PAIRING PATTERNS AND FITNESS IN A FREE-RANGING POPULATION OF PINYON JAYS: WHAT DO THEY REVEAL ABOUT MATE CHOICE?[1,2]

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Abstract. Pairing in 141 pairs of Pinyon Jays (*Gymnorhinus cyanocephalus*) was assortative for age, but was random for bill length and body weight. Assortative pairing for age may be favored because similar-aged partners produced slightly more young than dissimilar-aged ones and their young survived longer than young from dissimilar-aged pairs. We expected pairing to be disassortative for size because pairs consisting of heavy females and light males were more fit than pairs consisting of two heavy or two light birds. Pairs of heavy females and light mates fought less, lived longer, and produced young that lived longer and produced more offspring than young from partners of other size categories. Lack of significant disassortment for size may have resulted because large males may dominate small males and prefer to pair with some of the large, long-lived females. Large jays appear to have the highest genetic quality because they lived longer and body size was heritable. Genetic quality of a mate, however, may be negated if phenotypic properties of partners are not compatible.

Key words: Age; assortative mating; body size; dominance; fecundity; Gymnorhinus cyanocephalus; *heritability; longevity; mate choice; pair bond; randomization test.*

INTRODUCTION

The question of how individuals decide upon a particular mate has recently received much attention (e.g., Bateson 1983). Mate choice should be based on characters that have a positive effect on fitness, are variable enough to allow choice, and can be assessed accurately prior to mating (Searcy 1979a, 1982). Such characters may include physical and physiological features of the potential mate, quality of the mate's possessions, such as its territory, or quality of parental care provided by the mate.

Individuals selecting a mate on the basis of morphological features like plumage coloration (O'Donald 1972, O'Donald et al. 1974, Cooke and McNally 1975) or body size (Ankney 1977, Searcy 1979b, Cooke and Davies 1983) should rely on heritable characters that are difficult to falsely advertise. Such characters may insure inclusion of high quality genes in the individual's offspring.

Various characters appear to indicate quality of parental care in potential mates. Coulson

(1966), studying Black-legged Kittiwakes (*Rissa tridactyla*), and Burley and Moran (1979) studying Rock Doves (*Columba livia*) noted that age and experience, which influence parental care, were important characteristics of birds chosen for mates. Wiley (1973) and Howe (1982) showed that dominance and aggressiveness were important characters used in mate choice by Sage Grouse (*Centrocercus urophasianus*) and Willets (*Catoptrophorus semipalmatus*), respectively.

We have accumulated data on the characters of mated Pinyon Jays (*Gymnorhinus cyanocephalus*) for 14 years. These birds live in tightly knit flocks throughout the year, and breed colonially (Balda and Bateman 1971, 1972; Bateman and Balda 1973). Clutch size ranges from three to five and infertility is low (Balda and Bateman 1971, 1972; Ligon 1978). Over half of all nesting attempts are preyed upon or fail after late spring snowstorms (Ligon 1978, Marzluff 1988). Thus, few pairs succeed in producing independent young. Mate choice in the highly social Pinyon Jay may be unique because established pair bonds are rarely broken by divorce even if the pair continually fails to reproduce (Marzluff and Balda, in press a).

The process of pairing by free-ranging Pinyon Jays is poorly understood. Only slight sexual dimorphism exists in morphological features (Ligon and White 1974) and in plumage. No con-

spicuous intrasexual displays indicate male-male or female-female competition for mates. Instead, social structure, and hence access to mates, is mediated through subtle dominance gestures (Balda and Bateman 1972, Balda and Balda 1978). A recent laboratory study of mate choice by Pinyon Jays has shed some light on this species' process of pairing. Johnson (in press a, in press b) discovered that males and females both compete for and choose mates. She found that large, dominant males prefer large, dominant females, but females prefer brightly-colored males with large testes.

There are still gaps in our understanding of pairing in Pinyon Jays. Perhaps the largest remaining gap is a lack of information about the timing of mate acquisition. We only know the date of pair-bond formation for a few jays that lost their mates during the breeding season and quickly remated. Most unpaired jays apparently form pair bonds amongst themselves rapidly throughout the nonbreeding season. Because we do not know the temporal sequence in which bonds are formed we do not know the exact individuals from which a particular jay selected its mate.

