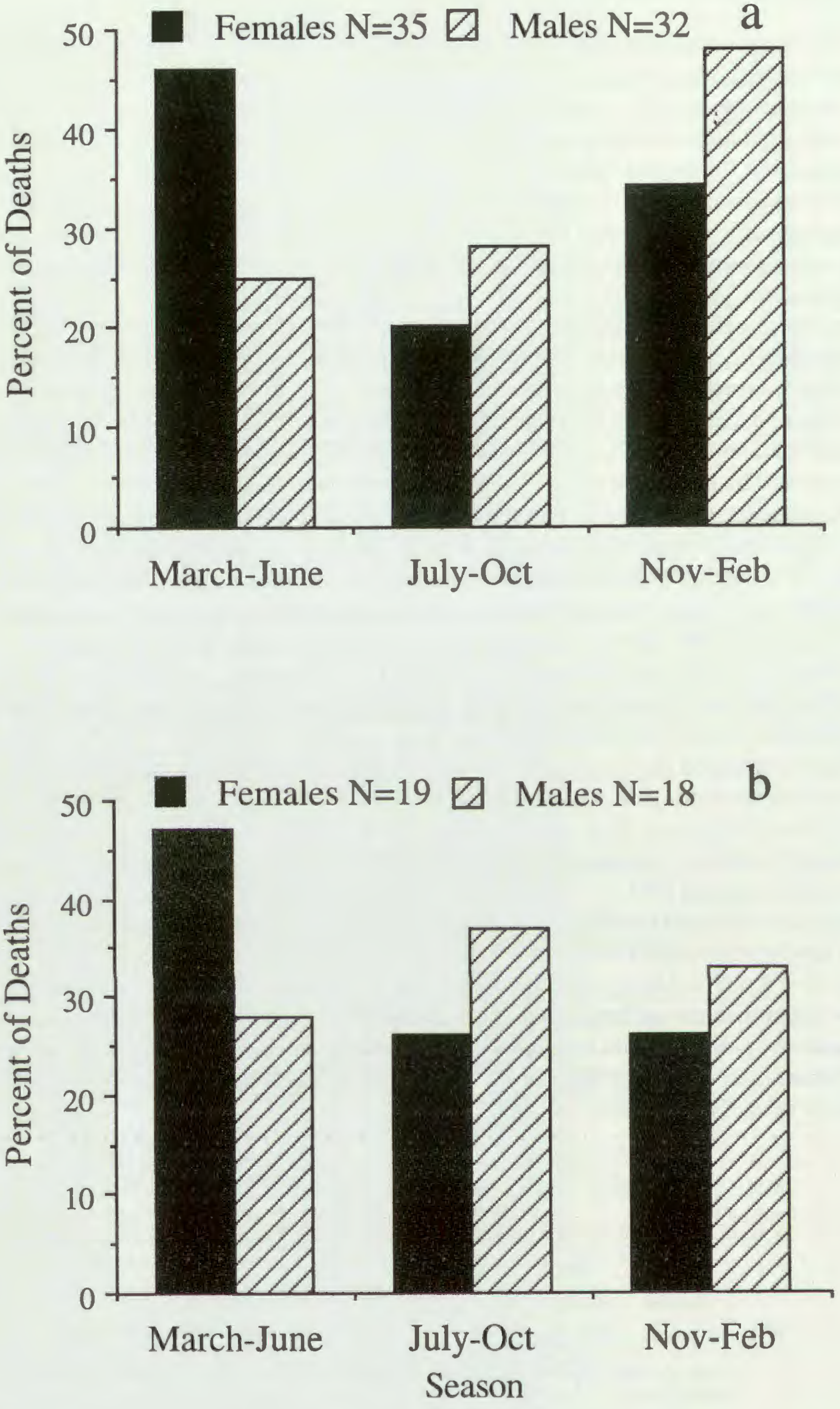

FIGURE 36. Seasonal pattern of deaths of males and females during the entire study period (a), and excluding deaths during the acorn crop failure (b).

Ignoring the possible decreased survivorship of jays acquiring a territory as yearlings, composite survivorship curves (Fig. 37) using all banded breeders, show an expected survivorship of 83% for males and 79% for females.

LIFE TABLES AND SURVIVORSHIP OF NONBREEDERS

Determining the survivorship of juveniles and older nonbreeders in any species is difficult because of dispersal in juveniles and wandering in older nonbreeders. In cooperative breeders some of these problems are overcome by delayed dispersal, absence of nonbreeding floaters, and a large number of sedentary helpers. Estimates of nonbreeder (helper) deaths can then be estimated from the number of helpers disappearing minus the number expected to have become breeders outside the study area (Woolfenden and Fitzpatrick 1984, Koenig and Mumme 1987). Custer and Pitelka (1977) used life-table analysis to estimate juvenile survivorship; their approach is used here and extended to estimate survivorship of older nonbreeders as well.

Assumptions

Several assumptions are necessary to carry out a life-table analysis. One is that the Hastings population has a stable age distribution (e.g., Caughley 1977). Few, if any, field studies meet this criterion. Both birth and death rate of fledglings and breeders varied considerably, especially in 1983–1984. However, if viewed over the five-year study period, the Hastings breeding population was relatively stable. It follows that the population's net reproductive rate (R_o) was approximately 1.0.

From a life table based on breeders, nonbreeder survivorship can be estimated, given that $R_o = 1$. This can be corrected further by checking the values against observed values, including the age that jays acquired a territory for the first time, and the proportion of territorial jays that were yearlings. With these checks the life table represents a reasonable model for the Hastings population. The life tables further allow estimation of other demographic variables considered to be important factors leading to cooperative or noncooperative social systems.

Life-table parameters

The proportion of each age class that acquires a territory can be estimated from the age distribution of jays acquiring a territory for the first time, the number of territory vacancies available for each age class of nonbreeder, and the number of jays competing for the vacancies.

The age distribution of males and females acquiring a territory for the first time (Fig. 14) are conservative estimates in which older age classes are probably under represented. Females filled vacancies earlier than males, with 50% of 34 territory vacancies taken by first-year females and 29% of 27 vacancies taken by first-year males. The oldest known female was three and the oldest known male four, but again, because the study lasted only five years the oldest known novice could only be four years old.

The number of breeding opportunities each year is determined by the mortality rate of breeders, and thus, in part, by turnover in territory occupants. Counting the mean annual number of openings in the population would underestimate the number of available vacancies because six more territories were lost than were added over the study period. I assumed that over time breeder density would have stabilized at prior levels. To calculate

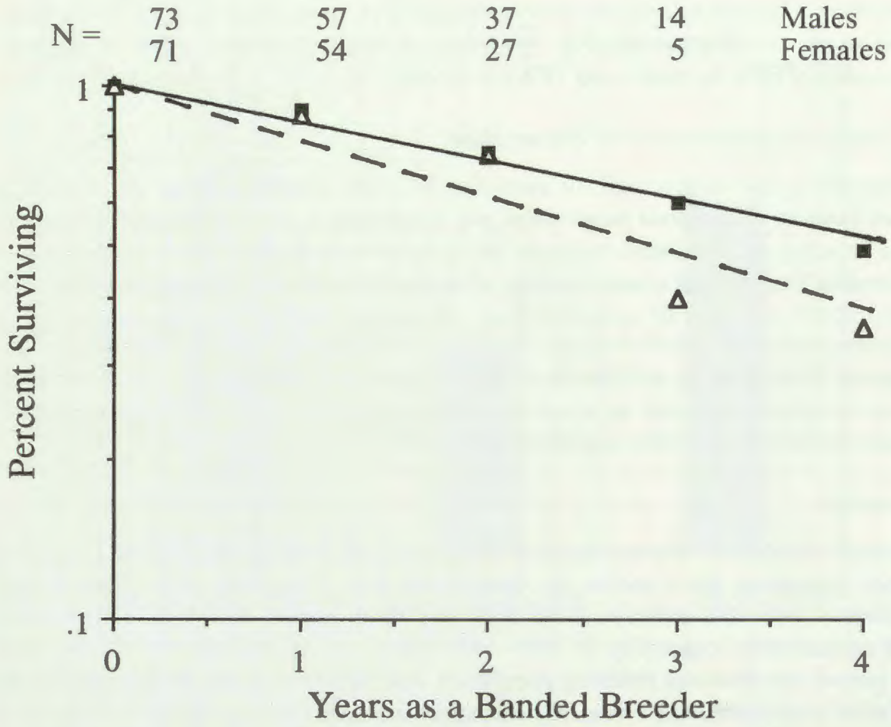

FIGURE 37. Survivorship of breeding California Scrub-Jays plotted as the proportion of banded breeders surviving from 1 to 4 years after banding. Sample sizes above points are the number of individuals at risk during the period and include breeders of all ages. The lines represent constant survivorship of 0.83% per year for males and 0.79% per year for females.

the number of vacancies I used the mean mortality rate, which averaged 16.6% for males and 22.1% for females (Table 20). Because female breeders have a higher mortality rate, more vacancies are available to and filled by first-year females.

The next step is to determine the number of individuals competing for these vacancies. The earliest age at which a jay could acquire a territory was set at 10 months, although a few jays may do so by six months. Survivorship from fledging to one month averaged 72% (Table 11). Past this age for unsettled young and older floaters survivorship was estimated iteratively using various combinations of survivorship values. Numerous combinations are possible, but lowering one value (e.g., juvenile survivorship) necessitates raising the other (e.g., older floater survivorship) to satisfy the conditions specified above. Survivorship values from one month to one year of 60% for both sexes, and 72% and 75% for older nonbreeding females and males, respectively, provided the most reasonable estimates.

The estimated number of male and female nonbreeders in each age class (Table 22) is dependent on age-specific survivorship and territory vacancies. For example, a hypothetical population of 1,000 pairs produces 1,200 fledglings (1.2 per pair; Table 10), half of which are males and half females. These fledglings survive to one year at 0.43 (0.72 survivorship to one month postfledging ×0.6 survivorship from one month to one year), when they either acquire a territory or become floaters. Each year there are 166 vacancies for males and 210 for females (1,000 × annual mortality rate). These vacancies are filled by different age classes in the proportions found on the study area (Fig. 14b). For example, 50% (105) of the 210 vacancies for females are filled by first-year jays, 37.5% (79) by two-year olds, and 12.5% (26) by three-year olds. Juvenile and older nonbreeder survivorship was adjusted so that all surviving females hold territories in their third year.

These data further allow calculations of the proportion of each age class that is territorial (P_{tx}), and the age-specific probability of acquiring a territory (P_{bx}; Table 22). Under the conditions outlined above, 40% of first-year, 83% of second-year, and 100% of third-year females are territorial, compared to 19% of first-year, 52% of second-year, 75% of third-year, and 100% of fourth-year males. These values reflect those actually observed: 12 jays banded as nestlings prior to 1984 acquired breeding status on the study area, 5 (42%) in their first year, 4 (33%) their second year, and 3 (25%) in their third year (Table 2).

However, only 8.7% of territorial first-year females and 40% of territorial first-year males bred, and after the acorn crop failure 32% of adult pairs failed to lay (Table 11). P_{tbx} (the proportion of each age class breeding) reflects this by reducing P_{tx} (the proportion territorial) by the relevant amounts for each age class.

