

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 (Woollfenden 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 Woollfenden 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, Woollfenden 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 <sup>a</sup>	-0.45 (44) P = 0.009	-0.48 (32) P = 0.002	-0.36 (58) P = 0.01
Clutch	0.21 (33) NS <sup>b</sup>	0.44 (26) P = 0.02	0.04 (48) NS
Fledge	0.24 (60) P = 0.06	0.41 (46) P = 0.005	0.12 (83) NS
Independent young	0.23 (60) P = 0.08	0.32 (46) P = 0.03	0.13 (83) NS

<sup>a</sup>First egg date standardized so that the first egg each year falls on the same date.

<sup>b</sup>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  $\pm$  SD) (N IN PARENTHESES)

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

<sup>a</sup>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.

<sup>b</sup>FED = first egg date. Ap=April, Mr=March.

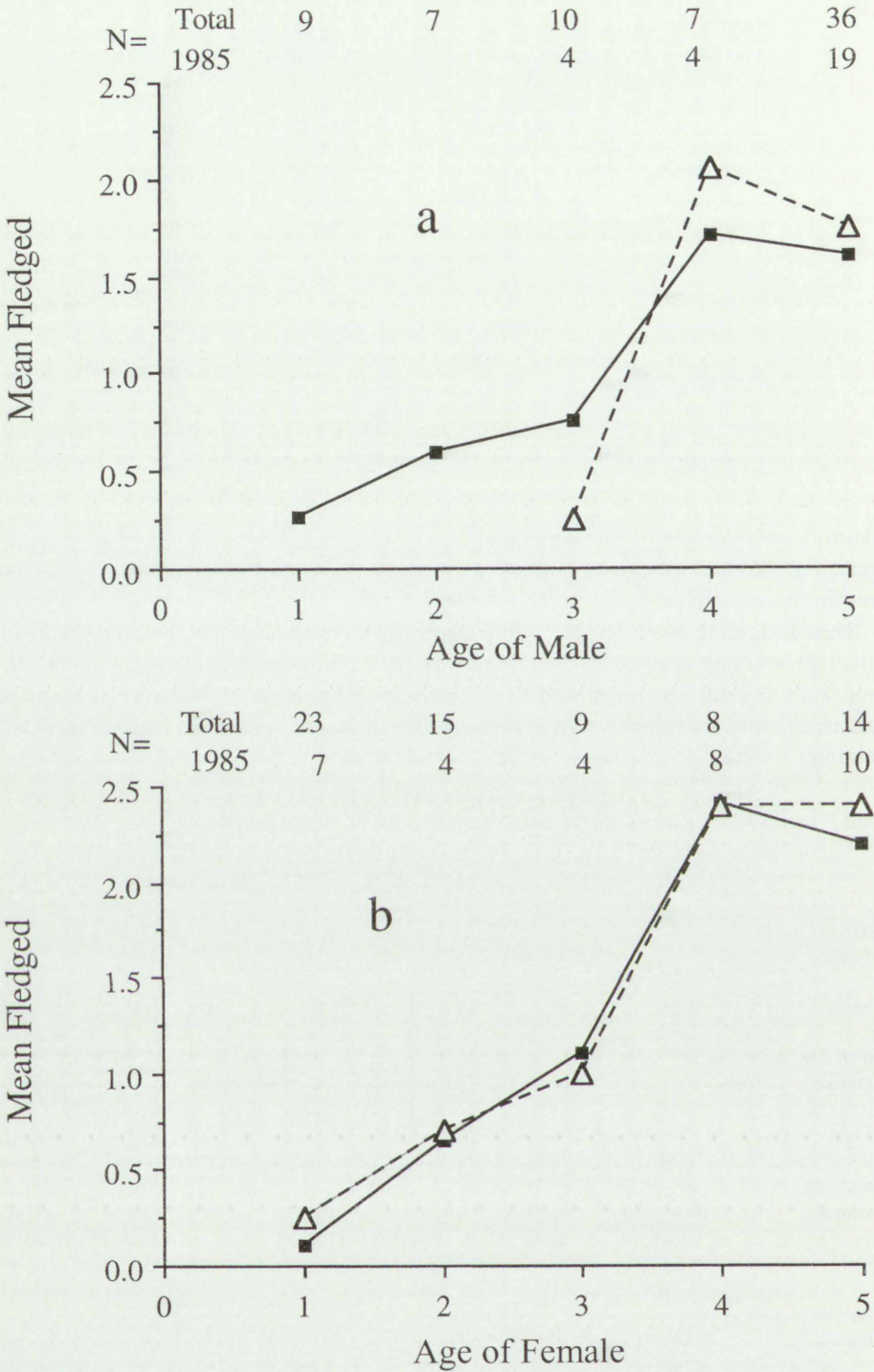


FIGURE 35. Age-specific fledgling production of breeding males (a) and females (b). Pooled data from all years, and for 1985 only, are plotted. Sample sizes for each year are plotted across the top.