An initial step in understanding mate choice is the documentation of nonrandom pairing patterns (Cooke and Davies 1983). Our first objective is to describe pairing with respect to age, body weight, and bill size of mates. These three characters fulfill Searcy's (1979a) requirements. All are difficult to falsely advertise, and all vary within the population. Bill length and body weight presumably can be assessed accurately. Well-developed individual recognition or changes in the brightness of plumage as birds age (Kris Johnson, pers. comm.) may allow for the assessment of age. Lastly, in other species, reproductive success and survival may be related to body size and age and/or breeding experience (Coulson and White 1958, Jehl 1970, Craig et al. 1977, Raveling 1981, Ryder 1981, Cooke and Davies 1983). Mate choice on the basis of territory quality, although potentially important in some species (Mayfield 1960, Zimmerman 1971, Lennington 1980) is not important because Pinyon Jays are not territorial (Balda and Bateman 1971, 1972).

Our second objective is to provide data on reproductive success and longevity of pairs that vary in age, body weight, and bill size. Investigating correlates of fitness and relating fitness to pairing patterns allows us to propose several testable hypotheses concerning mate choice.

METHODS

OBSERVED AND RANDOM PAIRING PATTERNS

This paper deals with a flock of color-banded, known-age jays living near Flagstaff, Arizona. This flock was closely monitored from 1972 to 1986 as it regularly visited feeding stations where sunflower seeds and pigeon grains were provided continuously. Pinyon pine (*Pinus edulis*) seeds were occasionally provided. We present data on 141 pairs. 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 constructed a nest and laid at least one egg in the nest. Family lineages were constructed for each pair in order to follow formation of pair bonds. Reproductive success of pairs, and pairing status of offspring was determined each breeding season.

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 have previously formed and broken (usually because one partner died) initial bonds with other jays (i.e., experienced breeders). If either partner was previously mated we classify the bond as subsequent. Five birds' initial pair bonds were classified as subsequent because they first paired with experienced breeders.

Mate availability each year was determined by inspection of yearly survivorship records. We called individuals that were alive and unmated between breeding seasons the yearly mate pool. Individuals retaining their former mates between years were not included in yearly mate pools. Because we did not know the temporal sequence of pairing during this interval our constructed mate pool overestimates the availability of mates to a given individual. In reality, choice of a mate occurred from some unknown subsample of our yearly mate pool. We assume this subsample contained a random sample from our yearly mate pool of those characters we investigated. Pairing patterns in the yearly mate pool should therefore be representative of patterns in the subsample.

We used a randomization procedure to test the significance of pairing patterns. There are $n!$ pos-

sible ways that n males and n females can be combined into pairs. In our procedure, we generated these possible pairing patterns and summarized each by the correlation between male and female characters. The uniqueness of the observed correlation between characters of mates was appraised relative to all possible correlations between unpaired males and females. All possible correlations were computed in mate pools of eight or fewer pairs. In larger pools, 500 simulations generated a random distribution of correlations to which the observed correlation was compared. Probabilities estimated from this procedure are more accurate than probabilities derived from standard correlation tests (Marzluff and Bell, unpubl.).

Choice of a mate based on one character may preempt choice for another character. We show below that pairing is assortative for partner age and previous success. We were interested in determining if assortment for age or previous success influenced pairing for other characters such as body size and if size was a secondary cue in mate choice. If age and breeding success were the first cues used to assess a potential mate and size was used as a secondary cue to choose among birds differing in age or success from the chooser, then variation in size differences among partners of similar age (partners differing in age by one year or less) or similar prior success (both partners either previously successful or both previously unsuccessful) should be greater than the variation in size among partners of disparate age (partners differing in age by two or more years) or disparate previous success (one partner previously successful, the other previously unsuccessful). We tested this prediction by comparing variances with Cochran's C-test.

CHARACTERS OF JAYS

Jays were measured and weighed periodically at local feeding stations. The vast majority of measurements were taken from August through December each year. Adult birds were captured and measured from one to eight times during their lifetime. When multiple measurements were taken on an individual we used the average values in this analysis. Bill length and body weight of individuals, as well as the sum and difference of bill length and weights 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. Two individuals (R.P.B. and Gene Foster) made over 90% of the measurements. We assured that these individuals made similar and consistent measurements by frequently comparing their measurements and calibrating their scales with the same objects.

