THE ADVANTAGES OF, AND CONSTRAINTS FORCING, MATE FIDELITY IN PINYON JAYS

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ABSTRACT.—Pinyon Jays (*Gymnorhinus cyanocephalus*) live in flocks composed primarily of pairs and their offspring. We describe characteristics of 107 pair bonds. Pair bonds appear to be monogamous, perennial, and last an average of 2.5 yr. Males average 1.63 mates/lifetime, and females average 1.43. Males initiate breeding at an average of 2 yr, and females at an average age of 1.56 yr. Initial bonds formed between morphologically similar jays lasted significantly longer than those formed between disparate-size jays. Pairs had emergent properties that could not be accounted for by considering only properties of the mated individuals. Annual reproductive productivity did not vary significantly with duration of pair bonds. We found two cases of mate desertion; all other bonds were broken by deaths of partners. Previously successful jays remated with other successful birds, and unsuccessful birds remated with other unsuccessful birds, more often than expected by chance.

Monogamy may have evolved because deserted females are incapable of rearing offspring, sex ratios are male biased, females are aggressive, and lifespan is long. Perennial pair bonds may have been imposed by social constraints more than favored by reproductive advantages. Three possible constraints were that previously unsuccessful individuals rarely mated with previously successful ones, that mates associated throughout the year, and that cooperation among group members may not have been maintained without long-term pair bonds between members of different extended families. *Received 19 May 1987, accepted 2 December 1987.*

MONOGAMY can be investigated by elucidation of the factors that favor its evolution and the factors responsible for the characteristic duration of a monogamous pair bond. Questions concerning the evolution of monogamy are best answered by quantifying the relative fitness of monogamous vs. polygamous individuals. Dispersion and quantity of resources, quality of care one parent can provide, availability of unmated individuals, male and female aggression, and lifetime productivity may influence the evolution of monogamy (Lack 1968, Emlen and Oring 1977, Maynard Smith 1977, Wittenberger and Tilson 1980, Ford 1983, Murray 1985). Questions concerning pair-bond duration, on the other hand, may be best answered by quantifying advantages of long-term bonds and identifying constraints that may force individuals into long-term bonds (Rowley 1983, Freed 1987).

Reproductive success is typically greater for older, established pairs than for newly formed pairs (Rowley 1983) and favors long-term pair bonds. In many monogamous species, however, individuals frequently choose new mates because their former mates have died or separated from them during migration (Rowley 1983) or because reproduction was poor (Coulson 1966, Mills 1973). Long-lived, permanent residents are likely to form perennial pair bonds (Rowley 1983). This mate fidelity need not occur because of advantages. It may be a consequence of environmental constraints that increase the costs of desertion and re-pairing. In the tropics, for example, House Wrens (*Troglodytes aedon*) are territorial, permanent residents (Freed 1987). They may be forced into perennial bonds because the costs (time and energy) of obtaining new mates, in an area saturated with breeders, may be greater than the costs of retaining the present mates (Freed 1987).

Social birds in which pairs do not defend territories are unlikely to have pair bonds constrained by resource availability. In these conditions pair-bond duration may be influenced primarily by advantages and disadvantages of mate fidelity. Colonial-nesting Black-legged Kittiwakes (*Rissa tridactyla*) are an example, and pair bonds are more likely to endure in previously successful pairs than in previously unsuccessful pairs (Coulson 1966). Pinyon Jays

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(*Gymnorhinus cyanocephalus*) are long-lived corvids that reside throughout the year in permanent flocks of several hundred individuals and nest colonially (Balda and Bateman 1971, 1972). This social system may facilitate the maintenance of perennial bonds by successful pairs and selection of new mates by members of previously unsuccessful pairs. As we report here, however, pairs of Pinyon Jays typically maintain perennial bonds regardless of past success.

We describe the duration and composition of Pinyon Jay pair bonds and postulate advantages of, and constraints affecting, long-term bonds. We also present anecdotal information that suggests why monogamy has evolved. Patterns of pairing based on phenotypic traits of jays and the influence of these characteristics on longevity and reproductive success are reported elsewhere (Marzluff and Balda 1988a).