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 <sup>a</sup>
First egg date	9 April $\pm$ 12 (6)	3 April $\pm$ 12 (52)	Z = 1.25 P = 0.21
Young fledged	0.73 $\pm$ 1.1 (11)	1.39 $\pm$ 1.6 (70)	Z = -1.13 P = 0.26
Independent young	0.6 $\pm$ 0.9 (10)	1.01 $\pm$ 1.3 (70)	Z = -0.82 P = 0.41

<sup>a</sup> 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 <sup>a</sup>	85.7% (14) <sup>c</sup>	84.0% (11)
Partial years <sup>b</sup>	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:  $G = 2.0$ ,  $df = 3$ ,  $P > 0.10$

<sup>a</sup> Entire years include only scrub-jays banded by 1 April.

<sup>b</sup> 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.

<sup>c</sup> 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  $\geq 5$  YR

Age	Males			Females			
	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	—	—	—
$\geq 5$	50	40	80	$\geq 5$	28	20	72

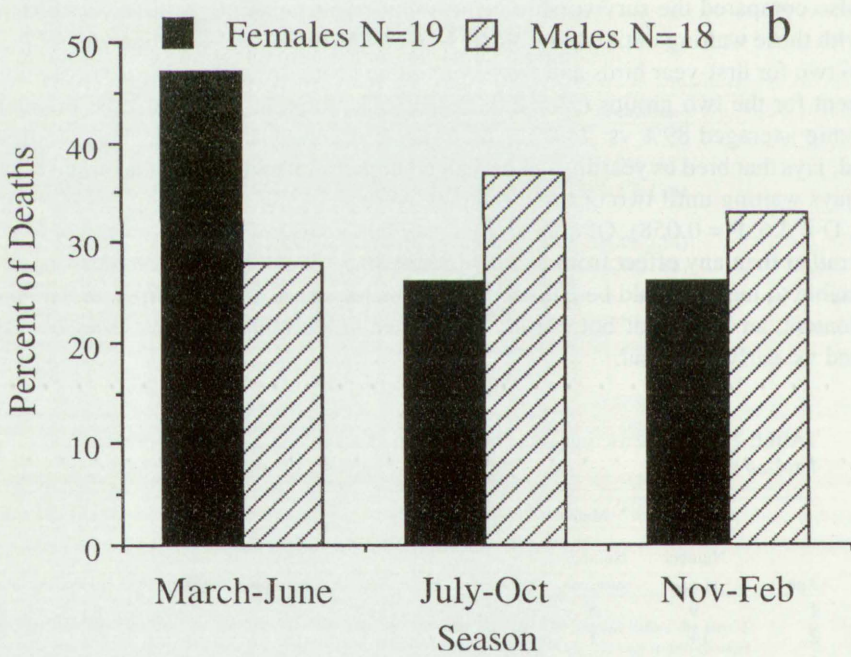
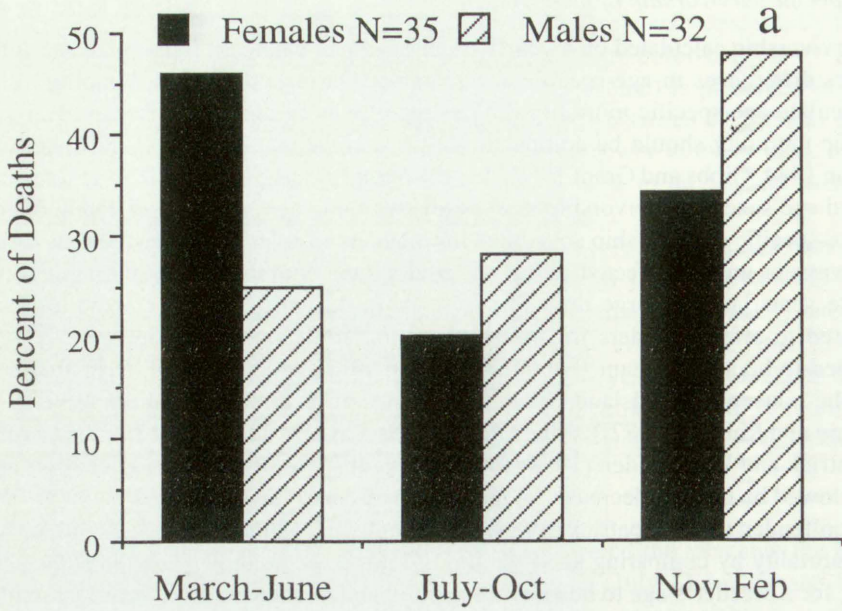