In the Hastings population, fecundity of territorial jays (f_x) increased with age (Table 18, Fig. 35), but these data slightly exaggerate average fledgling production because most of the data for older jays were obtained in 1985, a year of good reproduction; f_x values were, therefore, reduced by approximately 5% for the four- and five-year old age classes. The values in column f_x of the life table further differ from the values in Table 18, because f_x values in the life table are for jays that initiated breeding. Because not all jays bred, m_x (the average fecundity of all jays of age-class x) equals f_x (the average fecundity of breeders of age class x) multiplied by P_{tbx} (the proportion of each age class breeding). The maximum age of jays was set at 15.

TABLE 22. CALCULATING AGE THAT SCRUB-JAYS FIRST ACQUIRE TERRITORIES

Age	Survivorship		Age of territory	Number of			Proportion	Probability of getting
Age (x)	Breeders (Sb_x)	Floaters (Sf_x)	aquisition (A_x)	Vacancies (Ob_x)	Nonbreeders (Nf_x)	Breeders (Nb_x)	territorial (Pt_x)	territory (Pb_x)
Females								
Fledge	—	0.72	0	0[a]	600[b]	0	0	0
1 month	—	0.60	0	0	434	0	0	0
1 year	0.79	0.72	0.50	105	156	105	0.40	0.40
2 years	0.79	0.72	0.38	7	33	162	0.83	0.70
3 years	0.79	0.72	0.12	26	−2[c]	152	1.00	1.00
Males								
Fledge	—	0.72	0	0	600	0	0	0
1 month	—	0.60	0	0	434	0	0	0
1 year	0.83	0.75	0.29	49	212	49	0.19	0.19
2 years	0.83	0.75	0.37	61	96	102	0.52	0.39
3 years	0.83	0.75	0.17	28	44	129	0.75	0.39
4 years	0.83	0.75	0.17	28	+5[c]	136	1.00	1.00

Note: Values for breeder survivorship from Table 20; nonbreeders survivorship from life-table calculations; age distribution of scrub-jays filling territory vacancies from Figure 14b.

[a] Number of vacancies based upon a hypothetical population of 1,000 pairs, with all vacancies created by breeder deaths.

[b] Number of fledglings based upon 1,000 pairs producing 1.2/pair (Table 10).

[c] There were no excess female floaters (-2) in year 3, and 5 excess males floaters in year 4.

THE LIFE TABLES

Several assumptions used in deriving the life-table values warrant closer examination. First, many of the variables are estimates based on five-year averages. Mean breeder survivorship and reproductive output may actually be higher than observed because of the poor success in 1983–1984. Second, true survivorship rates of floating juvenile and adult nonbreeders is unknown. Such data are crucial for resolving questions concerning the costs and benefits of floating. Third, the demographic estimates are based upon 50 pairs of jays living in relatively high-quality habitat that attracted, in good acorn years, floaters from a wide area and fledged large numbers of independent young. For the life table, the study area was treated as a "closed system" such that the number of nonbreeders competing for the vacancies were those produced by the local breeders and the number of vacancies that opened were those resulting from the breeders' deaths. The implications of a regional (and more realistic) view are discussed below.

Although based on several assumptions, the life-table models for females (Table 23) and males (Table 24) closely fit observed population parameters. For example, all females breed by their third year (identical to observed), 10.7% of all territorial females are first-year birds (10.7% observed), and the total number of territorial jays in the life table ($\Sigma (l_x)(P_{tx})$) produces 1,000 fledglings, which equals 1.2 fledglings per pair (the overall average for the population; Table 10). Values for males are similarly close to those observed in the population.

The known age structure of the population in 1985 is shown in Table 25. In 1985, the exact ages of 37 (41%) of the 90 breeders were known. Because of the short duration of the study, known age older jays are few. Nevertheless, 22% of female breeders were known to be five years or older, and 45% of male breeders. The oldest known male was at least nine and the oldest female at least five.

Estimated age-specific reproductive value (V_x) and the contribution each age class makes to the net reproductive rate ($\Sigma l_x m_x$) are presented in Figure 38. The values are similar for males and females, despite the earlier age at which females acquire territories, because of the low reproductive success of young breeders, particularly first-year females, and the higher survivorship of male breeders. Reproductive value and $l_x m_x$ of males and females reaches a peak at age four, due to both delayed breeding and low fecundity and reproductive success of young territorial jays.

ESTIMATING LIFE-TIME REPRODUCTIVE SUCCESS

Mean life-time reproductive success (LRS) may be estimated from the life table as estimated LRS= $\Sigma l_x m_x$,where l_x and m_x are age-specific survivorship and fecundity (same sex fledglings per breeder) from breeding age (≥ 1) through age 15, the assumed reproductive life. Thus, LRS equals the expected number of same sex fledglings produced by an individual.

LRS estimates for males and females that acquire territories as yearlings, at age two, and as modeled in the life tables are given in Table 26. A female acquiring a territory at age one can expect to fledge 2.60 female offspring over her lifetime, and a male 3.17 male offspring. (These values can be doubled for total fledglings produced). Male LRS is higher due to slightly higher survivorship. How does a delay in breeding affect these LRS estimates? A female that delays breeding (floats) for a year and then acquires a territory at age two can expect to fledge 2.31 females, 11% fewer than a female acquiring a territory at age one. Because fecundity of territorial first-year females is only 0.04 fledglings,

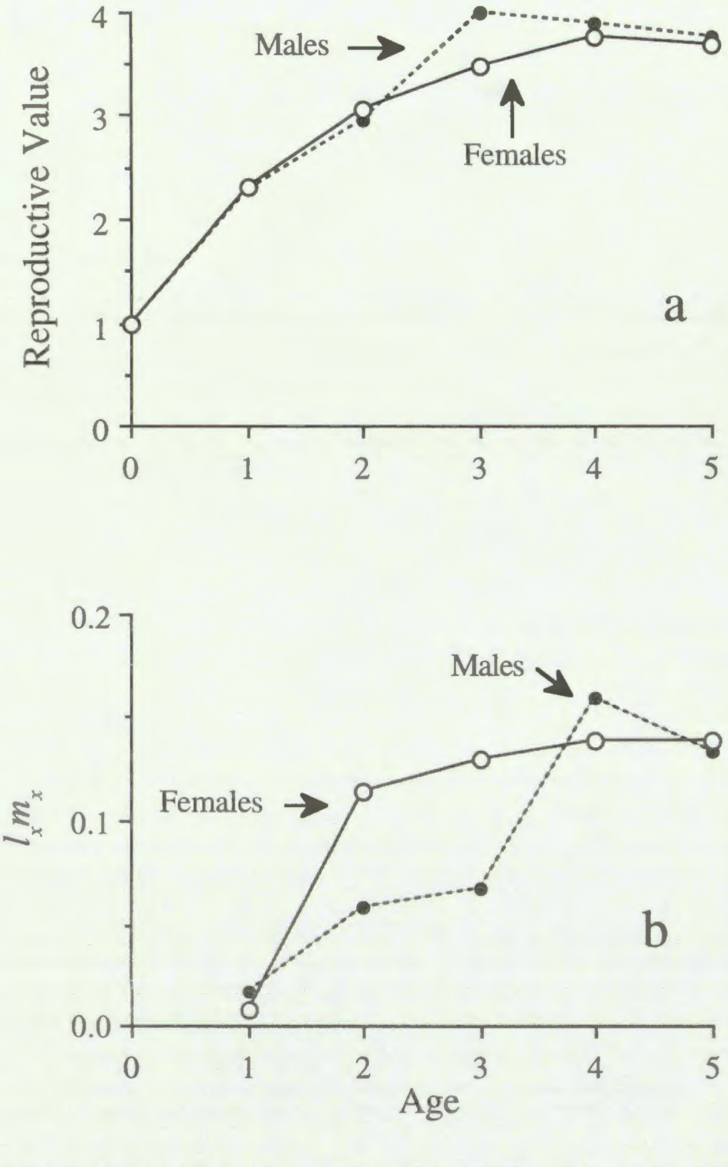

FIGURE 38. Life table estimates of reproductive value and $l_x m_x$. (a) Reproductive value (in fledglings) of males and females, and (b) $l_x m_x$ (the contribution each age class makes to the total reproductive output of the population).

the decline is due almost entirely to the probability of dying before breeding (survivorship is estimated to be higher for breeders than floaters). A male that delays breeding until age two produces 2.72 male fledglings, a 14% decline.

However, dispersing scrub-jays may be forced to delay breeding and float for several years; as modeled in the life tables, estimated LRS, discounted for age-specific probability (from age one onward) of acquiring a territory (Table 22) and the probability of dying, equals 2.42 fledglings for females (9.6% less than females acquiring territories as

TABLE 23. FEMALE LIFE TABLE ($R_o = 1.004$)

									Age structure	
Age *x*	S_{xb}	S_{xf}	S_x	l_x	P_{tbx}	f_x	m_x	$l_x m_x$	Total	Breeders
Fledge		0.724	0.724	1.000	0.000	0.000	0.000	0.000		
1 month		0.600	0.600	0.724	0.000	0.000	0.000	0.000		
1 year	0.79	0.720	0.748	0.434	0.035	0.500	0.018	0.008	0.228	0.110
2-yr	0.79	0.720	0.778	0.325	0.769	0.458	0.352	0.115	0.170	0.169
3-yr	0.79	0.720	0.790	0.253	0.927	0.555	0.515	0.130	0.133	0.159
4-yr	0.79	0.720	0.790	0.200	0.927	0.750	0.695	0.139	0.105	0.125
5-yr	0.79	0.720	0.790	0.158	0.927	0.950	0.881	0.139	0.083	0.099
6-yr	0.79	0.720	0.790	0.125	0.927	0.950	0.881	0.110	0.065	0.078
7-yr	0.79		0.790	0.098	0.927	0.950	0.881	0.087	0.052	0.062
8-yr	0.79		0.790	0.078	0.927	0.950	0.881	0.069	0.041	0.049
9-yr	0.79		0.790	0.061	0.927	0.950	0.881	0.054	0.032	0.039
10-yr	0.79		0.790	0.049	0.927	0.950	0.881	0.043	0.025	0.030
11-yr	0.79		0.790	0.038	0.927	0.950	0.881	0.034	0.020	0.024
12-yr	0.79		0.790	0.030	0.927	0.950	0.881	0.027	0.016	0.019
13-yr	0.79		0.790	0.024	0.927	0.950	0.881	0.021	0.013	0.015
14-yr	0.79		0.790	0.019	0.927	0.950	0.881	0.017	0.010	0.013
15-yr	0.79		0.790	0.015	0.927	0.950	0.881	0.013	0.008	0.013

yearlings) and 2.42 for males (24% less than those acquiring territories at age one; Table 26). Males that do not acquire territories their first year incur greater costs relative to females, because a male has a lower probability of acquiring a territory at any age than a female (Table 22).