METHODS

We studied a flock of color-banded, known-age jays near Flagstaff, Arizona. This flock regularly visited feeding stations where sunflower seeds (*Helianthus* spp.) and assorted pigeon grains were provided continuously. Meal worms and pinyon pine (*Pinus edulis*) seeds occasionally were provided. We have no evidence that this flock differed in any demographic or social properties from unprovisioned flocks (Marzluff and Balda 1988a). Data on 107 pairs, followed from 1972 to 1986, are presented. Mated pairs were determined yearly by field observations during courtship and nesting. We considered two jays to be paired in a given year if they built a nest together and laid at least one egg in it. Family lineages were constructed for each pair to follow the formation and termination of pair bonds.

The reproductive success of pairs was estimated each breeding season. We did not find all nests of all pairs each year. We assayed success for our purposes here primarily by the production of crechlings. Fledglings gather in creches where they are fed and guarded by their parents (Balda and Balda 1978). Young that survived through the creching period (approximately 2 months postfledging) were defined as crechlings. Production of crechlings was the best measure of reproductive success during the time parents have some control over the fate of their young. We also counted the number of yearlings (young that survive through their first winter and are alive as of 1 February) each pair produced.

We discuss two types of pair bonds: initial and subsequent. Initial bonds are formed between two jays that have never bred before. Subsequent bonds are formed between individuals that previously had formed and terminated initial bonds with other jays (i.e. between experienced breeders). If either partner

was mated previously, we classified the bond as subsequent. We did not count continuing bonds between the same two individuals as new bonds each year; all 107 bonds we discuss are unique combinations of males and females. We documented the annual production of yearlings and duration of each bond until it was terminated.

Individual survivorship of banded jays was monitored on a daily basis as the flock visited local feeding stations. An age-specific survivorship curve was calculated for 708 individuals banded as juveniles. Immigrants were not included in survivorship calculations. Based on this survivorship schedule and assuming that partner deaths were independent events, we predicted pair-bond duration of yearling-yearling, yearling-adult, and adult-adult pairs based on methods of Freund and Walpole (1980: 56). Because 81% of yearling breeders and 74% of adults survive each year (Balda and Marzluff unpubl. data), the probabilities that a yearling-yearling, yearling-adult, and adult-adult pair will remain intact for one year based solely on age-specific survivorship are 0.66, 0.60, and 0.55, respectively. Sex-specific absolute survivorship was unavailable for this population. From these rates, expected pair-bond durations were generated for each age combination in the study flock (i.e. 4 pairs of 2 yearlings, 24 of 1 adult and 1 yearling, and 79 of 2 adults). The number of pairs per age combination intact after one year was predicted by multiplying the number of pairs in each age group by the probability that such a pair would survive for one year. To generate the expected number of intact pairs remaining in each subsequent year, we multiplied the current composition by the probability that an adult pair would survive one more year. This procedure was continued until all pair bonds were terminated. The survivorship of initial and subsequent bonds was calculated separately.

Jays were measured and weighed periodically at local feeding stations. Most measurements were made by three individuals (R. Balda, J. Balda, and Gene Foster) from August through December each year. Adult birds were captured and measured 1–8 times during their lifetimes. Neither bill length nor body mass was correlated with age beyond a jay's first year (unpubl. data). When multiple measurements were taken on an individual, average values were used in analyses. The bill length and body mass of individuals, as well as the sum and difference of bill length and masses of mates, were calculated for each pair. Culmen length was measured to the nearest millimeter with a flexible ruler. Birds were weighed to the nearest gram on a triple-beam balance or Pesola scale.

Age was determined directly for birds banded as juveniles and indirectly by plumage characters for unbanded juveniles and yearlings (Bateman and Balda 1973, Ligon and White 1974). Male age, female age, total pair age (male plus female age), and male minus female age were calculated for each pair.
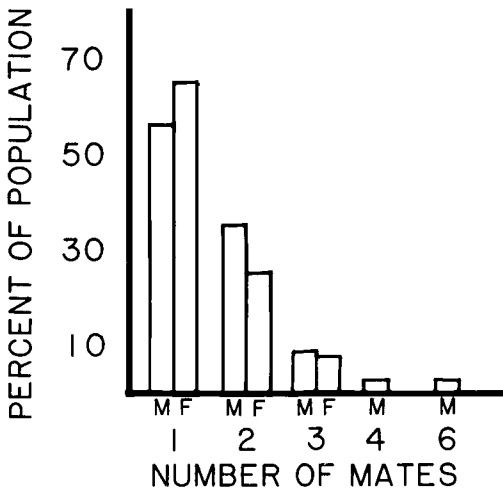
Fig. 1. Number of mates individual males (M) and females (F) obtained during their lifetimes. Percentages are based on sample sizes of 56 males and 60 females.