FIGURE 36. Seasonal pattern of deaths of males and females during the entire study period (a), and excluding deaths during the acorn crop failure (b).

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 ( $R_0$ ) was approximately 1.0.

From a life table based on breeders, nonbreeder survivorship can be estimated, given that  $R_0 = 1$ . 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 non-cooperative 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



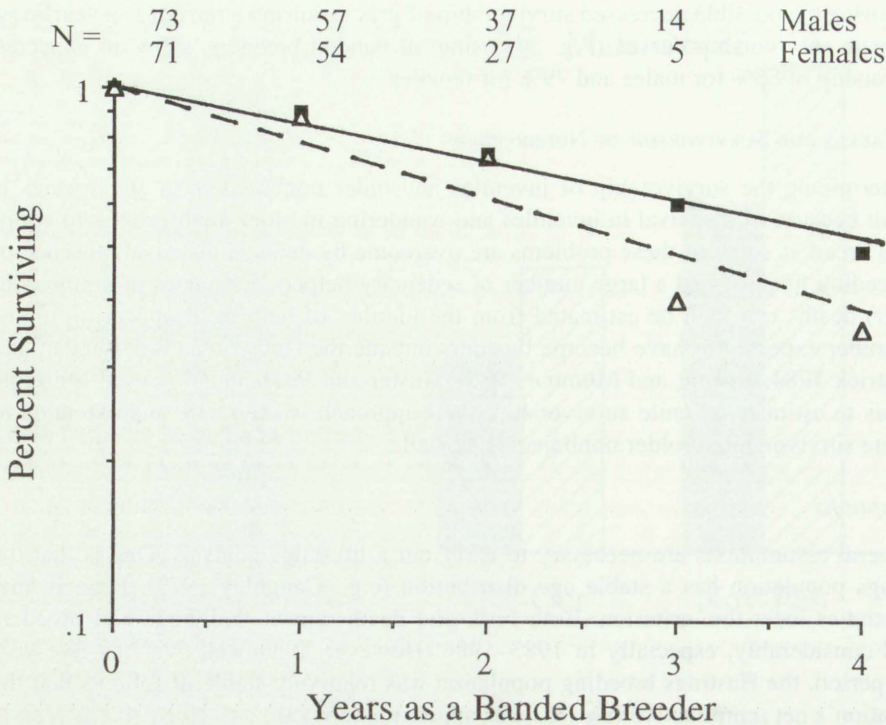


FIGURE 37. Survivorship of breeding California Scrub-Jays plotted as the proportion of banded breeders surviving from 1 to 4 years after banding. Sample sizes above points are the number of individuals at risk during the period and include breeders of all ages. The lines represent constant survivorship 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  $\times$  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  $\times$  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 ( $x$ )	Survivorship		Age of territory acquisition ( $A_x$ )	Number of			Proportion territorial ( $P_{tx}$ )	Probability of getting territory ( $P_{bx}$ )
	Breeders ( $Sb_x$ )	Floater ( $Sf_x$ )		Vacancies ( $Ob_x$ )	Nonbreeders ( $Nf_x$ )	Breeders ( $Nb_x$ )		
Females								
Fledge	—	0.72	0	0 <sup>a</sup>	600 <sup>b</sup>	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 <sup>c</sup>	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 <sup>c</sup>	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.