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 (male plus female) age, and male minus female age were calculated for each pair.

FITNESS OF BREEDERS AND THEIR OFFSPRING

We define breeding success, a component of parental fitness, on the basis of production of young which survive the winter in the natal flock (i.e., production of nondispersing yearlings). In addition, we define a pair as being reproductively successful if it produced at least one nondispersing yearling. Comparisons between successful and unsuccessful pairs are meaningful because most pairs (81.3%) either produced one ($n = 31$) or no ($n = 34$) nondispersing yearlings.

A second component of parental fitness, for species lacking a postreproductive life, is individual lifespan. We compared lifespan with bill size, body weight, and age variables calculated for pairs and individuals.

Heritability of physical characters was estimated with father-son regressions (Hartl 1981). Samples were insufficient for mother-daughter or midparent regressions.

AGGRESSION BETWEEN ADULTS

We recorded the occurrence and outcome of aggressive interactions while jays were foraging at feeding stations in 1972, 1973, and 1974. Interactions occurring between two birds resulted in the subordinate bird either leaving the feeder, moving away from the food but staying at the feeder, giving a bill-up or begging appeasement display (Balda and Bateman 1972), or fighting with the dominant bird. Here we provide data only for encounters between adult males and adult females. We divided the year into three periods: breeding season (January to May), late breeding/molting season (June, July), and nonbreeding season (August to December).

RESULTS

COMPARISON OF OUR STUDY FLOCK TO AN UNPROVISIONED ONE

The study flock regularly visits feeding stations and therefore might be more sedentary, have an atypical age and/or sex structure, or have unusual breeding habits relative to unprovisioned flocks. Despite the availability of supplemental foods, our flock actively harvests and caches seeds of pinyon and ponderosa (*Pinus ponderosa*) pine during the fall of each year. In years of seed crop failure our flock and other flocks wander widely, presumably in search of pine seeds (Bock 1982). The age and sex structure of the study flock is virtually identical to a randomly sampled unprovisioned flock (Ligon and White 1974, table 8). The Magdalena flock studied by Ligon and White (1974) consisted of 49% adult males, 29% adult females, 12% yearling males, and 10% yearling females, whereas our study flock averaged 47% adult males, 28% adult females, 15% yearling males, and 9% yearling females. In particular, the subordinate juveniles, who should benefit the most from abundant foods, were equally prevalent in the two flocks. In one year breeding was 1 month earlier in the study flock than in an adjacent less provisioned one (Balda and Bateman 1972); however, clutch size, fledgling production, and nest success rates do not differ between these flocks (Balda and Bateman 1972; Marzluff and Balda, in press b) or between ours and another wild flock (Ligon 1978). Onset of breeding is not as strongly correlated with the size of pine crops in our study flock; however, this appears to be a result of cold and snowy spring weather, and not a result of provisioning (Marzluff and Balda, in press b). Adults in our study flock have bill lengths and body weights within the range of measures from the wild flock studied by Ligon and White (1974). We assume that acquisition of a quality mate is just as important to an individual's fitness in this flock as in any other flock.

INFLUENCE OF PARENTS ON NESTING SUCCESS

Mate choice influences the fitness of an individual only if a mate's activities are important determinants of reproductive success or survival of that individual. Predation is the major source of nest failure and it may be avoided by concealed nest placement and by behaving cautiously around the nest (Marzluff 1985, 1988). Early spring snowstorms are another important source of nest failure, the effect of which can be minimized by appropriate nest placement (Cannon 1973, Marzluff 1988). Males appear to select nest sites (Gabaldon 1978), thus female breeding success may depend in part upon her mate's ability to select successful nest sites. From 1981 to 1985 variation in fledgling success among all pairs within a year (average variance = 0.231, $n = 5$ years) was consistently higher than variation within individual pairs across years (average variance = 0.142, $n = 41$ pairs). This indicates that success or failure at producing fledglings is more consistent within pairs than within years and suggests that pair quality may be an important influence on nesting success.