When assumptions of parametric statistical procedures were not met (e.g. when population variances were not equal), we used Mann-Whitney U-tests (W statistics) and Kruskal-Wallis tests (H statistics).

RESULTS

Description of the pair bond.—Pinyon Jays apparently (Gowaty 1985) form monogamous pair bonds. We have never observed more than one adult of either sex attending a nest. Yearling males occasionally (11% of nests each year; Marzluff and Balda 1988b) help their parents defend and clean the nest and feed the nestlings. The yearlings rarely associate with the pair during nest building or egg laying, however, and we never observed them near a copulating pair. We have never observed extrapair copulation or associations between unmated males and females, but we lack genetic evidence of strict monogamy.

Pair bonds appear to be perennial. Mates remain in close spatial proximity throughout the year as members of the same flock. We could not identify mated pairs in the wild outside of the breeding season by any behavioral criterion. Laboratory results suggest that mates are recognized during the nonbreeding season (Berger and Ligon 1977, Marzluff and Balda unpubl. data). Such recognition strongly suggests that pair bonds are maintained through subtle

TABLE 1. Reasons for the termination of 103 pair bonds.

Type of pair bond	n	Male died	Female died	Both died	Desertion
Initial	54	18	30	4	2
Subsequent	38	13	11	14	0
Initial/subsequent[a]	11	1	7	3	0

[a] Bonds that were initial for one partner and subsequent for the other.

vocal and postural behaviors throughout the year.

An individual may have several mates during its lifetime, but pair bonds usually remain intact until one partner dies. Most jays had only one mate during their lifetimes (Fig. 1). One male mated with 6 females, but on average males (n = 56) had 1.63 mates/lifetime (SD = 0.95) and females (n = 60) had 1.43 (SD = 0.65). This difference was not significant (W = 3,426.5, P = 0.41). We documented only two cases of mate desertion (Table 1). Initial bonds usually ended because of the female's death, but subsequent bonds were equally likely to dissolve because of the death of either or both mates before the next breeding season (Table 1). Initial and subsequent bonds differed significantly in this respect (comparing the number of bonds broken by the death of males, females, or both between initial and subsequent bond types; χ^2 = 13.31, df = 2, P < 0.005).

We never observed jays delay first breeding beyond 3 yr of age. Most individuals bred when 2 yr old (Fig. 2). Females bred more commonly as yearlings and less commonly as 2- and 3-yr-olds than did males (comparing 3 breeding-age categories by sex; χ^2 = 18.66, df = 2, P < 0.005). On average males (n = 63) initiated breeding when 2 yr old (SD = 0.54), and females (n = 66) initiated breeding when 1.56 yr old (SD = 0.56).

Pair-bond duration.—Pair-bond duration was variable, but averaged 2.52 yr (SD = 1.78, n = 107). Thirty-nine (36.4%) remained intact for 1 yr, and 11 (10.3%) for more than 5 yr, including 1 (0.9%) for 10 yr. Median duration did not differ between initial (n = 64) and subsequent (n = 43) bonds ($\bar{x}_{int} \doteq 2.58$ yr, $\bar{x}_{sub}$ = 2.44 yr; W = 3,390.5, P = 0.68).

