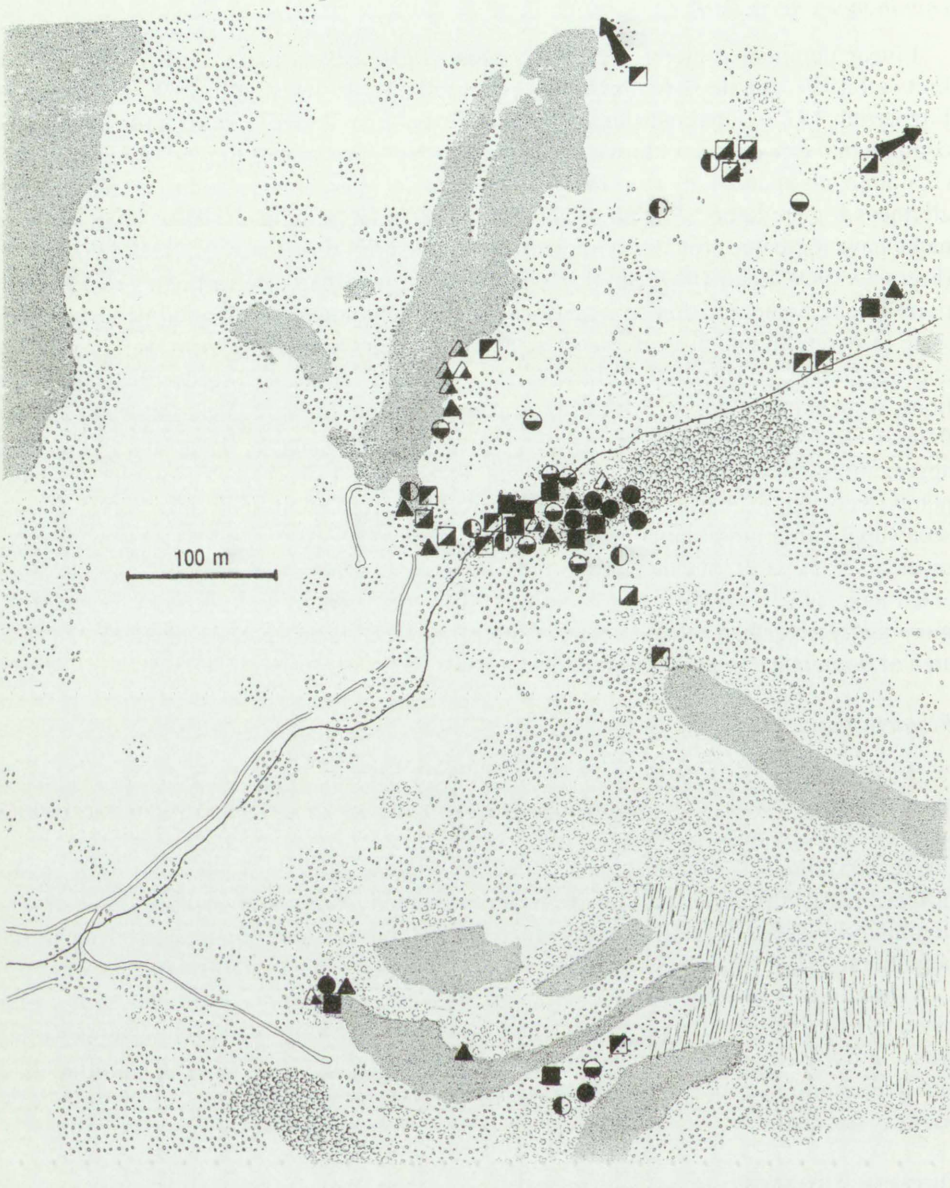

FIGURE 31. Floater association and movements of seven individuals during the breeding season. Eight simultaneous radio-locations were taken one hour apart from 0600 to 2000 hours on 7 May, 1985. The eight different geometric shapes represent the eight simultaneous locations of seven individuals.