OBSERVED AND RANDOM PAIRING PATTERNS

Age of mates. Unpaired jays typically mated with jays of similar age (Figs. 1, 2). In all bonds, pairing was assortative for age ($r = 0.53$, $n = 141$, $P < 0.002$). This was especially evident among jays forming initial pair bonds; 89.6% of initial bonds were between jays within 1 year of age of each other ($r = 0.41$, $n = 87$, $P < 0.002$) (Figs. 1, 2). The majority of subsequent pair bonds were between jays within 1 year of age (51.8%), despite the wide age range of jays forming these bonds (1 to 14 years) (Figs. 1, 2). Subsequent pairings were not significantly assortative ($r = 0.11$, $n = 54$, $P = 0.23$).

Pair bonds formed within a year were also typically assortative for age (Table 1). Availability of similar-aged mates in a given year appeared to influence the strength of assortative mating. In 1975, for example, there were three unpaired 5-year-old males but only one 5-year-old female. All of these old jays mated with young jays producing the least assortative mating for age we observed. In 1981 eight old females died (an unusual event) leaving their partners mateless. These males mated with young females in 1982 resulting in the most extreme partner age differences in 11 years. In spite of these differences, pairing was significantly assortative for age. In 1979 all available mates were within 1 year of each year. The observed pairing pattern was as assortative as possible, but because only three ages were represented, this pattern would be formed by chance 21% of the time.

FEMALE AGE

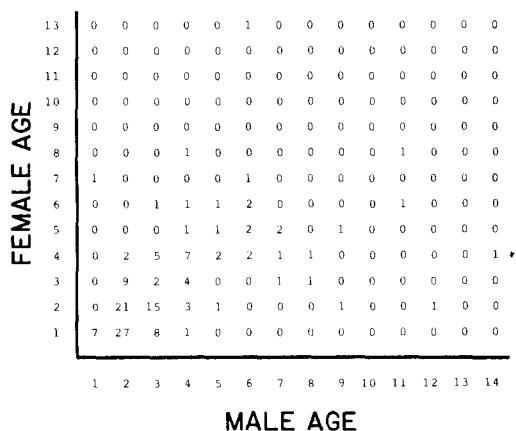|	1	2	3	4	5	6	7	8	9	10	11	12	13	14
13	0	0	0	0	0	1	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	1	0	0	0	0	0	0	1	0	0	0
7	1	0	0	0	0	1	0	0	0	0	0	0	0	0
6	0	0	1	1	1	2	0	0	0	0	1	0	0	0
5	0	0	0	1	1	2	2	0	1	0	0	0	0	0
4	0	2	5	7	2	2	1	1	0	0	0	0	0	1
3	0	9	2	4	0	0	1	1	0	0	0	0	0	0
2	0	21	15	3	1	0	0	0	1	0	0	1	0	0
1	7	27	8	1	0	0	0	0	0	0	0	0	0	0

MALE AGE

FIGURE 1.   Matrix showing age composition (in years) of 141 pairs in their first year of breeding together. The number of pairs composed of each age combination is given in the matrix. All pairs involving a male or a female 3 years old or younger are initial bonds, except two subsequent bonds between 3-year-old males and 2-year-old females. All pairs involving a male or a female 4 years old or older are subsequent bonds.

Bill size. Pairing with respect to bill size was not strongly assortative or disassortative. For all pair bonds ($n = 59$) bill sizes of partners were weakly negatively correlated ($r = -0.15$, $P = 0.10$). Initial ($n = 33$, $r = -0.14$, $P = 0.24$) and subsequent ($n = 26$, $r = -0.22$, $P = 0.14$) pair bonds were also weakly disassortative. Within yearly mate pools, pairing was also random and tended towards disassortative patterns in three of four years (Table 1).

FIGURE 2.   Frequency distribution of differences in ages of mates. Entire histogram gives distribution for all pair bonds ($n = 141$). Shaded portion is initial bonds only ($n = 87$). Unshaded portion is subsequent bonds only ($n = 54$).

The differences in partners' bill sizes formed a bimodal pattern for all bonds and especially initial bonds (Fig. 3). Nearly one-third of all pairs (30.5%) had a difference in bill size of 1 to 2 mm and 40.6% had a difference of 4 to 5 mm. Average bill lengths of all males and females differ by 3.1 mm.