Because death of a partner is virtually the only means to terminate the pair bond (Table 1), we expected that a model of pair-bond duration based on individual survivorship (see
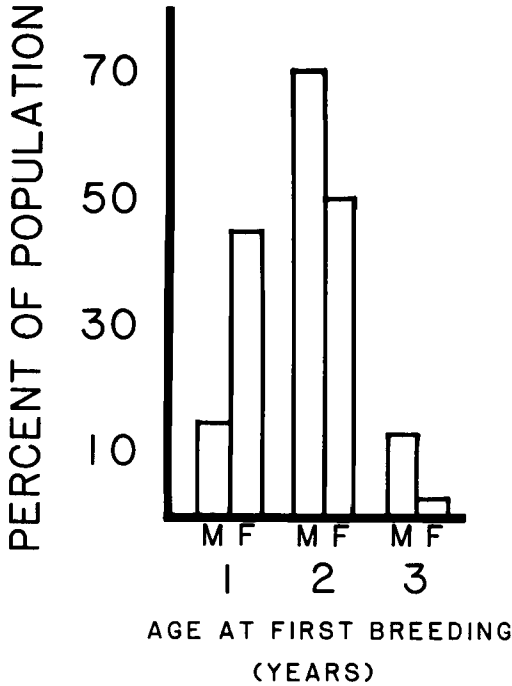
Fig. 2. Age at first breeding in Pinyon Jays. Percentages are based on sample sizes of 63 males (M) and 66 females (F).
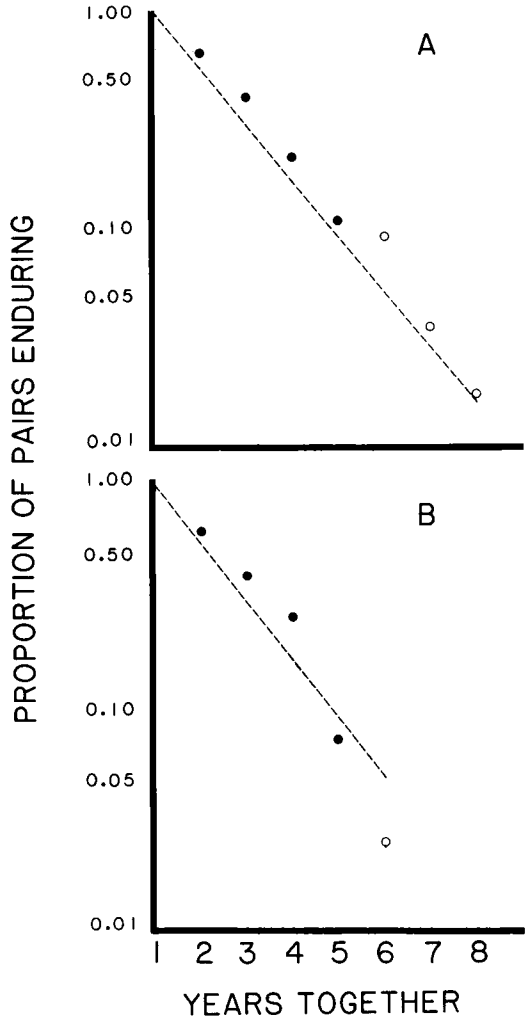

Fig. 3. Survivorship of initial (A) and subsequent (B) pair bonds as a function of pair-bond duration. Dots and circles represent observed survivorship. Dashed lines are survivorship expected based purely on individual age-specific survivorship. Open circles represent observations based on samples of fewer than 10 pairs.

Methods) would provide a rate of pair-bond dissolution similar to that observed in our study flock. Our model accurately fit the observed survivorship rate of initial and subsequent pair bonds (Fig. 3). The equations that describe the relationship between pair-bond duration (x) and the number of pairs surviving a given duration (y) were virtually identical for observed and expected initial or subsequent bonds (initial, observed: $y = 48.2 - 6.96x$; initial, expected: $y = 44.6 - 6.61x$; subsequent, observed: $y = 43.6 - 7.1x$; subsequent, expected: $y = 38.7 - 6.33x$). None of the slopes or y-intercepts in these equations differed significantly. Each value was included in the 95% confidence interval for the others (95% confidence intervals for slopes: -6.96 ± 2.42, -6.61 ± 2.79, -7.14 ± 2.03, -6.33 ± 2.77; 95% confidence intervals for intercepts: 48.2 ± 12.2, 44.6 ± 14.1, 43.6 ± 9.1, 38.7 ± 12.4). The average annual survival rate was 58.1% for initial bonds and 50.2% for subsequent bonds.

Pair-bond duration was correlated with physical characteristics of mates. Durations of initial bonds were negatively correlated with the dif-

ferences in mates' masses and mates' bill lengths (Table 2). Initial bonds between mates of similar size lasted longest (i.e. bonds between larger-than-average females and smaller-than-average males; Table 3). This does not appear to result solely from exceptional survivorship of large females or small males. Heavier-than-average females did not live significantly longer than lighter ones ($\bar{x}$ longevity: heavy $= 7.1$ yr, $n = 17$; light $= 6.1$ yr, $n = 9$; $F = 0.56$, $P = 0.46$).

TABLE 2. Correlations between pair-bond duration and characteristics of mated pairs.