<sup>a</sup> Number of vacancies based upon a hypothetical population of 1,000 pairs, with all vacancies created by breeder deaths.

<sup>b</sup> Number of fledglings based upon 1,000 pairs producing 1.2/pair (Table 10).

<sup>c</sup> 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 ( $\sum (l_x)(P_{ix})$ ) 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 ( $\sum l_x m_x$ ) 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  $LRS = \sum l_x m_x$ , where  $l_x$  and  $m_x$  are age-specific survivorship and fecundity (same sex fledglings per breeder) from breeding age ( $\geq 1$ ) 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,

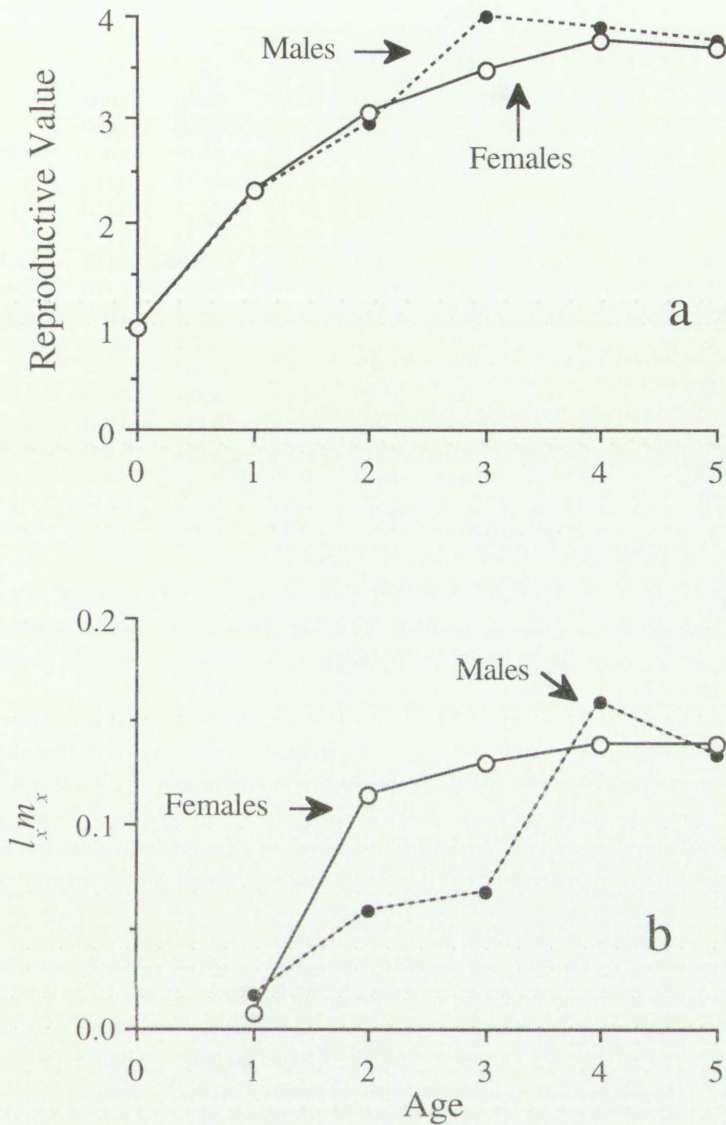


FIGURE 38. Life table estimates of reproductive value and  $l_x m_x$ . (a) Reproductive value (in fledglings) of males and females, and (b)  $l_x m_x$  (the contribution each age class makes to the total reproductive output of the population).

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 ( $R_0 = 1.004$ )

Age $x$	$S_{ab}$	$S_{af}$	$S_x$	$l_x$	$P_{mx}$	$f_x$	$m_x$	$l_x m_x$	Age structure	
									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 ( $R_0 = 0.998$ )

Age $x$	$S_{ab}$	$S_{af}$	$S_x$	$l_x$	$P_{mx}$	$f_x$	$m_x$	$l_x m_x$	Age structure	
									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

Age	Females (N = 45)		Males (N = 45)	
	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			Indirect benefits*
	1-year	2-years	Life table	
Males	3.18	2.72	2.42	0.25
Females	2.60	2.31	2.35	0.24

\* 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