REPRODUCTION

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

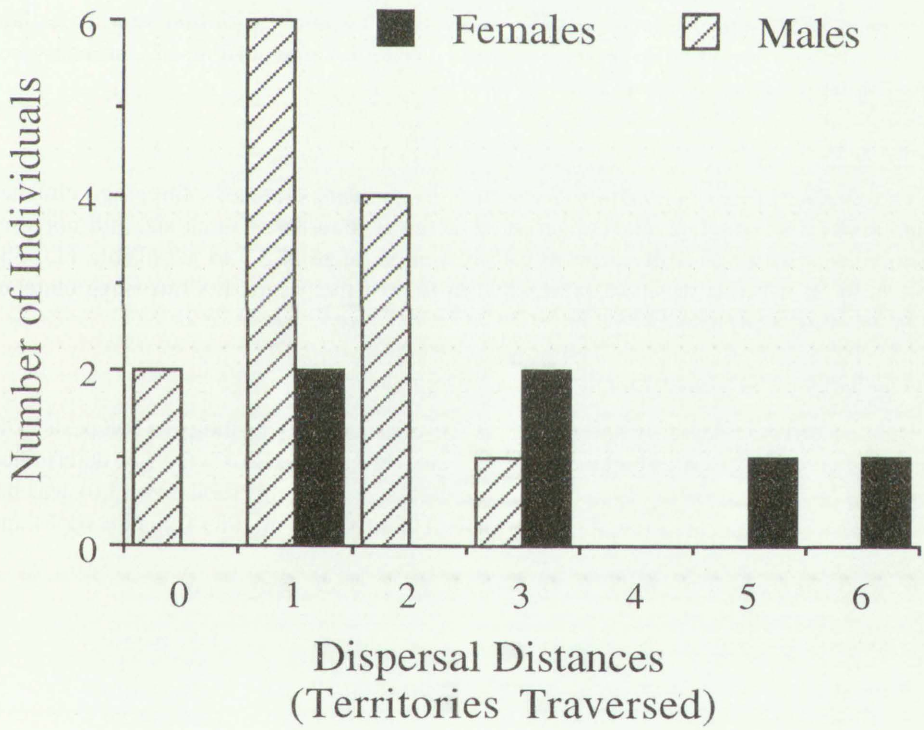

FIGURE 32. Natal-to-breeding dispersal distances within the study area and immediate vicinity. Distance is measured in territories traversed.