Pair characteristic	Initial bonds			Subsequent bonds		
	r^a	n	P	r^a	n	P
Male mass (g)	−0.21	17	0.21	−0.03	9	0.47
Female mass (g)	+0.35	17	0.08	−0.18	9	0.32
Male + female mass (g)	+0.08	17	0.38	−0.17	9	0.34
Male − female mass (g)	−0.45	17	0.04	+0.15	9	0.35
Male bill length (mm)	−0.28	17	0.14	+0.44	9	0.12
Female bill length (mm)	+0.47	17	0.03	−0.58	9	0.05
Male + female bill length (mm)	+0.23	17	0.19	−0.25	9	0.26
Male − female bill length (mm)	−0.53	17	0.01	+0.57	9	0.06
Difference in age of partners	−0.15	39	0.19	+0.31	17	0.12

[a] Pearson correlation coefficients.

Lighter-than-average males lived longer than heavier ones, but not significantly so ($\bar{x}$ longevity: heavy = 5.0 yr, n = 6; light = 7.4 yr, n = 14; F = 3.30, P = 0.08). Size-specific male survivorship was related to the size of their mates; smaller-than-average males lived longer (although not significantly longer than larger males) when mated with heavier-than-average females ($\bar{x}$ longevity: heavy males = 5.8 yr, n = 4; light males = 8.1 yr, n = 8; F = 1.28, P = 0.28). Birds with longer-than-average bills, especially males, survived longer than those with shorter bills ($\bar{x}$ longevity: short-billed males = 5.0 yr, n = 9; long-billed males = 7.93 yr, n = 15; F = 6.10, P = 0.02; short-billed females = 5.25 yr, n = 8; long-billed females = 7.39 yr, n = 18; F = 2.93, P = 0.10). Durations of subsequent bonds did not show similar trends. In fact, bonds involving small-billed females lasted longer than those involving large-billed females. Therefore, the morphological similarity of partners was related inversely to the duration of subsequent bonds (Table 2).

Advantages of mate fidelity.—Experience with the same mate did not significantly increase annual fecundity. There was no clear and significant increase in the production of crechlings nor in the probability of successful reproduction with increasing pair-bond duration. We cannot statistically appraise this relationship with our largest data set (Table 4) because some pairs were measured repeatedly and other pairs only once. We found that the reproductive success of pairs mated for identical lengths of time, but measured during 1 of 14 breeding seasons, was extremely variable (note the standard deviation relative to mean for each pair-bond duration). Variability may be due to individual pair differences when pooled (Table 4). We fac-

tored out this variability by using a smaller data set that included only pairs for which we had repeatedly measured success. We performed four paired t-tests on the success of the same pairs at different levels of experience. None of the comparisons was statistically significant (initial bonds: duration of 1 yr vs. 2 yr, n = 18, t = 1.61, P = 0.13; duration of 2 yr vs. 3 or more years, n = 8, t = −1.16, P = 0.29; subsequent bonds: duration of 1 yr vs. 2 yr, n = 17, t = −0.78, P = 0.45; duration of 2 yr vs. 3 or more years, n = 7, t = 1.55, P = 0.17). The greatest difference (greater success in year 2 vs. year 1 of initial bonds) was only marginally significant (one-tailed test, P = 0.065). Another way to test for the effect of experience on success is to compare success by experienced pairs in subsequent bonds with success by initially inexperienced birds in initial bonds. Pairs in initial bonds are independent of those in subsequent bonds

TABLE 3. Duration of initial pair bonds in relation to size of mates. Heavy birds weighed more than average males (112.1 g) or average females (98.9 g); light birds weighed less than the average. Long-billed birds had longer bills than average males (35.0 mm) or average females (31.9 mm); short-billed birds had shorter-than-average bills.

Size of male	Size of female	n	Average pair-bond duration (yr)
Heavy	Heavy	10	3.2
Heavy	Light	2	1.0
Light	Heavy	7	3.4
Light	Light	7	2.6
Long bill	Long bill	8	2.8
Long bill	Short bill	2	1.0
Short bill	Long bill	10	3.7
Short bill	Short bill	6	2.5

TABLE 4. Influence of pair-bond duration on annual production of crechlings and nesting success. Sample sizes are all pairs of a given bond duration for which reproductive data were known. Reproductive data were known for some pairs at only one bond duration and for others at several durations.

Duration of pair bond (yr)	Initial bonds				Subsequent bonds			
		Crechlings		Proportion of pairs successful[a]		Crechlings		Proportion of pairs successful[a]
	n	Mean	SD		n	Mean	SD	
1	49	0.88	1.15	0.40	38	1.26	1.33	0.58
2	24	1.54	1.26	0.71	24	1.08	1.26	0.54
3	14	1.14	1.19	0.57	11	1.91	1.24	0.82
4	7	1.57	0.91	0.86	6	1.83	1.86	0.50
5–10	12	1.25	1.48	0.50	3	3.00	1.41	1.0

[a] Successful is defined as production of at least 1 crechling.