Body weight. Pairing with respect to body weight was not strongly assortative or disassortative (for all pair bonds $n = 57$, $r = 0.14$, $P = 0.15$). No tendency toward assortment for weight was evident in initial bonds ($r = 0.09$, $n = 32$, $P = 0.29$), subsequent bonds ($r = 0.21$, $n = 25$, $P = 0.14$), nor bonds newly formed within years (Table 1).

Partners typically weighed within 22 g of each other (Fig. 4). Differences were concentrated within two ranges: 29.6% of all pairs were within
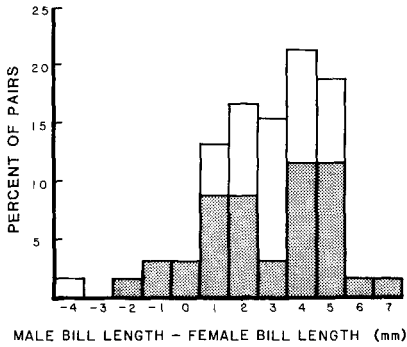
TABLE 1.   Patterns of pairing within yearly mate pools. n refers to the number of new pair bonds (initial and subsequent) formed each year for which characters were known. The observed Pearson correlation coefficient between partners' characters is r. P is derived from a randomization procedure (see Methods) and refers to the probability of observing a correlation as extreme or more so given the structure of the mate pool.

Year	Age of mates			Bill size of mates			Body weight of mates		
	n	r	P	n	r	P	n	r	P
1974				4	+0.49	0.13	4	+0.28	0.39
1975	9	−0.08	0.33						
1976	10	+0.57	0.10	8	−0.22	0.30	8	+0.18	0.36
1977	6	+0.81	0.02	4	−0.52	0.26	4	+0.68	0.09
1979	8	+0.58	0.21						
1980	5	+0.69	0.14	4	−0.19	0.43	4	+0.47	0.22
1981	12	+0.85	0.002						
1982	15	+0.60	0.02						
1983	14	+0.77	0.002						
1984	7	+0.64	0.07						
1985	13	+0.69	0.002						
1986	15	+0.76	0.006						

FIGURE 3. Frequency distribution of differences in bill sizes of mates. Entire histogram gives distribution for all pair bonds (n = 59). Shaded portion is initial bonds only (n = 33). Unshaded portion is subsequent bonds only (n = 26).
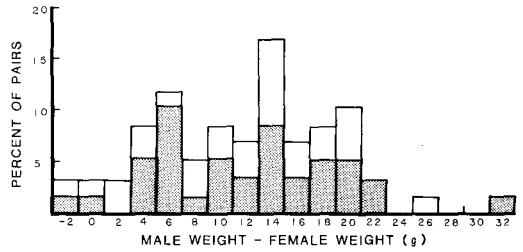

FIGURE 4. Frequency distribution of differences in body weights of mates. Entire histogram gives distribution for all pair bonds (n = 57). Shaded portion is initial bonds only (n = 32). Unshaded portion is subsequent bonds only (n = 25).

6 g while 32.2% had differences from 10 to 14 g. Concentration of weight differences in this latter interval is to be expected because the average weight of all males and females differed by 13.2 g. It should be noted that the average difference between partners' characteristics is an inherent property of the range of characteristics in the mating population. Average difference is fixed for a given mate pool and does not depend upon who pairs with whom.

Pairing patterns of parents and their sons. Body weight and bill size of sons were correlated with their fathers' sizes and were heritable. Bill size was highly heritable (h^2 + SE = 1.05 + 0.25, n = 22). The correlation between fathers' and sons' bill sizes approached significance (r = 0.31, n = 22, P = 0.07). Body weight was also heritable (h^2 + SE = 0.95 + 0.30, n = 22) and was correlated among fathers and sons (r = 0.31, n = 22, P = 0.07). Heritability in excess of 1.0 is a result of doubling a regression slope with high SE (see also Boag and Grant 1978).