An interesting question is how estimated LRS would be affected if California Scrub-Jays delayed dispersal, remained at home, and helped. The increase in fledgling production due to a single helper in the Florida Scrub-Jay averages 51% (Woolfenden and Fitzpatrick 1984); a similar increase in the California Scrub-Jay would raise production from 1.2 to 1.8 fledglings/pair. When this increase is converted to genome-equivalents (see Brown and Brown 1981b for details of this method; these values may be doubled for

TABLE 24. MALE LIFE TABLE ($R_o = 0.998$)

									Age structure	
Age *x*	S_{xb}	S_{xf}	S_x	l_x	P_{tbx}	f_x	m_x	$l_x m_x$	Total	Breeders
Fledge		0.724	0.724	1.000	0.000	0.000	0.000	0.000		
1 month		0.600	0.600	0.724	0.000	0.000	0.000	0.000		
1 year	0.834	0.750	0.766	0.434	0.075	0.500	0.038	0.016	0.200	0.051
2-yr	0.834	0.750	0.793	0.333	0.438	0.400	0.175	0.058	0.153	0.107
3-yr	0.834	0.750	0.812	0.264	0.635	0.400	0.254	0.067	0.121	0.123
4-yr	0.834	0.750	0.834	0.214	0.855	0.875	0.748	0.160	0.099	0.135
5-yr	0.834	0.750	0.834	0.179	0.855	0.875	0.748	0.134	0.082	0.112
6-yr	0.834	0.750	0.834	0.149	0.855	0.875	0.748	0.112	0.069	0.094
7-yr	0.834		0.834	0.124	0.855	0.875	0.748	0.093	0.057	0.078
8-yr	0.834		0.834	0.104	0.855	0.875	0.748	0.078	0.048	0.065
9-yr	0.834		0.834	0.086	0.855	0.875	0.748	0.065	0.040	0.054
10-yr	0.834		0.834	0.072	0.855	0.875	0.748	0.054	0.033	0.045
11-yr	0.834		0.834	0.060	0.855	0.875	0.748	0.045	0.028	0.038
12-yr	0.834		0.834	0.050	0.855	0.875	0.748	0.038	0.023	0.031
13-yr	0.834		0.834	0.042	0.855	0.875	0.748	0.031	0.019	0.026
14-yr	0.834		0.834	0.035	0.855	0.875	0.748	0.026	0.016	0.022
15-yr	0.834		0.834	0.029	0.855	0.875	0.748	0.022	0.013	0.018

TABLE 25. AGE DISTRIBUTION OF BREEDERS IN 1985

	Females (N = 45)		Males (N = 45)	
Age	Number	Percent	Number	Percent
1	8	18%	3	7%
2	3	7%		
2+	3	7%	2	4%
3	5	11%	7	16%
3+	8	18%	4	9%
4	5	11%	5	11%
4+	3	7%	4	9%
5				
5+	10	22%	12	27%
6+			1	2%
7+			4	9%
8+			2	4%
9+			1	2%

TABLE 26. ESTIMATED LIFE TIME REPRODUCTIVE SUCCESS (IN SAME SEX FLEDGLINGS) OF MALE AND FEMALE CALIFORNIA SCRUB-JAYS THAT ACQUIRE TERRITORIES AS YEARLINGS, AT AGE TWO, AND IN THE DISTRIBUTION AS MODELED IN THE LIFE TABLES

	LRS for jays acquiring territories at age			
	1-year	2-years	Life table	Indirect benefits[a]
Males	3.18	2.72	2.42	0.25
Females	2.60	2.31	2.35	0.24

[a] Hypothetical indirect benefit of helping for one year (see text for explanation).

"offspring equivalents"), the estimated indirect benefits for helping for one year equals 0.24 genome-equivalents for a single female helper and 0.25 for a single male helper. These hypothetical indirect benefits are significantly greater than the direct benefits derived from acquiring a territory and breeding status for a first-year jay. For example, a first-year female acquiring a territory will, on average, fledge 0.08 offspring (Table 18) or 0.04 genome-equivalents (and a male 0.17). This suggests that a jay would do best by helping for a year and then breeding independently rather than breeding at age one or floating, all else being equal. However, differences in survivorship on and off the natal territory and in the probability of securing a suitable territory may easily outweigh these hypothetical indirect fitness benefits (Woolfenden and Fitzpatrick 1984, Walters et al. 1992a). Analyses of life-time reproductive success for several cooperative breeders (Florida Scrub-Jays, Woolfenden and Fitzpatrick 1984; Acorn Woodpeckers, Koenig and Mumme 1987) indicate that the highest LRS is achieved by breeding as early as possible on a suitable territory. In Florida Scrub-Jays, success in acquiring a territory at an early age is, together with breeder life-span, the most important contributor to a jay's lifetime reproductive success (Fitzpatrick and Woolfenden 1988, Fitzpatrick et al. 1989).

Not surprisingly, relative survivorship of floaters and breeders and the age of first breeding are critical factors affecting estimated LRS. In their long-term study of Florida Scrub-Jays, Woolfenden and Fitzpatrick (1984; Fitzpatrick and Woolfenden 1986, 1988) concluded that the indirect benefit to nonbreeders of raising the reproductive output of relatives is small (and decreases rapidly with group size) compared to those of (1) higher survivorship on the natal territory, (2) increasing the chance of getting or creating a high-quality territory vacancy, and (3) increasing the survivorship of related breeders (see also Brown 1974, Koenig and Mumme 1987; Stacey and Ligon 1987, 1991). Hence, except for the latter benefit, the general conclusions regarding factors affecting LRS and selecting for alternative dispersal strategies in cooperative and noncooperative scrub-jays are similar. The specific ecological factors that promote delayed dispersal in one population and early dispersal and floating in another are examined below.

TEST OF THEORIES AND COMPARISONS

In this section, I compare data from the California Scrub-Jay with those from several closely related cooperative *Aphelocoma* and other cooperative breeders to test hypotheses and predictions of models for the evolution of cooperative breeding. These comparisons are used to answer the following questions: Do the models adequately explain why one species is cooperative and a closely related species or conspecific is not? What are the critical ecological, demographic, and behavioral differences that select for the alternative social systems in these species? There are, however, three potential complications in drawing conclusions based on such comparisons: (1) the models examined are for the evolution of cooperative breeding, not its loss; (2) it is difficult to separate the effects of historical vs. current ecological factors; and (3) observed behaviors may be relics of ancestral, cooperative populations.

The models discussed are for the evolution of delayed dispersal and cooperative breeding. But are the conditions hypothesized to select for the evolution of a character state such as cooperative breeding the mirror image of those leading to its loss? Not always. In *Aphelocoma* jays, phylogenetic studies reveal that cooperative breeding occurred before the diversification of the genus (Peterson and Burt 1992) and that it was lost in the western North American lineage (Pitelka 1986). Studies of *Aphelocoma* examine factors important to the maintenance of cooperative (or noncooperative) breeding rather than its evolutionary origins; current conditions may not reflect those that led to the evolution of the observed traits and would therefore not be responsible for observed differences in social behavior. For example, cooperative breeding in Australian babblers (*Pomatostomus* spp.) apparently arose in rain forest habitats (Schodde 1982) but has been maintained as the group diversified and spread into arid interior Australia; cooperative breeding still occurs but under far different ecological conditions under which it evolved. In a similar vein, noncooperative populations derived from cooperatively breeding ancestors may exhibit behaviors or demographic components that are relic of ancestral, cooperative populations. In Western Scrub-Jays these may include tolerance of young and nonbreeders on territories, delayed breeding, very low reproductive success in territorial first-year birds, and aspects of territorial acquisition.

Despite these potential complications, for the first time detailed ecological, demographic, and behavioral comparisons can be made among closely related cooperative and noncooperative species and may provide evidence of the key factors selecting for a switch from delayed dispersal and cooperative breeding to early dispersal and floating.

BROWN'S THEORY OF HABITAT SATURATION AND GROUP LIVING

Brown (1969) developed a model for the role of territorial exclusion in creating a nonbreeding surplus, and later for group living and cooperative breeding in New World jays and the genus *Aphelocoma* in particular (Brown 1974, 1978; see also Verbeek 1973). This habitat saturation (HS) theory incorporates both ecological and demographic arguments, and with various modifications and elaborations has served as the underlying framework for most other theories for the evolution of cooperative breeding in permanently territorial species.

Brown argues that in nonmigratory, long-lived species residing near carrying capacity in habitats characterized by stable mature vegetation, territory vacancies will be rare, as all suitable habitats will be "saturated." Under these conditions, the best strategy for young birds is to delay breeding and remain on their natal territory. Early dispersal and floating are not precluded, but young that delay dispersal stand a better chance of eventually getting a territory and reproducing successfully due to competitive advantages that come with increased age and experience and through territorial inheritance. And once young delay dispersal, those that "help" relatives are at selective advantage (through direct and indirect fitness benefits) over ones that do not. Advantages also accrue to breeders via decreased defense costs and enhanced reproductive success due to helper aid. In addition, larger groups have a competitive advantage over smaller ones in securing and keeping territorial space. Brown (1974) suggests that this process is self-reinforcing, leading to a build up of nonbreeders and eventually to multi-pair territories and is mirrored in the progression from the noncooperative California Scrub-Jay, to a single breeding pair with helpers as in the Florida Scrub-Jay, and finally to the multi-pair territories with helpers as in the Mexican Jay.

Brown (1974:78) listed six attributes of cooperative as compared to noncooperative breeders under the "K-selection phase" of his model: (1) delayed maturity, (2) higher survivorship, (3) lower reproductive rate, (4) reduced dispersal, (5) a higher proportion of nonbreeders, and (6) narrower habitat tolerance. These predictions are tested below with data from the California Scrub-Jay and provide a framework for exploring other hypotheses as well.

Delayed maturity and the "Skill Hypothesis"

Delayed maturation is common among cooperative breeders, but controversy exists over whether this leads to group living and cooperation per se (Skutch 1961, Lack 1966) or is merely a correlate of some other causal factor(s) (Brown 1978, Lawton and Lawton 1986). Retention of juvenile or subadult morphological characteristics for a year or two could be a consequence of delayed breeding, but such characteristics occur in both cooperative and noncooperative species (Pitelka 1945). Delayed maturation or "lack of skill" in foraging efficiency, territorial defense, predator avoidance, and reproductive skills may favor delayed breeding (Stearns and Crandell 1981; Brown 1985, 1987), and some suggest this may lead to group living and cooperative breeding as well (Skutch 1961, Rowley 1965, Lack 1966; Heinsohn et al. 1988, 1990; Heinsohn 1991).

Numerous studies have demonstrated that young of cooperative breeders are less skillful than older individuals, including those on cooperative *Aphelocoma* jays (Stallcup and Woolfenden 1978, Brown 1985, DeGange 1976, McGowan 1987), but this is also true for numerous noncooperative species that delay breeding (Sæther 1990). It is also true that young nonbreeders may learn from experienced group members (e.g., White-winged Choughs, *Corcorax melanorhamphos* [Heinsohn et al. 1988]; Seychelles Warblers, *Acrocephalus sechellensis* [Komdeur 1996]; White-throated Magpie-Jays [Langen 1996a,c; Langen and Vehrencamp 1999]; and Long-tailed Tits, *Aegithalos caudatus* [Hatchwell et al. 1999]).

Delayed maturation and overall lack of skill in young birds in both cooperative and noncooperative breeding systems is indicated by a steep increase in age-specific reproductive success of breeders. In California Scrub-Jays, Florida Scrub-Jays, and Mexican Jays, reproductive success is quite low at age one and increases to peak at age four or five (Fig. 39). More California than Florida scrub-jays acquire territories as yearlings, but few breed and those that do have very low success. Some of the few Florida Scrub-Jays that acquired a territory their first year bred successfully (Woolfenden and Fitzpatrick 1984). In some cooperative breeders, such as the Gray-crowned Babbler (*Pomatostomus temporalis*), the gonads are usually small and presumably nonfunctional their first year, and do not reach full size until the third year (Brown and Brown 1981b). However, this may be more an inability of young individuals to acquire a territory and breeding status as young Gray-crowned Babblers that are able to acquire a territory and breed are nearly as productive as adults (Brown and Brown 1981b).