(means in Table 4). We used two-sample t-tests to compare success in initial and subsequent bonds for pair-bond durations of 1, 2, 3, and 4 or more years. No test was statistically significant (all P-values > 0.14). Collectively, the results suggest that mate fidelity did not result in higher annual reproductive success.

Future reproductive success could be predicted from past success. Twenty-one of 27 pairs (77.8%) successful at producing crechlings their first year were successful in subsequent years. Fifty-five percent ($n = 11$) of pairs unsuccessful during their first year never produced crechlings, and 45% ($n = 9$) succeeded eventually. Future production of crechlings was dependent on past production of crechlings ($x^2 = 5.36$, df = 1, $P < 0.025$); thus, mate fidelity appears to be advantageous only following successful reproduction. Many pairs of jays, however, remained mated despite failure to reproduce. Thirty-eight pairs failed to produce crechlings their first year; 10 of these also failed the next year, and 2 even failed the third year. Five other pairs remained mated but failed to produce crechlings during 4 or more consecutive years.

Constraints forcing mate fidelity.—Previously unsuccessful pairs are likely to remain unsuccessful, but unsuccessful partners remained paired instead of deserting the current mate and obtaining another. Subsequent mate choice appears constrained by past reproductive performance (Table 5). Only 17.6% of previously unsuccessful or inexperienced females ($n = 17$) obtained previously successful males, and only 33.3% of previously unsuccessful or inexperienced males ($n = 21$) obtained previously successful females. The majority of previously successful individuals (72.7% of males, 53.3% of females) mated with other previously success-

ful birds. Previously successful jays mated with other successful jays and previously unsuccessful jays mated with other unsuccessful jays more often than expected by chance (Table 5).

Most jays sampled were not exceptionally successful when they remated with previously successful jays. We observed 27 males mate with females of known reproductive history. Sixty percent (9 of 15) of the males that mated with previously successful females reproduced successfully, but only 50% (6 of 12) of males mated with unsuccessful females did so (comparing productivity of crechlings by female reproductive history; $x^2 = 0.30$, df = 1, $P > 0.10$). We observed 25 females mated with males of known reproductive history. Regardless of the male's past success, females had a 50% chance of future success ($x^2 = 0.03$, df = 1, $P > 0.10$). A subsequent bond formed between two previously successful jays produced the greatest number of young we observed (17 crechlings and 5 yearlings during 5 yr). On an annual basis, however, pairs of previously successful males and females ("SS" pairs) did not produce significantly more crechlings or yearlings than pairs of previously

TABLE 5. Assortative mating for previous success. Number of pair bonds with respect to previous reproductive history of males and females is given. Previous history of mates is more similar than expected ($x^2 = 4.5$, df = 1, $P < 0.05$).

Female reproductive history	Male reproductive history		Total
	Successful	Unsuccessful	
Successful	8	7	15
Unsuccessful	3	14	17
Total	11	21	32

unsuccessful jays ("UU" pairs) or pairs in which only one partner was successful previously ("US" pairs) ($\bar{x}$ crechlings/yr: UU = 1.84, n = 12; US = 1.70, n = 7; SS = 1.15, n = 7; H = 0.76, df = 2, P > 0.10; $\bar{x}$ yearlings/yr: UU = 0.71, n = 12; US = 0.93, n = 7; SS = 0.62, n = 7; H = 0.37, df = 2, P > 0.10). Previous success with one partner apparently does not guarantee immediate success with a new partner. Conversely, reproductive failure with one partner does not guarantee continued failure with a new partner.

DISCUSSION

Evolution of monogamy.—The origin of monogamy in Pinyon Jays presumably is due fundamentally to the inability of deserted jays to rear nestlings successfully to independence. We observed two cases where females lost their mates while caring for nestlings (one male was killed, and the other re-paired with his former mate; see below). Neither female fledged any young after mate loss. Moreover, deserted females did not fledge reduced broods. In the case where the male was killed, the nestlings died in order. The female could not successfully raise even the last individual. Male desertion would not be favored under these conditions because the probability of the deserted offspring surviving would be zero (Lack 1968, Maynard Smith 1977).