Do males pair with females that resemble their mothers? There was only a slight, nonsignificant trend for female partners to resemble their mothers-in-law in weight (r = 0.35, n = 8, P = 0.20) and in bill size (r = 0.23, n = 8, P = 0.30). Difference in weight between parents was weakly correlated with weight difference between their sons and sons' mates (r = 0.63, n = 7, P = 0.07). Bill differences of parents were inversely related to bill differences between their sons and their sons' mates (r = −0.73, n = 7, P = 0.03).

Influences of choice for one character on choice for other characters. In initial pair bonds, non-random pairing for age apparently had little effect on pairing for size. Pairs of similar-aged vs. disparate-aged jays (see Methods) did not differ in the variance of their bill sizes (C = 0.59, P = 0.51) or body weights (C = 0.59, P = 0.51). Mean difference in weight also did not differ between such pairs (F = 0.29, df = 1, 28, P = 0.60). Pairs of similar-aged jays had slightly more similar bill sizes than did pairs of disparate-aged jays (difference in bill size: $\bar{x}_{similar-aged}$ = 2.3 mm, n = 15; $\bar{x}_{disparate-aged}$ = 4.0 mm, n = 14; F = 3.37, P = 0.08).

In addition to age, assortment for success in previous breeding attempts may influence pairing patterns in subsequently formed pair bonds. Elsewhere we document assortative pairing for previous success (Marzluff and Balda, in press a). Here we show how this assortment may influence pairing with respect to size and age.

Assortment for success may influence options for selection based on age or bill size. Jays that paired with previously successful breeders (those producing at least one yearling) had more variation in age difference (C = 0.94, P = 0.001), less variation in bill size difference (C = 0.89, P = 0.01), and similar variation in weight difference (C = 0.56, P = 0.78) than did jays who paired with previously unsuccessful breeders. Mean differences for each character did not differ significantly between jays pairing with previously successful vs. previously unsuccessful breeders (all P-values >0.33).

Pairing with respect to body size in subsequent bonds may be affected by preference for similar-aged partners. Pairs of similar-aged jays were more variable in bill size difference (C = 0.93, P = 0.001), and slightly more variable in weight difference (C = 0.78, P = 0.09) than were pairs differing in age by two or more years. Pairs of

TABLE 2. Fitness correlates of mate size.[1]

Male	Female	n	Male	n	Fe-male	n	Per year	n	Per bond	n	Fecun-dity	n	Longev-ity	n	Mean
			Life span				Number of yearlings				Fitness of sons			Interactions	
Body weight[2]															
Heavy	Heavy	4	5.75[a] 0.48[b]	9	6.44 1.24	11	0.45 0.13	10	1.50 0.48	1	0.00 0.00	1	4.00 0.00	3	1.00
Heavy	Light	2	3.50 1.50	3	5.33 1.76	10	0.71 0.22	2	0.50 0.50	3	0.67 0.33	4	5.00 1.41	6	2.00
Light	Heavy	9	8.44 1.30	8	7.75 0.65	12	0.24 0.08	7	0.86 0.46	5	2.00 0.63	9	5.33 1.05	5	0.60
Light	Light	9	6.44 0.50	6	6.50 0.48	12	0.53 0.09	7	1.28 0.15	8	0.88 0.30	14	4.07 0.55	11	1.82
Bill size[3]															
Long	Long	6	6.50 0.53	8	7.00 0.50	13	0.42 0.09	8	0.75 0.12	4	1.25 0.95	8	4.50 1.00	7	1.57
Long	Short	4	10.25 1.89	3	5.33 1.76	10	0.51 0.22	2	0.50 0.50	1	0.00 0.00	1	5.00 0.00	6	0.83
Short	Long	7	6.57 1.11	10	7.70 0.78	12	0.52 0.12	10	1.70 0.52	9	1.11 0.31	13	4.69 0.81	5	1.80
Short	Short	7	5.43 0.87	5	5.20 0.86	10	0.44 0.14	6	1.16 0.60	3	1.33 0.33	6	4.50 0.56	7	1.86

[1] Descriptive statistics for each size category are given without hypothesis testing because of unequal sample sizes and unequal variances per category.
[2] Light refers to jays less than or equal to the average weight. Heavy jays are greater than the average weight.
[3] Short refers to jays with bill sizes less than or equal to the average. Long-billed jays have bills greater than the average.
[a] Mean.
[b] Standard error. Mean is presented above SE throughout table.

similar-aged jays had smaller differences in bill size than did pairs of disparate-aged jays ($\bar{x}_{similar-aged}$ = 2.2 mm, n = 8, $\bar{x}_{disparate-aged}$ = 4.2 mm, n = 9, F = 4.63, P = 0.05).