In both the Florida Scrub-Jay (Woolfenden and Fitzpatrick 1984) and Mexican Jay (Brown 1974), larger groups are more successful than smaller ones in securing and expanding territorial space. Although this makes it difficult to establish and defend a territory independently, group living and cooperative behavior may in some cases allow young individuals to be more successful breeders than otherwise would be possible by providing aid in feeding young, territorial defense, detecting and fighting off predators, and nest building. For example, inexperienced Florida Scrub-Jays breeding as pairs average 1.24 fledglings/pair, mixed pairs 1.34, and experienced pairs 1.8. With helpers, the same pairs raise 2.2, 2.5, and 2.4 fledglings, respectively; inexperienced (young) and experienced (older) pairs with helpers fledge the same number of young (Woolfenden and Fitzpatrick 1984).

These comparisons suggest that young in both cooperative and noncooperative birds may be less efficient at foraging, exhibit delayed maturity, and lack reproductive skills compared to older age classes. Although lack of skill and delayed maturity in Western Scrub-Jays may also be relic of ancestral cooperative populations, no reason exists to expect that differences in delayed maturity or skill have led to group living rather than having arisen as a consequence of it.

Higher survivorship

Higher survivorship of breeders was predicted for cooperative breeders (as this contributes to lower breeder turnover and fewer breeding vacancies; see Arnold and Owens 1998, 1999) but no significant difference exists among the California and Florida scrub-jays and Mexican Jays (Table 27), or *A. californica obscura*, another noncooperative population (83%; M. J. Alpers, pers. comm.). Survivorship was even higher (94%) in the Island Scrub-Jay (Atwood et al. 1990).

Lower Reproductive Rate

Reproductive rate is not related to social behavior in *Aphelocoma* jays (Table 27). Clutch size is slightly smaller in the Florida Scrub-Jay than in either the Mexican Jay or California Scrub-Jay, although populations of the Western Scrub-Jay in drier habitats have significantly smaller clutch sizes overall (Atwood 1978). Fledging success is lower in California compared to simple pairs in Florida (43% vs. 66%), and considerably lower compared to pairs with helpers (80%).

Percentages of egg and nestling survivorship are similar. In California, 60.6% of eggs laid hatched and 48% of hatchlings fledged. In Florida, for pairs without helpers, 60% of

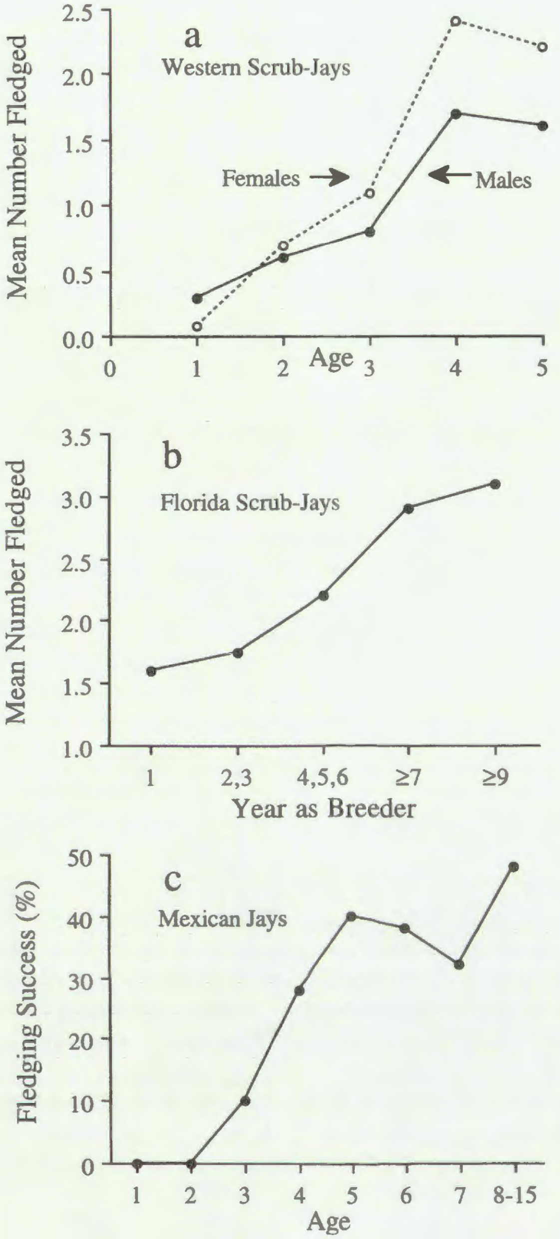

FIGURE 39. Increase in reproductive success with age for the noncooperative California Scrub-Jay, the cooperative Florida Scrub-Jay, and the Mexican Jay. (a) Age-specific reproductive success (fledgling production) in California Scrub-Jay breeders; (b) relationship between past breeding experience and fledgling production in Florida-Scrub Jays (because few first-year jays breed, the *x*-axis begins roughly at age 2; from fig. 8.15 in Woolfenden and Fitzpatrick 1984); and (c) fledging success with age in Mexican Jay breeders (from fig. 3 in Brown 1986).

eggs laid hatched and 54% of hatched eggs fledged. For pairs with helpers in Florida, corresponding values increase significantly to 69% and 68% (Woolfenden and Fitzpatrick 1984). Overall, fledgling production averaged 1.2 per pair at Hastings and 1.59 in Florida, rising to 2.31 for pairs with helpers (Woolfenden and Fitzpatrick 1984).

Given these similarities, what accounts for the higher reproductive output in Florida? First, although nest predation rates are similar, a major difference between the Florida and California populations is the rate of starvation (4.8% vs. 17.2%). Second, virtually all breeding pairs in Florida initiate breeding every year (G. Woolfenden, pers. comm.), and 13% of pairs attempt to raise second broods. At Hastings, however, in 215 breeding pair-years, 40 pairs failed to lay eggs. If these pairs are excluded, the overall average climbs to 1.5 fledglings per pair, quite close to 1.59 per pair without helpers in Florida. Third, pairs with helpers in Florida show a significant increase in fledgling production, which is attributable to lower predation rates on eggs and nestlings compared to those of unassisted pairs.

Reduced dispersal

Comparisons among *Aphelocoma* jays generally support Brown's prediction of reduced dispersal (see also Zack 1990). Mean natal to breeding territory distance in Florida Scrub-Jays is 0.9 territories for males and 3.4 for females (these distances include nearly all dispersal events). In comparison, values from scrub-jays at Hastings were 1.3 and 3.2 territories traversed for males and females; however, these data include but a small percentage of the estimated successful dispersal events. Many California Scrub-Jays float in the vicinity of their natal territories but others make wide-ranging movements and most acquired territories off the study area; hence, actual natal to breeding distances, though unknown, are certainly greater. Brown and Brown (1990) found that Mexican Jays may never leave high-quality territories or at most move to adjacent territories to breed, but their sample was small (6 territories) and evidence of immigration existed.

TABLE 27. DEMOGRAPHIC COMPARISONS AMONG *APHELOCOMA* JAYS

	Scrub-Jays			
	California[a]	Island[b]	Florida[c]	Mexican Jay[d]
Breeder survivorship	♂ 0.83	Both 0.94	Both 0.82	0.86
	♀ 0.79			0.81
Mean clutch size	3.7	3.7	3.4	4.0
Mean fledglings/pair	1.2	—	1.4 (pairs)	—
			2.4 (w/helpers)	
Percent non-breeders	♂ 29%	~50%[e]	31%	30%[e]
	♀ 16%		22%	
Age of transition to breeding status (yr)	1–3	2-3	2–3	3–4
Mean age first territorial (yr)	♂ 2.2	—	2.9	—
	♀ 1.6	—	2.4	—
Mean age first breeding (yr)	♂ 2.4	—	3.0	—
	♀ 2.1	—	2.4	—

[a] Estimates derived from demographic values as used in the life tables for females (Table 23) and males (Table 24).

[b] Data from Atwood et al. (1990); clutch size from Atwood (1980b); percent nonbreeders from an independent life table estimate.

[c] Data from Woolfenden and Fitzpatrick (1984).

[d] Data from Brown (1974, 1985, 1986) and Brown and Brown (1990).

[e] Combined estimate, not broken down by sex.

Prebreeders

A salient feature of Brown's (1974, 1978) theory is that permanently territorial noncooperative species either should not have a significant nonbreeding surplus, or that the surplus is due to factors other than habitat saturation, such as an unbalanced sex ratio (Rowley 1965), inability of simple pairs to raise young (Rabenold 1984, 1985), or general lack of skill in young individuals (Brown 1985, 1987).

The "nonbreeding surplus" can be a significant in both cooperative and noncooperative breeders. In field experiments where breeders were removed or high-quality habitat created, breeding positions were filled by nonbreeding helpers in cooperative species (Hannon et al. 1985, Pruett-Jones and Lewis 1990, Komdeur 1991, Walters et al. 1992b) and by floaters in noncooperative species (Watson and Moss 1970, Rutberg and Rohwer 1980). A substantial percentage of nonbreeders may occur in other permanently territorial, noncooperative species, with estimates of 35% in Carrion Crows (*Corvus corone*) in Scotland (Charles 1972, as cited by Patterson 1980) to 50% in the Rufous-collared Sparrow (Smith 1978). Cooperative species also show a wide range in the percentage of nonbreeders, from a low of 8% in one population of Bicolored Wren (*Campylorhynchus griseus*; Austad and Rabenold 1985), to 25% in Acorn Woodpeckers at Hastings (Koenig and Mumme 1987), and up to 80% in the African Yellow-billed Shrike (*Corvinella corvina*; Grimes 1980).

The percentage of nonbreeders (one year and older) averaged 31% for the Florida Scrub-Jay and 30% for the Mexican Jay, compared with an estimated 22% for scrub-jays at Hastings (Table 27) and perhaps 50% on Santa Cruz Island (data calculated from Atwood 1980b, Atwood et al. 1990).

Evidence that scrub-jays at Hastings may not acquire territories for several years includes: (1) the small proportion of territorial first-year females and males (10.7% and 4.9%, respectively, N = 223 breeding years; Table 12); (2) the percentage of jays banded as nestlings that eventually acquired territories on the study area (42% did so at age one, 33% at age two, and 25% at age three (Table 2); and (3) in four of five years, floaters were present in large numbers in March through early May and had no chance of breeding. Thus, noncooperative scrub-jays can have as high, or sometimes higher, proportions of nonbreeders than their cooperative relatives.

But is the "surplus" in noncooperative populations due to other factors besides habitat saturation? In Western Scrub-Jays, the sex ratio of floaters is roughly equal, simple pairs are the breeding unit, and lack of skill does not prevent young from acquiring territories and attempting to breed given the opportunity. More to the point, neither lack of mates or skill has any bearing on whether prebreeders delay dispersal or float. A lack of mates may prevent individuals from breeding but has no bearing on whether delayed dispersal or floating would be favored. Similarly, genetic or age effects ("skill") may deter individuals from attempting to set up territories and breed independently, but are unlikely to be important in determining whether delayed dispersal or floating is favored. However, in species where a critical group size is required for successful reproduction (e.g., *Campylorhynchus* wrens), breeding as part of a simple pair is not a viable option and delayed dispersal may be favored over floating.