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%

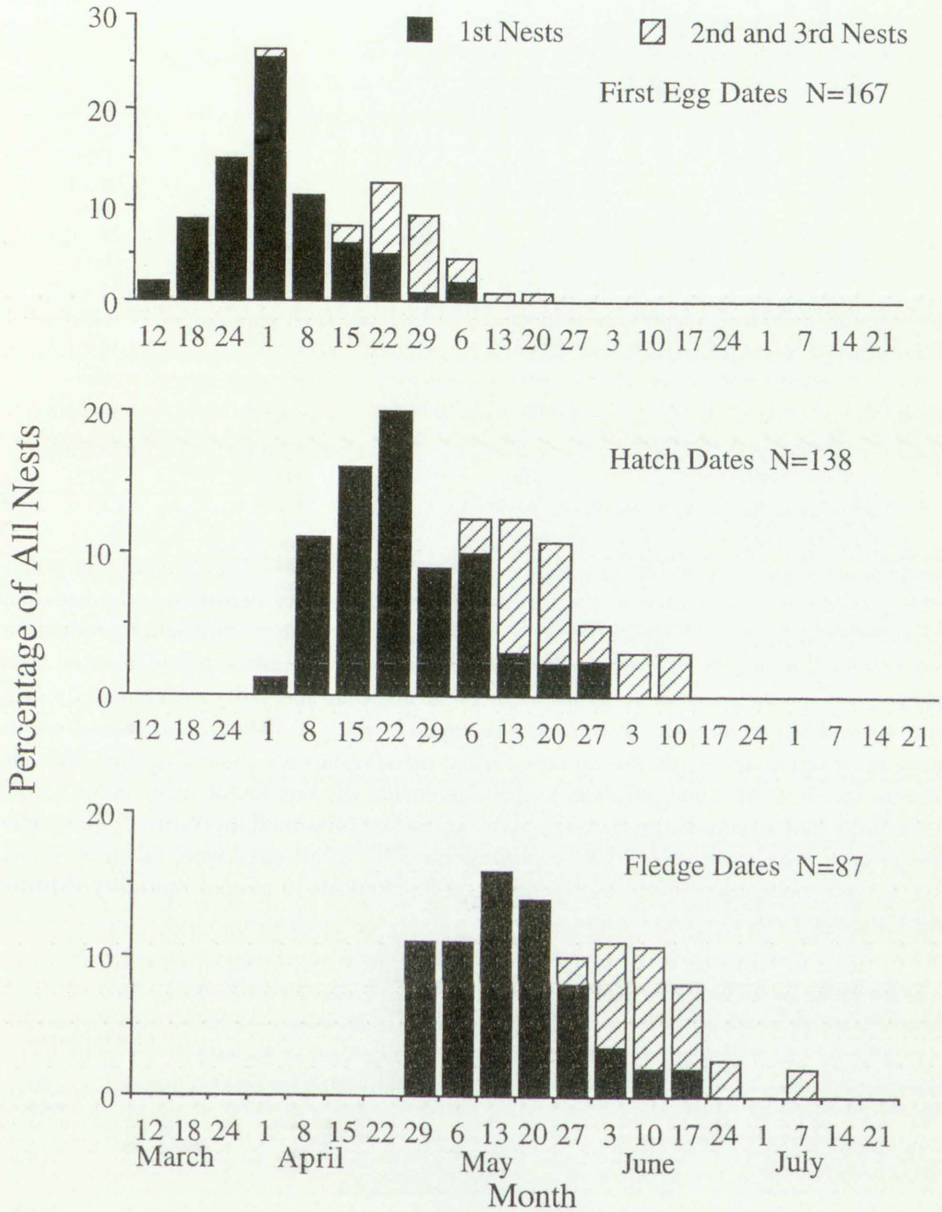

FIGURE 33. Nesting chronology of Hastings scrub-jays, 1981–1985.

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.

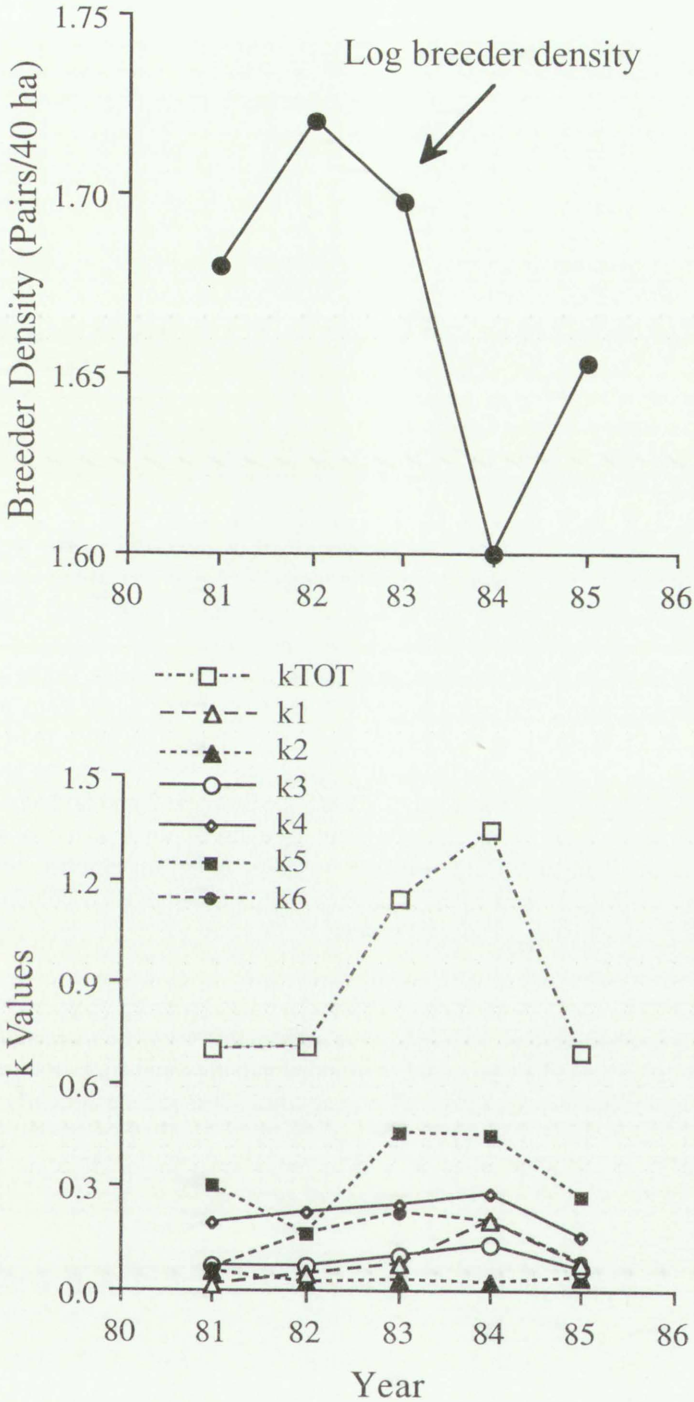

FIGURE 34. Log of breeder density (pairs/40 ha) and k-values 1981–1985 (see text for explanation of key-factor analysis). k1: failure to lay eggs; k2: failure to lay four eggs in clutch; k3: failure to renest; k4: egg loss; k5: nestling loss; k6: fledgling loss.

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

	Predation on				Starvation of
Year	Eggs	Nestlings	E+N combined	Nests	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