INFLUENCE OF MATES' CHARACTERS ON FITNESS

Survivorship of breeders. Bill size, but not body weight, was correlated with lifespan. Males with large bills lived longer than those with small bills (correlation of male life span with male bill size: r = 0.45, n = 24, P = 0.01). Neither female bill size nor body weight was correlated with female survivorship (r = −0.07, n = 26, P = 0.37; r = 0.02, n = 26, P = 0.46). Females with larger than average bills, however, had slightly longer life spans than females with shorter bills (Table 2; $\bar{x}$ long = 7.39 years, n = 18; $\bar{x}$ short = 5.25 years, n = 8; F = 2.43, P = 0.10).

Jays mated with partners similar in weight to themselves lived longest (Table 2). Pairs of similar-sized jays include small males mated to large females because males are larger, on average than females (Ligon and White 1974; Marzluff and Balda, in press a). Light males lived on average 2.0 years longer when mated to heavy females

than when mated to light females. Heavy females lived on average 1.3 years longer when mated to light males than when mated to heavy males. Lifespan was less affected by a mate's bill size; long-billed jays lived longer than short-billed ones regardless of their mates' bill sizes.

Breeding success. Production of young that remained in the flock paralleled known production of emigrants. We have identified 22 yearlings from our population that became established breeders in a neighboring flock (Marzluff and Balda, in press a). The parents of 11 of these emigrants were known and all but one pair also produced yearlings which remained in the study flock. Parents that produced emigrants also averaged very high production of yearlings that remained in the study flock ($\bar{x}$ = 2.45). It appears that the most successful breeders are also the most likely pairs to produce emigrants. We conclude that production of yearlings which remain in the flock is a realistic measure of a pair's reproductive success because pairs that do poorly in this measure do not compensate by producing dispersing offspring.

Duration of the pair bond was significantly correlated with production of yearlings. This is

TABLE 3. Mean values of characters of pairs producing none, less than two, or greater than two surviving yearlings. Averages, listed first, are for initial and subsequent bonds together. Sample sizes in parentheses. Due to the large number of statistical tests on these data we use $\alpha = 0.01$ as our significance level in this table.

| Character | Number of yearlings while paired | | | F | P[1] |
	0	1–1.99	2–5		
Male age[2]	2.93 (28)	2.80 (25)	2.58 (12)	0.20	0.82
Female age[2]	2.71 (28)	3.04 (25)	2.58 (12)	0.35	0.71
Ending male age[3]	3.13 (23)	5.15 (20)	4.20 (10)	5.74	0.006
Ending female age[3]	2.83 (23)	5.05 (19)	3.90 (10)	6.76	0.003
Male + female age[2]	5.09 (23)	5.68 (19)	4.64 (11)	0.48	0.62
Male − female age[2]	1.07 (27)	1.00 (20)	0.45 (11)	1.38	0.26
Male body weight[4]	110.84 (15)	113.15 (21)	112.87 (9)	1.19	0.31
Female body weight	99.39 (15)	98.39 (21)	100.30 (9)	0.35	0.71
Male + female weight	216.89 (15)	211.54 (21)	213.17 (9)	0.57	0.57
Male − female weight	9.68 (15)	13.63 (21)	10.43 (9)	1.48	0.24
Male bill size	34.78 (15)	35.24 (21)	34.67 (9)	0.74	0.48
Female bill size	31.67 (15)	31.66 (21)	32.67 (9)	1.29	0.28
Male + female bill	66.45 (15)	66.90 (21)	67.33 (9)	0.57	0.57
Male − female bill	3.51 (15)	3.16 (21)	2.84 (9)	0.54	0.59
Pair-bond duration[5]	1.89 (28)	3.33 (21)	3.10 (10)	5.04	0.01

[1] From one-way ANOVA.
[2] Age in years when pair bond was formed.
[3] Age in years when pair bond was broken.
[4] All body weights are in g, bill sizes in mm.
[5] Duration in years.