Habitat differences

Brown (1974) originally predicted that permanently territorial cooperative breeders should inhabit mature stable vegetation types, but later acknowledged many exceptions

(Brown 1978). Of all the *Aphelocoma*, Western Scrub-Jays occupy the greatest geographic range and diversity of habitats (Pitelka 1951, Peterson and Vargas 1992). Florida Scrub-Jays occur in periodically burned oak scrub (Woolfenden and Fitzpatrick 1984) but may also inhabit fire suppressed and suburban landscapes that include oak scrub, although the latter may function in most years as population sinks (Breininger et al. 1995, 1996). Mexican Jays mostly inhabit mature oak-pine woodland, and Unicolored Jays are found in humid tall, luxuriant hardwood forest (Pitelka 1951, Webber and Brown 1994). Even on a local level, Western Scrub-Jays use a wider variety of habitats than their relatives. For example, where Mexican Jays and scrub-jays are sympatric, the latter use habitats that are rarely used by Mexican Jays. However, in similar habitats without Mexican Jays, scrub-jays expand into the former's preferred habitat (Marshall 1957; P. Stacey, pers. comm.). Burt and Peterson (1993) found that a cooperatively breeding population of scrub-jay in Oaxaca, Mexico, used a diverse assemblage of habitats and that conversion of its natural habitat has allowed expansion of the population.

Brown's (1974) generalization that cooperative breeders inhabit "mature, stable vegetation" followed from the idea that good quality habitat had to be saturated, so that the chance of a nonbreeder finding a good territory would be low. In contrast, Brown (1974: 73) suggested that "...the [western populations of] Scrub Jay inhabits a variety of habitats, including scrubby areas and chaparral, much of which is transient and created by forest fires. ...the higher reproductive rate and wider dispersal of the Scrub Jay may be viewed as adaptations for finding and exploiting newly available suitable habitat." The key idea is that some ecological factor acts to keep breeding habitat available or "unsaturated" in noncooperative breeders. As shown in the previous section, however, the large nonbreeding surplus in Western Scrub-Jays suggests that other factors are needed to explain the loss of delayed dispersal and group living.

THE MARGINAL HABITAT HYPOTHESIS

Koenig and Pitelka (1981) proposed that for group living to evolve in permanently territorial species, not only must high-quality habitat be saturated but marginal habitat must be relatively rare with a relatively sharp division between the two. Under these conditions, territories in high-quality habitat will be continuously occupied by established groups; those of intermediate quality will relatively rarely be occupied, and offspring will have a low probability of acquiring breeding status on a suitable territory. The key factor, however, is that because of a steep gradient between good and poor habitats, young individuals attempting to breed or even subsist in unoccupied habitat face a low probability of success and are "forced" to delay dispersal and remain on their natal territories.

If, however, a large proportion of intermediate and low-quality "marginal" habitat allows young individuals either to settle on territories, or float, early dispersal is favored. Predictions of the marginal habitat hypothesis (MHH) are contrasted with those of other models in Table 28, and examined below.

The MHH not only provides an ecological explanation for habitat saturation, it attempts to explain conditions that would preclude floating and favor delayed dispersal. Studies of cooperative breeders generally supported the MHH, including field experiments in which helpers actively competed for and filled artificially created breeding vacancies (Brown et al. 1982, Hannon et al. 1985, Pruett-Jones and Lewis 1990, Komdeur 1991). Prior studies of *Aphelocoma* also fit the predictions of the model. In the Island Scrub-Jay, Atwood (1980a) found breeding habitat "saturated" and floaters, including juveniles, only in "marginal" unoccupied habitat (open grassland with scattered shrubs or young trees and low *Baccharus* thickets that would be unsuitable for floaters on the mainland). In Florida, breeding space in high-quality habitat is always filled, and juveniles have a low probability of acquiring a territory. Juveniles do wander off their natal territories and are generally tolerated by unrelated adults until their post-juvenile molt in fall (Woolfenden and Fitzpatrick 1984). Group members, both breeders and helpers, then evict virtually all non-natal juveniles and older trespassers, and juveniles return to their natal territories and become helpers. Woolfenden and Fitzpatrick (1984; Fitzpatrick and Woolfenden 1986) demonstrate that jays breeding in marginal habitat have both lower survivorship and lower production of breeding age offspring, and therefore conclude that nonbreeding juveniles and adults would also experience low survivorship compared to staying on their natal territories.

Although these patterns support the MHH, evidence from the California Scrub-Jay does not. Nonbreeders, tolerated except during the height of the breeding season, used occupied territories and aggregated in habitats with the most abundant food resources. During the breeding season, breeders evicted floaters from their territories and floaters were rarely observed. In one year (1985) floaters were evicted only from the nest area and remained in the highest quality habitats, and microhabitat use and foraging behavior of floaters was identical to that of breeders. Thus, in the California Scrub-Jay, marginal or unoccupied habitat does not appear to be a factor in allowing nonbreeders to disperse and float. Tolerance of floaters by breeders and floaters' use of occupied habitat was also found in an study of *A. c. obscura* in southern California (M. J. Alpers, pers. comm.). This tolerance, in particular that of allowing nonbreeders access to territories but not to nests, is similar to the pattern in Florida Scrub-Jays and may be a relic behavior. In other territorial species, such as the Rufous-collared Sparrow (Smith 1978), floaters sneak through territories, which again suggests that floating does not depend on unoccupied or marginal areas for dispersal.

The MHH may explain higher levels of delayed dispersal and larger group sizes under different ecological conditions in cooperative breeders, but fails as a general explanation as to why another population is noncooperative (i.e., why nonbreeders float) for several reasons. The MHH predicts that the shape of the distribution in territory-habitat quality is fundamental. For example, Acorn Woodpecker territories at Hastings exhibit a steep territory-habitat gradient curve (little marginal habitat) and the birds are highly social

TABLE 28. Predictions of ecological models for the evolution of delayed dispersal, group living, and cooperative breeding (HS = Habitat Saturation[a]; MHH = Marginal Habitat Hypothesis[b]; FSJ = Florida Scrub-Jay Model[c]; EC = Ecological Constraints[d]; RCW = Red-cockaded Woodpecker Model[e]; BOP = Benefits of Philopatry[f]; WSJ=Western Scrub-Jays[g])

Predictions	HS	MHH	FSJ	EC	RCW	BOP	WSJ
Habitat saturated?	yes	yes	yes	yes	—	no	yes
Level of breeding constraints critical?	yes	no	yes	yes	yes	no	no
Floating ecologically constrained?	no	yes	yes	yes	no	no	no
Benefits of philopatry of primary importance?	yes	no	no	no	—	yes	no
Variance in rank order of territory quality	high	low	low	?	?	high	low

[a] Brown (1974, 1978, 1987).

[b] Koenig and Pitelka (1981), Koenig and Mumme (1987).

[c] Woolfenden and Fitzpatrick (1984), Fitzpatrick and Woolfenden (1986).

[d] Emlen (1982a).

[e] Walters et al. (1992b).

[f] Stacey and Ligon (1987, 1991).

[g] This study.

(Koenig and Mumme 1987); in New Mexico where a shallow gradient exists, group size is smaller. However, even in the latter, floating appears to be infrequent. Floating in cooperative breeders is usually rare (<5%; Woolfenden and Fitzpatrick 1984, Koenig and Mumme 1987, Brown 1987, Walters 1990). Further, Woolfenden and Fitzpatrick (1990) found nonbreeders "declining" available breeding space in high-quality habitat, and the presence of available but unused "suitable" territorial space in cooperative breeders is difficult to reconcile with a strict reading of the MHH (see also Stacey and Ligon 1991).

Under what habitat gradient (range of habitat conditions) is floating precluded? In Florida Scrub-Jays (Woolfenden and Fitzpatrick 1984), Acorn Woodpeckers in both California (Koenig and Mumme 1987) and New Mexico (Stacey and Ligon 1987), and other cooperative breeders (e.g., Grey-backed Shrikes, *Lanius excubitorius* [Zack and Ligon 1985b]), some unoccupied lower quality habitat is usually available. For example, Florida Scrub-Jays breeding in overgrown scrub fledge as many young as do unassisted pairs in high-quality habitat, although fledgling survival is lower in the former habitat due possibly to higher predation pressures (Woolfenden and Fitzpatrick 1984). If overgrown scrub can support successful breeding, floating should also be possible, although higher predation rates may also apply to floaters in this habitat (G. Woolfenden, pers. comm.). Indeed, nonbreeders in Florida do occasionally disperse into unoccupied habitats, forming small flocks that may persist for a month or two (Woolfenden and Fitzpatrick 1984).

Adults may force their offspring off territories even when marginal habitat may not be present. An extreme example is the Red Grouse (=Willow Ptarmigan, *Lagopus lagopus*), where nonbreeders are evicted from breeding habitats and are forced into areas where survivorship is so low that few survive through the winter (Watson and Moss 1970, Watson 1985).

Finally, the MHH also fails to explain how floating, and delayed dispersal and helping, could coexist as alternative strategies in the same population. In Purple Gallinules (*Gallinula martinica*), juveniles help but nonbreeding adults float in nonbreeding habitat (Hunter 1987). Young Green Jays (*Cyanocorax yncas*) in Texas delay dispersal for 15 months and assist their parents in defending the territory, but the nonbreeders are evicted after the next year's offspring are fledged (Gayou 1986) and evidently float until a vacancy is located. White-throated Magpie-Jay males disperse and a substantial number may float in unoccupied habitat, whereas most females are philopatric (Innes and Johnston 1996, Langen 1996b). In a population of western American Crows, Caffrey (1992) found that nonbreeders could delay dispersal, float, or switch between the two. The best documented example is the Australian Magpie (Carrick 1963, 1972; Veltman 1989), where some nonbreeders float in nonbreeding habitat and others remain on group territories.

THE FLORIDA SCRUB-JAY MODEL

Woolfenden and Fitzpatrick (1984, Fitzpatrick and Woolfenden 1986) developed a demographic model for the evolution of cooperative breeding in the Florida Scrub-Jay and the other *Aphelocoma*. Three variables are crucial to their model: D_o, the probability that early dispersers will become established successfully as breeders; B, the summed annual probabilities that a surviving helper remaining on its natal territory will encounter or create a breeding vacancy it can successfully fill; and L_h, the survival rate of a helper at home. The model predicts that as B and L_h increase, relative to early dispersal, delayed breeding and group living will be favored so long as D_o is low, even without any indirect fitness benefits (Table 28). In the Florida Scrub-Jay, D_o is low (high constraints on independent breeding); L_h is high (in comparison to that estimated for early dispersants floating in marginal overgrown scrub or sneaking through hostile occupied territories); and *B* is large, for males at least, due to territorial budding (Woolfenden and Fitzpatrick 1984).