The importance of male provisioning and guarding nestlings may favor monogamy; however, females' reliance on males for over 80% of their food during incubation (Balda and Bateman 1972) may be a more important factor that favors monogamy (Ford 1983). Pinyon Jays are not territorial, and flocks usually have a surplus of males (Marzluff and Balda 1988b). Monogamy may thus be favored because the majority of males in such a population can reproduce most successfully by defending exclusive access to a single female (Wittenberger and Tilson 1980, McKinney 1985).

Female aggression may also prevent males from acquiring additional mates. For example, in 1972 a mated female was removed from the flock for 7 weeks during which her mate formed a new bond and produced young (R. Balda and G. Foster unpubl. data). When the original female was reintroduced into the flock, she badgered the new pair for one week until the new pair bond was broken and the original bond reestablished. The deserted female did not rear the brood successfully.

Lastly, the long lifespan of Pinyon Jays (Marzluff and Balda 1988b) may allow monogamy because monogamous pairs may be able to rear enough offspring to replace themselves in the population (Murray 1985). Certainly, a combination of factors may be partially responsible for the evolution of monogamy.

Mate fidelity.—In our study flock, mate fidelity did not produce a great reproductive advantage. Crechling production and the proportion of successful pairs did not increase significantly with increased pair-bond duration (Table 4). Florida Scrub Jays (*Aphelocoma coerulescens*) gain only slight annual reproductive advantages with increasing pair-bond duration and also have low desertion rates ("divorce" rate of 7.6%; Woolfenden and Fitzpatrick 1984). Enduring Florida Scrub Jay pairs, however, have an additonal advantage: recruitment of helpers (Woolfenden and Fitzpatrick 1984). Helping is relatively rare in Pinyon Jays and is not associated with increased annual reproductive success or with enhancement of pair-bond duration (Marzluff and Balda 1988b, unpubl. data).

Lack of a consistent increase in success with pair-bond duration may result from age-specific vulnerability of nesting jays (Marzluff 1983). Older Pinyon Jays are more prone to nest failure from cold weather and less prone to loss from predation because they nest earlier and in more concealed locations than younger jays (Marzluff 1988a). The relative importance of these two sources of nest failure varies annually. Therefore, pairs of old jays do not always out-reproduce pairs of young jays. This yearly variation in age-related success may obscure age-related trends in success accumulated over several years (Table 4).

Parenting by Pinyon Jays affects nesting success, as indicated by higher variation in fledging success between pairs within years than within pairs between years (Marzluff and Balda 1988b). Parents influence success in at least three ways. First, males select nest sites (Gabaldon 1978), and selection of concealed locations within the nest tree increases success (Marzluff 1988a). Second, nests that are visited by parents for longer periods of time are more prone to loss than those visited for short periods of time (Marzluff 1983). Finally, parents mob nest pred-

ators and may increase vigilance around the nest after predators remove part of the brood, thus enabling remaining young to fledge successfully (Marzluff 1985).

Mate desertion may be uncommon because constraints force jays to remain mated. Rasmussen (1981) proposed two constraints on desertion after unsuccessful reproduction. First, if reproductive success is low among all members of the population, then desertion provides no advantage. Second, if courtship and bond-formation costs are high or the quality of resources controlled by the focal pair relative to other pairs is high, then desertion may be too costly. These explanations do not apply to Pinyon Jays, however. Reproductive success in jays was highly variable. Courtship and bond-formation costs are either low or equal among pairs forming initial or subsequent bonds (Balda and Bateman 1971). Finally, Pinyon Jays are not territorial, and few resources are controlled by pairs of birds.

Resource availability may also constrain desertion. Lesser Snow Geese (*Anser c. caerulescens*) do not terminate pair bonds, even after failure, probably because pairs are better able to defend resources jointly (Cooke et al. 1981). Ring-billed Gulls (*Larus delawarensis*) also remain paired after failure because of a lack of potential mates and available nest sites (Kovacs and Ryder 1981). These reasons do not apply to Pinyon Jays. Jays do not jointly defend resources, and mates and nest sites are available each year.

In Pinyon Jays the highly social environment may constrain desertion. The chances that a previously unsuccessful jay will gain a better (i.e. previously successful) mate are reduced. Within flocks, members recognize each other as individuals (Balda and Balda 1978, McArthur 1982, Marzluff 1988b) and may assess the reproductive success or failure of other pairs. Reproductive output may be monitored when individuals visit other nests in the colony (which we have often observed) and during the creching stage when newly fledged young from all nests in the colony group together and the parents feed them (Balda and Balda 1978). Memory of past events in this species (Marzluff 1985, 1988; Balda and Kamil unpubl. data) may explain how successful birds apparently avoid mating with unsuccessful or inexperienced individuals.