Because the model does not include floating as an option, it assumes that nearly all Western Scrub-Jays breed as yearlings. Woolfenden and Fitzpatrick (1984:339) predict that D_o values for Western Scrub-Jays are high enough to favor early dispersal: "a wide range of acceptable habitats means that dispersing juveniles need only to stay alive in order to be more or less certain of obtaining space in which to breed as yearlings." D_o values, estimated from life-table variables, provide an index of breeding space competition (see Fitzpatrick and Woolfenden 1986). Similar D_o estimates for California, Island, and Florida scrub-jays, and for other taxa (Table 29) suggest that the level of breeding constraints per se is not sufficient to explain why one population is cooperative and another noncooperative; in fact, the level of breeding constraints provides absolutely no clue as to a population's social organization. More meaningful comparisons in D_o values could be made using fledgling production from simple pairs only; the added increment in fledgling production of breeders attributable to helpers may be important in the maintenance of delayed dispersal and cooperative breeding, but these secondarily derived benefits should not be used to assess the importance of breeding constraints leading to its evolution. When D_o is calculated for pairs only, this lowers the values for cooperative breeders, further blurring any relationship between breeding constraints and breeding system (Table 29).

L_h (adult helper-survivorship) and *B* (probability of a helper acquiring a breeding vacancy), on the other hand, may be much different between Florida and Western scrub-jays; unfortunately, both are impossible to measure for noncooperative species. Woolfenden and Fitzpatrick (1984, 1990) present a convincing argument why L_h may be relatively high compared to early dispersal in Florida. However, in California the converse may be true because jays can float, or even settle temporarily, in high-quality, occupied habitats as well as float and merely move through marginal ones. *B* (the summed annual probability of finding or creating a breeding vacancy) for Western Scrub-Jays, as for female Florida Scrub-Jays (which do not benefit from territorial budding, rarely inherit territories, and disperse farther), is even harder to evaluate; however, an increase in *B* in Florida Scrub-Jays must be a secondarily derived benefit of group living, rather than a primary casual factor.

The Florida Scrub-Jay model overemphasizes the importance of breeding constraints in the evolution of delayed dispersal, but provides valuable insight into the role of relative survivorship of nonbreeders pursing different strategies and other demographic factors. However, it falls short in its application to noncooperative populations simply because the model considers only two options for young birds: (1) disperse and breed, or (2) stay and delay breeding. The third option, floating, is not considered.

Walters et al. (1992a) applied a similar demographic model to empirical data from Red-cockaded Woodpeckers to evaluate fitness payoffs of young males that "depart and search" (DAS) for territories and those that "stay and foray"(SAF); all females employ the former strategy. Of males surviving to age one, 31% employed the DAS strategy and of these 39% became breeders on territories; 56% were solitary on territories and an estimated 5% remained as floaters. Walters et al. estimate that mean fitness for males

TABLE 29. INDEX OF BREEDING SPACE COMPETITION[a] FOR NONCOOPERATIVE CALIFORNIA AND ISLAND SCRUB-JAYS, COOPERATIVE FLORIDA SCRUB-JAYS, AND TWO OTHER COOPERATIVE BREEDERS

		Breeding space competition	
Species	Sex	Overall (with helpers)	Pairs only
Scrub-Jay			
California	Male	—	0.31 (0.23)[b]
	Female	—	0.54 (0.43)
Island	Both	—	0.07[c]
Florida	Both	0.27	0.44[d]
Acorn Woodpeckers	Male	0.08	0.09[e]
	Female	0.21	0.25
Green Woodhoopoes	Male	1.10	5.30[f]
	Female	0.43	0.92

[a] Lower values indicate higher levels of competition; a value of 0.1 would mean one breeding vacancy for every 9 nonbreeders.

[b] Values for breeder, juvenile, and adult nonbreeder survivorship as used in life tables (Table 23 and 24), where adult nonbreeder survivorship is 10% less than that of breeders; values in parenthesis are assuming nonbreeder survivorship equals breeder survivorship.

[c] Value calculated assuming 94% breeder survivorship (Atwood et al. 1990), adult nonbreeder survivorship 20% less than breeder survivorship, and juvenile survivorship and fecundity the same as for the Hastings population.

[d] Calculated from data in Woolfenden and Fitzpatrick (1984).

[e] Calculated from data in Koenig and Mumme (1987).

[f] Calculated from data in Ligon and Ligon (1978) and Ligon (1981).

employing the two strategies is nearly equal even without indirect fitness benefits as the potential advantage of early reproduction in DAS is balanced by a low probability of successful dispersal and increased survival in those adopting SAF. Walters et al. identify four variables that may be responsible for a reduced payoff in DAS relative to noncooperative species: (1) a high survivorship in males adopting SAF compared to birds in noncooperative species; (2) a low probability of surviving DAS birds attaining breeding status; (3) poor performance of males that do attain breeding status at a young age; and (4) a striking increase in reproductive success with age. These variables are nearly identical to those identified by Emlen (1982:32) as the key factors in favoring delayed dispersal and that "Such situations are expected to be rare, and philopatry (remaining at home) should occur only when the option of early personal reproduction is severely constrained." As noted before, these attributes were shown to differ little between cooperative and noncooperative *Aphelocoma.*

THE BENEFITS OF PHILOPATRY MODEL

Stacey and Ligon (1987) developed a model for the evolution of cooperative breeding in Acorn Woodpeckers that they term the benefits of philopatry (BOP) model. Based on their long-term study of Acorn Woodpeckers in New Mexico, they concluded that, contrary to previous models (Table 28), all suitable habitats are not saturated and no sharp gradient exists between good and poor habitats. Accordingly, nonbreeders remain on high-quality territories because helping for up to three years, and then breeding on a high-quality territory, accrues higher LRS than early dispersal and independent breeding on a territory of lower quality.

Similar results, albeit with a different interpretation, were found by Fitzpatrick and Woolfenden (1988) and Fitzpatrick et al. (1989). Analyses of life-time reproductive success in Florida Scrub-Jays indicate that the highest LRS is achieved by breeding as early as possible on a suitable territory; success in acquiring a territory at an early age is, together with breeder life-span, the most important contributor to a jay's lifetime reproductive success. However, when lifetime fitness is compared for Florida Scrub-Jays breeding in different habitats, they found that jays could delay breeding for several years in the good habitat and still have higher fitness than early breeders in the poor habitat (overgrown scrub). Thus, in both Florida Scrub-Jays and Acorn Woodpeckers, individuals that breed early in the always available but less suitable habitats will have lower life-time fitness than individuals delaying dispersal but eventually breeding on better territories, assuming the choice of a territory is final and permanent. Fitzpatrick and Woolfenden see this as a high cost of early dispersal, whereas Stacey and Ligon see it as a high benefit of philopatry (i.e., opposite sides of the same coin). Interestingly, when Fitzpatrick et al. (1989) examined how the production of breeding descendants varied within high-quality habitat, profound differences became evident; some areas showed much higher production of breeding descendants than others. Although this may result from differences in individual (genetic) quality, if it is due to long-term differences in habitat, then high-quality habitats are passed down through families, resulting in high variation in the success of different lineages (Brown 1974, Fitzpatrick et al. 1989). Such variation in habitat quality would lend support to the variance hypothesis and some of Brown's predictions (Table 28). However, Fitzpatrick et al. (1989) could find no evidence that individuals differentially compete for these areas, a necessary requisite for the BOP model.

Stacey and Ligon (1991; see also Waser 1988, Powell 1989) propose that natal philopatry is favored when a high and stable variance exists in territory quality, and/or group size affects the quality of a breeding opportunity. Under the BOP hypothesis, young in small groups on high-quality territories should delay dispersal in anticipation of inheriting breeding space, whereas young born into very large groups or on low-quality territories should disperse and breed as soon as possible. If group size is critical, nonbreeders should remain only in groups of some critical mass that assures the groups of high reproductive success and survivorship. For example, in *Campylorhynchus* wrens (Rabenold 1984, 1985; Austad and Rabenold 1985, Zack and Rabenold 1989), reproductive success of pairs is near zero and increases with group size so that reproductive output (per capita) peaks in groups of either three (*C. griseus*) or four (*C. nuchalis*). In these species, nonbreeders are effectively prevented from independent breeding by high nest predation rates, and neither habitat saturation nor differences in territory quality are implicated (Austad and Rabenold 1985). Under these conditions, floating is not precluded, but the advantages of group living and helping for nonbreeders make floating, or even breeding in simple pairs, a poor alternative.

The BOP model predicts that young in noncooperative species should disperse at independence either because: (1) the habitat is more uniform and territories are of similar quality; (2) interterritory quality fluctuates unpredictably over time (therefore high-quality territories are not "inheritable"); or (3) individuals do not benefit from living in groups.

Despite such clear examples of species that may form groups because of "group-living effects," two problems exist with this suggestion. First, the BOP hypothesis does not clearly distinguish between primary and secondary group-living effects. For example, Stacey and Ligon (1991) suggest that Florida Scrub-Jays and other cooperatively breeding New World jays delay dispersal because of anti-predator benefits of group living. The orchestrated sentinel system (McGowan and Woolfenden 1989) and other group behaviors in Florida Scrub-Jays may lessen predation; pairs with helpers do experience lower nest predation rates (Schaub et al. 1992). Another group-living effect is territorial expansion with increased group size in Florida Scrub-Jays. This not only lessens any adverse impact from resource depression, but allows for territorial "budding," which Woolfenden and Fitzpatrick (1984) identify as an important factor in maintaining cooperative breeding in the Florida population. Such secondarily derived benefits may be substantive but cannot be attributed as a primary cause of delayed dispersal, although they may be important in its maintenance (current utility). Because it is always possible to point to some benefit of group living, one cannot suggest that another population is noncooperative because group benefits do not apply.

Other predictions of the BOP concern how variance in territory quality differs among populations that vary in social behavior. To date, tests have involved comparisons between widely separated populations of cooperative species (e.g., Acorn woodpeckers in California and New Mexico; Koenig and Mumme 1987, Stacey and Ligon 1987). A more appropriate test can be between the closely related Western and Florida scrub-jays. Scrub-jay territories at Hastings were ranked from Type 1 to Type 3 on the basis of occupancy rate and vegetation characteristics. Of approximately 45 territories (range of 40 to 52 over the study period), five (~11%) were of very low quality. In Florida, the quality of the habitat depends on whether it has been burned recently, but all of the area in the periodically burned scrub is continuously occupied in nearly all years (therefore Type 1 and Type 2 territories). Fledgling production over the study area at Hastings also appears to be more variable than in Florida. In Figure 40, both the Hastings and Florida study areas are arbitrarily divided into 9 parts. Within high-quality habitat, fledgling production is relatively uniform in Florida, ranging from 1.9 to 2.2 (Woolfenden and Fitzpatrick 1984), whereas in California it ranged from 0.6 to 1.4.

While this suggests greater variance in territory and habitat quality in the noncooperative population, it could be argued that the "marginal" unburned, overgrown scrub in Florida should be included, despite the fact that unburned scrub is rarely colonized but rather "grows up" and eventually takes over what was formerly high-quality habitat. Stacey and Ligon (1991) suggest that comparisons of high- and low-quality habitat in Florida would reveal marked variation in habitat-territory quality, implying that this would run counter to both the Florida Scrub-Jay model (Woolfenden and Fitzpatrick's 1984) and the MHH (Koenig and Pitelka 1981). However, one could argue that this difference is exactly the basis for the latter model (a steep drop-off in quality in rarely occupied, marginal habitats). The fact that these low-quality habitats are not continuously "saturated" only refutes Koenig and Pitelka and Woolfenden and Fitzpatrick to the extent one stretches the definition of "suitability," and once again illustrates the problem in defining "suitable" and "marginal" habitats (see also Koenig et al. 1992). In a study of Florida Scrub-Jays at the Kennedy Space Center, where habitat is generally more marginal, Breininger et al. (1995) found that some areas acted as source populations and others as population sinks. All areas may appear "saturated," but only because of immigration from source habitats. Over a three-year period, demographic performance was related to landscape features; as at Archbold, open scrub oak was higher quality habitat, but territories also included a matrix of low-quality and unsuitable habitat.

According to the BOP, a shortcoming of prior analyses is that they compared habitat, not territory, quality (Stacey and Ligon 1991). For delayed dispersal to be favored under the BOP, high-quality territories must be inheritable, i.e., long-term differences in quality on a per-territory basis. Early dispersal will occur in situations with low variance in territory quality, which can arise either by very low correlation and large differences in quality among years, or high correlation but uniform quality among years. For example,

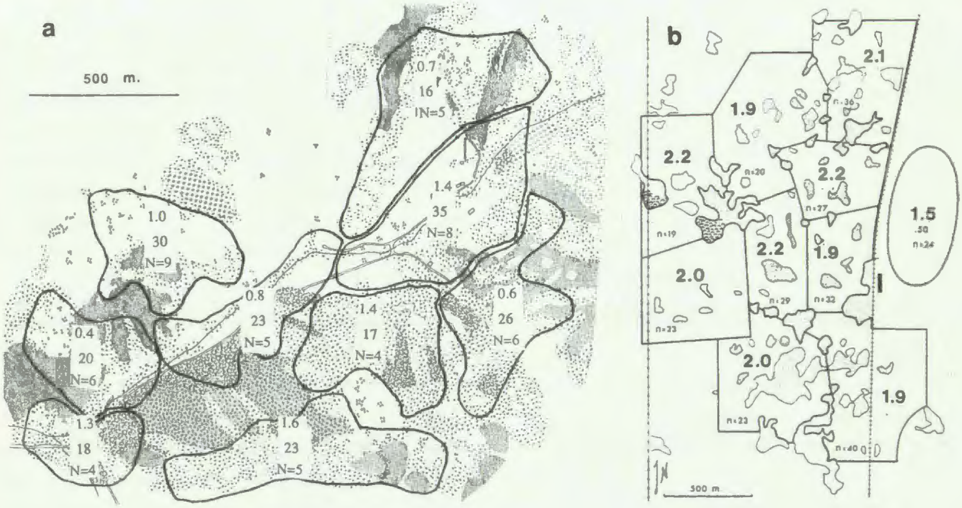

FIGURE 40. Variation in fledgling production over nine randomly drawn geographic segments of the California and Florida scrub-jay study areas. (a) California Scrub-Jay study area at the Hastings Reservation, (b) Florida Scrub-Jay study area at the Archbold Biological Station (from Woolfenden and Fitzpatrick 1984). Numbers are overall mean fledgling production calculated by averaging mean fledgling production for all breeding pairs (or family groups) on each territory in each area; N = breeding-pair years in each area.

Waser (1988), in relating philopatry to variance in home range quality, hypothesized that the banner-tailed kangaroo rat (*Dipodmys spectabilis*) dispersed, despite all other conditions favoring philopatry, because no correlation existed between home range quality among years.

However, as with defining "marginal habitat" under the MHH, it is not clear how much or little variance is required to favor one social system over another. Also, interterritory comparisons among cooperative and noncooperative species are difficult to make for several reasons. Because territories are occupied and defended by groups in cooperative species, and better territories are more continuously occupied by larger groups, this may result in more stable boundaries and greater permanence of groups on higher quality territories, and combines (and confounds) group effects with effects of territory quality. In noncooperative populations, because only pairs occupy territories, no group effects occur and territory boundaries often fluctuate upon the death of one of the breeders. The BOP model also assumes that the choice of a territory is permanent. However, movements in noncooperative breeders from low-quality to higher quality habitat may be common (e.g., Great Tits, *Parus major* [Krebs 1971]; Eurasian Magpies [Baeyens 1981]). At Hastings, 20% of all territory vacancies were filled by breeders changing territories. This suggests that young nonbreeders are able to breed initially in low or intermediate quality habitat and later acquire a better site. In cooperative breeders, on the other hand, young that disperse to low-quality habitats may not be able to shift back because nondispersing individuals are present to fill vacancies on territories in high-quality habitats. A third problem involves scale; the MHH generally examines habitat gradients over a wide geographic area, whereas BOP focuses on interterritory differences within a small, local area.

DELAYED DISPERSAL THRESHOLD MODEL

None of the models (Table 28) are fully supported by comparisons among the cooperative and noncooperative *Aphelocoma*. Most treat only two options (disperse and breed or stay and delay breeding) and sidestep the question of floating. In populations where floaters are restricted to the same degree as helpers from independent breeding, the relevant comparisons are between early dispersal (and floating) vs. delayed dispersal (and helping), not between delayed dispersal and independent breeding. The Delayed Dispersal Threshold Model (Koenig et al. 1992) addressed some of the short comings of the previous models by giving equal treatment to early dispersal and floating, delayed dispersal and helping, and independent breeding. Rather than specific predictions, the model provides a general guide for organizing and evaluating the relative importance of ecological factors under which the different dispersal strategies, including floating, are favored. The model lists 13 factors influencing the dispersal options available to offspring, most of which have been discussed in the context of the other models. Here, I focus closely on how three factors—resource depression on territories, habitat available for floating, and habitat variability—influence dispersal options in *Aphelocoma* jays and show why floating is the preferred option in Western Scrub-Jays.

Resource depression on territories

Models developed by Waser (1981, 1988) and Brown (1982, 1987) explore the relationship of territory quality and resource depression to group living. If territories have limited resources or low rates of resource renewal, the addition of individuals beyond the breeding pair may lower survival and reproductive success to such a degree that breeders should evict offspring, or offspring should choose to leave, or both. Where resource renewal is slow, group size may be limited to pairs despite other factors favoring retention of offspring. Nonbreeders may, however, increase the fitness of breeders by helping to defend the territory, or by helping to raise young. These secondarily derived benefits may lower the absolute costs to breeders of allowing offspring to remain. Lowered defense costs were used by Brown (1969) to explain why adults would tolerate young in Mexican Jays and other cooperative breeders. In contrast, on high-quality territories, specifically those with rapid resource renewal or those with "nondepreciable resources" (Waser 1988), additional group members will have relatively little effect on survival and reproductive success.

Does resource depression explain the different patterns of territorial behavior, dispersal, and group living in *Aphelocoma* jays? Both territory size and habitat productivity contribute to resource levels, but data on the latter are scant. Comparisons of territory size suggest that on large territories resource levels are lower per unit area, more patchy, or fluctuate more strongly. In this context, it is noteworthy that in Florida, scrub-jay territories are extremely large (mean of 7.2 ha for pairs and increasing significantly with group size; Woolfenden and Fitzpatrick 1984) compared to those recorded for Western Scrub-Jays (1.5 to 2.5 ha). Mexican Jay territories in Arizona are extremely large (20 to 25 ha), support large groups (ranging from 5 to 22 jays), but territory size apparently does not fluctuate with group size (Brown 1987, Brown et al. 1997). Brown (1987) suggested that Mexican Jay territories are larger than needed except at peak densities, but data are lacking, particularly with respect to winter conditions. Unicolor Jay territories may be even larger; the one territory Webber and Brown (1994) were able to map in its entirety ranged between 41 and 45 ha, and was held by a group of six.

Several lines of evidence suggest that territories in Western Scrub-Jays are not of such low quality as to preclude group living. First, breeders at Hastings tolerated their own young and unrelated floaters in the nonbreeding season and, in 1985, even in the breeding season. Second, Western Scrub-Jays occupy habitats that support group-living Mexican Jays when the latter are absent. Third, acorns, an important resource for *Aphelocoma* jays, are unlikely to limit group size because they are a "time-limited" resource (Waser 1988); processes other than consumption by scrub-jays limit their availability. Acorns remain on oaks for several months and numerous seed cachers and seed predators remove acorns before and after seed fall. In most years, acorns are superabundant with respect to a jay's (or an aggregation of jays) ability to eat or cache them, and this decreases the cost of sharing a territory either with related offspring or unrelated floaters. Little information on insect productivity is available for comparison, but nestling starvation in Florida Scrub-Jays is extremely low, and adults (with helpers) foraged only 40% of daylight hours during the breeding season. Nestling starvation averaged 17% at Hastings and breeders foraged 70% of daylight hours, suggesting potential for resource depression effects. Additional work on food resources of these jays would be required to provide a definitive answer regarding the importance of resource depression on their dispersal options (see also Burt 1996).

Habitat available for floating

In some cooperative species, special features of their habitat can strengthen ties of helpers to home groups. For example, roost-holes in Green Woodhoopoes (*Phoeniculus purpureus*; Ligon 1988) and granaries in Acorn Woodpeckers (Koenig and Mumme 1987) appear to be critical for breeders and nonbreeders alike; when limited, offspring that either attempt to set up a territory or float will do poorly. When the critical resource is important only for breeding (e.g., nest cavities), this does not constrain floating, and some other explanation for delayed dispersal must be invoked. When breeding space itself is in some way limited, as has been suggested for the cooperative *Aphelocoma* jays, it is more difficult to pin-point the resources that make space or other habitat features critical for nonbreeders. However, a complete theory for group living in any species must include an explanation of what ecological factors make adjacent habitat unsuitable for floating by nonbreeders.

Access to high-quality habitat should result in high floater survivorship, but actual floater survivorship is unknown. Data on relative age-specific survivorship of juveniles, adult nonbreeders, and territorial jays are particularly crucial for resolving questions concerning the costs and benefits of floating. In many cooperatively breeding species, nonbreeding helpers have higher survivorship than breeders (e.g., male Florida Scrub-Jays [Woolfenden and Fitzpatrick 1984], Acorn Woodpeckers [Koenig and Mumme 1987]). In contrast, nonbreeder survivorship in noncooperative species is thought to be lower than that of breeders, due to risks of dispersal (Brown 1974, Emlen 1982), being forced into marginal habitats (Watson 1985), or not having the benefits of unrestricted access to critical resources and microhabitats (Ekman and Askenmo 1984). However, Ekman and Askenmo (1986) found that nonbreeding adult male Willow Tits (*Parus montanus*) had higher survivorship than adult male breeders.

In *Aphelocoma* jays, the types of habitat available to nonbreeders are strongly influenced by the territorial behavior of breeders. In Florida Scrub-Jays, juveniles wander and are tolerated on all territories prior to their post-juvenile molt (Woolfenden and

Fitzpatrick 1984). Later, however, they are not tolerated on non-natal territories, and either return to their natal territories (the preferred option), or move to unoccupied areas, usually non-breeding habitats. Survivorship of helpers does not stabilize at adult breeder levels until age two, but this seems to be caused primarily by the risks of dispersal forays (Woolfenden and Fitzpatrick 1984, Fitzpatrick and Woolfenden 1988). Nonbreeders in Florida must trespass occupied, hostile territories in search of breeding vacancies, or float in unoccupied habitats with high predation rates (Woolfenden and Fitzpatrick 1984, 1990) and possibly also a paucity of acorns.