The interaction of the pair during the non-breeding season also may constrain an individual's ability to obtain a new mate (Rowley 1983). The major proximate cause of desertion in the Black-legged Kittiwake was a failure of the pair to return to the colony at the same time after migration (Coulson and Thomas 1983). In species that maintain bonds throughout the year, asynchronous returns to the breeding grounds would be precluded. Pinyon Jays, which flock year-round (Balda and Bateman 1971, 1972), Snow Geese (Cooke et al. 1981), which migrate as family units, and Florida Scrub Jays and tropical populations of House Wrens, which reside in habitats saturated with breeders that maintain permanent territories throughout the year (Woolfenden and Fitzpatrick 1984, Freed 1987), are four such species. In all four mate fidelity is the rule.

Maintenance of a large, stable, cohesive, and cooperating association, such as a flock of Pinyon Jays, may not be possible if desertion and re-pairing occurred yearly. This would be especially true if these events lead to instability and intraflock strife. In a flock structured into numerous extended families, we have no evidence of interfamily hostility or rivalry. Aggressive interactions between flock members were rare, and cooperation was apparently prevalent. Flock members foraged together, guided each other to novel food sources, warned each other of impending danger, and cooperatively mobbed predators at all times of the year. Pair bonds between members of different families may be the reason discrete family lineages are united into a cooperative flock. If unsuccessful pair bonds were broken at the end of each breeding season, deserted individuals might not cooperate with their former mates. This could divide the flock into small competing factions. Competition for mates and establishment of new pair bonds after desertion would demand extra time and energy. This might reduce the time available for activities such as extended parental care; harvesting, eating, and caching pine seeds; and predator detection. Establishment of new pair bonds might also delay the onset of the next breeding attempt (Wilson 1975, McKinney 1985) and hinder the adjustment of reproduction to the availability of spatially and temporally variable food (Ligon 1978, Marzluff and Balda 1988b). The existence of social flocks suggests that the benefit-to-cost ratio of such life is greater than the

benefit-to-cost ratio of solitary life. Mate fidelity, although a cost in terms of current reproductive success for some flock members, may enhance sociality, which provides long-term reproductive and survival benefits to individual flock members.

Emergent properties of pairs.—Although a model of pair-bond duration based solely on individual survivorship closely matched the observed data, bond survivorship was constantly higher than expected in initial bonds and through four years of subsequent bonds. After this time it was lower than expected. There appears to be a lack of independence between the death rates of mates. Both mates died the same fall or winter 20.8% of the time (Table 1). If death rates of breeders were independent, partner deaths should co-occur only 6.8% of the time. Mated individuals may affect each other's lifespan, resulting in higher or lower than expected bond survivorship. For example, similar-size partners had longer initial pair bonds than dissimilar-size ones (Tables 2 and 3). We believe that longer pair-bond duration is not solely a result of large females or small males having exceptional survivorship. Instead, intrapair dominance and aggression may enhance survivorship of similar-size pairs relative to disparate-size pairs. Dominance is related to body size, and larger birds are dominant (Johnson in press a, b; Marzluff and Balda 1988a). Perhaps small males and large females have relatively equal dominance status. This may explain the lower intrapair aggression between similar-size mates (Marzluff and Balda 1988a). Reduced aggression and similar dominance among mates may enhance survivorship and increase pair-bond duration.

Partner similarity may be a factor in the decision to desert. In one case of desertion the partners were morphologically more dissimilar than any other partners measured (mass difference = 33.3 g, bill difference = 7.0 mm). The male in the other deserted pair had a crippled wing, which may have impaired his parenting. Similar arguments were given for Florida Scrub Jays (Woolfenden and Fitzpatrick 1984).

Pairs of Pinyon Jays apparently have emergent properties that are not simple products of the properties of the individuals forming a pair bond. We found that partner death rates are not independent events. Further, the reproductive productivity of a pair is predictable from year to year, but it is not dependent on the produc-

tivities of the mates in previous pair bonds with other jays. We are unaware of discussions concerning emergent properties of pairs and suggest that such properties are most likely to occur in species that form permanently monogamous bonds in which both members of the pair contribute substantially to rearing offspring. If emergent properties are common in such pairs, it may not be appropriate to consider the success of individuals in isolation from the success of pairs. The pair may be a functional evolutionary unit.

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