At Hastings, scrub-jay breeders tolerated both offspring and unrelated floaters of all ages on their territories except in May and June, and the floaters aggregated primarily where acorns were in good supply. Most remained sedentary throughout the winter and early spring, storing and recovering acorns as did the resident territorial breeders. By late April in most years, aggregations dissolved and floaters were rarely seen until early July when some of the same individuals returned and joined independent juveniles. Their disappearance coincided with increased aggression by territorial jays, but they also disappeared from areas unoccupied by breeders. In all months but May and June, floaters had unrestricted access to the best habitats, aggregated in loose flocks, and did not invest time and energy in territory defense or reproduction, and it is possible that their survivorship may be near (or even exceed) that of breeders.

In contrast, juvenile Island Scrub-Jays move to unoccupied areas by early August as breeders aggressively exclude them, including their own offspring, from their territories (Atwood 1980a; J. Atwood, pers. comm.). Yet, they do well, even though they must encroach on territories to gain access to acorns (Atwood 1980a). Few details are available on dispersal in Mexican Jays, but young retain juvenile characteristics for several years (Brown 1963), which may extend the period of tolerance and lessen the aggression of adults (Lawton and Lawton 1986). Degree of sociality varies within the range of the Mexican Jay (Brown and Brown 1990); they occur primarily in montane oak-woodland, but no obvious habitat or vegetation feature(s), separate high- and low-quality habitats, either for breeders or potential floaters (Edwards 1986).

Habitat variability

It is necessary to attempt to separate variability on a per-territory basis from phenomena that occur on a larger scale. For example, at Hastings, territory quality (occupancy rate) was correlated with vegetation characteristics, including the number of oak species and area of oak canopy. Both of these variables are indicators of reliable acorn production on a per territory basis. Hence, on the local scale, territory quality is predictable and the relative ranking of territories probably does not vary greatly from year to year. However, on a broader regional scale in California, acorn production is highly variable and strongly affects scrub-jay population density and dispersal options. This may be a key point in the secondary loss of cooperation in Western Scrub-Jays.

Acorn production in high-quality scrub-jay habitat in Florida shows little annual and spatial variation relative to that in California. In Florida, scrub oaks form continuous, shrub-like stands covering many hectares, and each scrub oak produces few seeds. Estimated production on the average territory was 128,000 acorns, and ranged from 14,000 to 331,000 (DeGange et al. 1989). Group size ranges from 2 to 10 jays in Florida, and each jay eats and caches approximately 8,700 acorns per year. It seems probable that in the poorest acorn years demand may exceed production for some large groups, but during their 25 years of study, no complete acorn crop failure occurred on the study tract (G. Woolfenden and J. Fitzpatrick, pers. comm.). Whether acorn production declines with time since last burning in Florida scrub oak species as in some other scrub-oaks (Wolgast and Stout 1977) is not known, but this would contribute to low suitability of long unburned areas in Florida for both floaters and breeders. Relatively uniform production of acorns contributes to a situation where nonbreeders would gain little by intruding on neighboring territories, intruder pressure is slight, and territory defense is economical (DeGange et al. 1989). The rarity of acorn crop failures in Florida would also prevent the local populations crashes that occur in California, thereby eliminating the benefits of the wide-ranging movements by floaters (i.e., locating areas where acorn crop crashes have created low population densities and territory vacancies) observed in Western Scrub-Jays.

Mexican Jays and Western Scrub-Jays co-occur throughout much of their range, and although Mexican Jays locally exclude scrub-jays from their preferred habitat, both can be found in oak woodlands that are generally more typical of those in California than those in Florida, that is, with highly variable acorn production (Bock and Bock 1974, Stacey and Bock 1978). However, specific details on acorn production patterns and acorn use and dependency by jays in Arizona are not known.

On the scrub-jay study area at Hastings, the three common species of oaks are distributed as isolated individuals, extensive monotypic stands, and mixed closed-canopy forest. The oaks are generally quite large and a single tree can produce well over 400,000 acorns (W. Carmen, unpubl. data). An average scrub-jay territory at Hastings includes 0.55 ha of oak canopy and two oak species, and although acorn production per territory was not measured, acorns are probably produced far in excess of jay demand in all but the poorest years. Acorn production was highly variable among years, with relatively frequent crop failures on a local habitat level and more rarely on a regional level. Acorn crop failures resulted in territory abandonment, high mortality, emigration by breeders and floaters, and poor reproductive success the following breeding season. Early dispersal and floating allows nonbreeders to respond most efficiently to spatial and temporal variation in acorn production patterns and to locate breeding vacancies. These tactics yield three patterns: (1) localized home-range movements by floaters during the fall-early spring period in most years; (2) emigration to locate acorns during local acorn crop crashes; and (3) either local or wide-ranging movements in early spring to locate breeding vacancies, particularly to areas where population density has been reduced by acorn crop failures.

SYNOPSIS

The fundamental result of this study is that floating should be considered an important strategy for acquiring breeding space, just as is delayed dispersal and helping. When floating is ignored or treated as a one-dimensional phenomenon, not only do theories for the evolution of delayed dispersal and cooperative breeding fall short, but a interesting and complex part of the social behavior of a species is overlooked. 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, as are the varied responses of floaters to these conditions. 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. Below, I provide a synopsis of the range of scrub-jay dispersal, movement and behavioral patterns.

SCRUB-JAY DISPERSAL AND FLOATING IN CENTRAL COASTAL CALIFORNIA

Figure 41 illustrates a landscape representing an idealized mosaic of habitat qualities for scrub-jays as are found in central coastal California. Higher quality habitats occur where oak diversity is high, live oaks predominate, and insects and berries are abundant. These features are most commonly found along stream channels in the area.

Figure 41a depicts clusters of territories in high- and low-quality habitat (territories in better habitat are more tightly clustered and smaller) and the dispersal movements of floaters during the nonbreeding season (August–April). Tolerance by breeders allows floaters to aggregate in high-quality habitat where acorns are abundant and floater survivorship is expected to be high. As shown, floaters fledged in low-quality habitat move into high-quality habitat, whereas those fledged in high-quality habitat may remain on or near their natal territories; both may also move considerable distances. Floaters appear to be as dependent on cached acorns as breeders and may be closely tied to their stores during the winter. When acorns are few, jays experience significantly higher mortality, reproductive failure, and territory abandonment. Poor acorn production in local areas (e.g., X and Y in Fig. 41a) results in emigration by both offspring and a substantial number of territorial breeders. They search for locations with high acorn production in which to spend the fall-early spring period.

Beginning in April, floaters and residents are less dependent on their cached acorns as invertebrate food becomes more abundant. This seasonal pattern of food abundance may contribute to the tolerance of floaters by local, settled breeders in the winter (when acorns are superabundant), and their intolerance in the breeding season (when insect prey is important and starvation rates of nestlings are high). At this time (Fig. 41b), floaters may move out of high-quality habitat where breeding vacancies are few to potentially high-quality habitat where an interval of poor acorn production has reduced breeder density (e.g., area X), or to poor quality habitat where breeding space may be available intermittently for a number of reasons, including frequent poor acorn crops and movement of breeders from there to higher quality habitat. Surviving breeders may also return to the locations they abandoned due to poor acorn production the previous fall, only some of which are able to reestablish their territories. In such areas in high-quality habitat, occupied space is unchanged but territory size has increased (Fig. 41b area X); in low-quality habitat, territories simply may be abandoned and the space go unused (area Y). Over time breeding density returns to prior levels as new territories are established.

At the onset of the breeding season, individual floaters employ different behaviors, including establishing pseudo-territories, sneaking through territories and unoccupied habitat and, as observed in one year, moving substantial distances in large cohesive flocks (as indicated by the large arrows in Fig. 41b). Floaters also may remain in aggregations

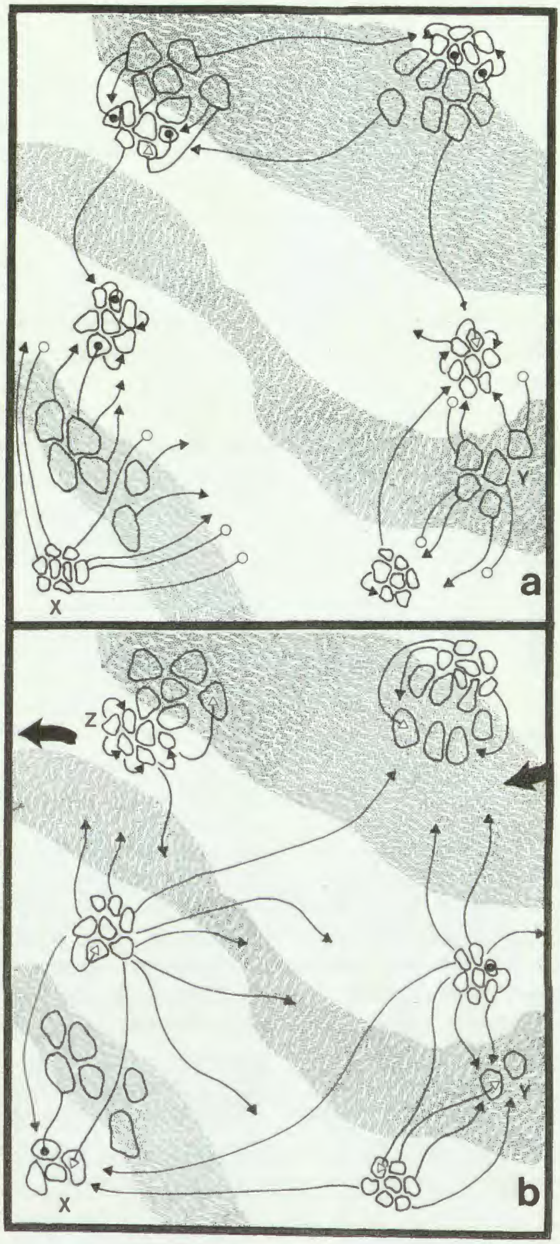

FIGURE 41. Floater and breeder (territorial jay) movements in an idealized mosaic of habitat qualities as found in central coastal California. The unshaded area represents high-quality habitat and the shaded area low-quality habitat. A few representative territories are drawn showing smaller, denser territories in high-quality habitat. Lines with closed arrows denote movement of floaters, open arrows denote floater-to-breeder transition, closed circles denote breeders changing territories, open circles denote breeders abandoning territories, and large arrows denote flock movements. Poor acorn crops occur in area X and Y with exceptional production in area Z. (a) Movement patterns during the nonbreeding season (August–April). (b) Movement patterns during the breeding season (May–July).

on high-quality habitats throughout the breeding season (e.g., area Z in Fig. 41b) as a result of increased tolerance by breeders given unusually abundant acorns into the summer months.

During the year, floaters search for and fill available breeding vacancies as shown in Figure 41. Although breeding vacancies arise from breeder death throughout suitable habitat, floaters have the greatest probability of gaining a breeding vacancy either in poor quality habitat where breeder turnover may be greater or in high-quality habitat where breeder density has been reduced by an acorn crop failure. Also as shown in Figure 41, there is movement of breeders from one territory to another, often from lower to higher quality habitat. Not illustrated are the relatively rare regional acorn crop failures that may result in breeder density decline and subsequent low reproductive output over a broad area, providing increased opportunity for dispersing offspring and older floaters to gain a territory and breeding status.

These patterns of habitat quality and acorn production, the varied behaviors floaters employ to acquire breeding space and exploit resources, the behavioral interactions between territorial jays and floaters, and the ability of breeders to move and improve the quality of their territories all promote selection for early dispersal and floating in scrub-jays in central coastal California, and selection against cooperative breeding.

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