not due to a gradual accumulation of yearlings each year. Annual reproductive success is slightly lower for initial pairs in their first breeding attempt than it is for more experienced pairs, however, annual success does not increase with increasing pair-bond duration beyond 2 years (Marzluff and Balda, in press a). Few pairs (<20% of breeders) produced yearlings in any given year and nearly half of all pairs we studied failed to produce any young (note sample sizes in Table 3). Long-lasting pairs were apparently successful because they had more breeding opportunities of which one or two might produce yearlings. Successful pairs remained together for over 3 years, but unsuccessful breeders were together less than 2 years (Table 3). Pair-bond duration of successful pairs and unsuccessful pairs differed to a greater extent in initial bonds ($F = 4.81$, df = 2, 15, $P = 0.01$) than in subsequent bonds ($F = 1.27$, df = 2, 15, $P = 0.31$).

The mean values of bill size and body weight did not differ significantly between pairs producing zero, one, or two yearlings (Table 3). Pairs composed of heavy females and light males had relatively poor annual reproductive success; however, total success during their tenure together was high (Table 2). Pairs of large males and large females also were relatively fecund (Table 2).

Difference in partners' ages showed a weak relationship with reproductive success that was consistent for initial and subsequent bonds. Those pairs producing two or more yearlings were twice as similar in age as those failing to produce yearlings (Table 3). Similar-aged mates had a greater chance of breeding successfully. Sixty-three percent of pairs with 1 year or less difference in age produced at least one yearling. In contrast, only 43% of pairs in which the partners showed greater age difference had equal success. Pairs with 1 year or less difference in age ($n = 47$) averaged 0.46 yearlings per year, whereas pairs with greater age difference ($n = 10$) averaged only 0.18 yearlings per year ($F = 1.84$, $P = 0.18$). Pairs with one year or less difference in age ($n = 46$) produced on average 0.95 yearlings during the time they were paired, whereas pairs with greater age differences ($n = 9$) only produced 0.33 yearlings during their tenure together ($F = 2.5$, $P = 0.11$).

The relationship between reproductive success and age difference of partners was confounded by a relationship between age difference and lineage of descent. Analysis of the family lineages revealed that helping behavior occurred in some lineages but never in others (Marzluff and Balda, unpubl). Lineages in which helping occasionally occurs are referred to as H-lineages ($n = 36$ pairs); all other lineages are termed NH-lineages ($n = 25$ pairs). Helping by male, yearling off-

spring did not increase annual success of the pair. Despite an apparent lack of help, H-lineage pairs were more successful than NH-lineage pairs. Fifty-six percent of successful pairs, but only 18% of unsuccessful pairs were H-lineage descendents. H-lineage pairs were nearly twice as similar in age as NH-lineage pairs (mean age difference: $\bar{x}_H = 0.69$ years, $n = 29$; $\bar{x}_{NH} = 1.26$ years, $n = 23$; $F = 3.7$, $P = 0.06$).

We investigated the influence of parental characters on the quality of their young by examining two components of offspring fitness: lifetime reproductive success (production of yearlings) and life span. Life span was closely related to lifetime reproductive success in young for which complete data were available ($r = 0.61$, $n = 18$, $P = 0.003$). Sample size ($n = 30$) was sufficient to investigate the influence of parental characters only on sons.

Sons produced by pairs of equal-aged partners survived significantly longer ($\bar{x} = 7.2$ years, $n = 5$) than sons produced by pairs with greater age difference ($\bar{x} = 3.9$ years, $n = 7$, $t = 4.83$, df = 5, $P < 0.005$). Young produced by equal-aged partners had an average lifetime production four times that of young produced by unequal-aged partners ($n = 4$ pairs).

Physical characters of parents were correlated with their sons' fitness. Weight difference of parents was negatively correlated with their sons' lifespans ($r = -0.35$, $n = 21$, $P = 0.029$). Sons produced by heavier than average mothers mated to lighter than average fathers averaged longer life spans and greater lifetime production of offspring (Table 2).

In summary, we have shown that physical characters were correlated with fitness of breeders in the following ways: (1) pairs of heavy females and light males (similar partner weights) lived longer, and produced young that lived longer and produced more offspring than young from partners disparate in weight, and (2) long-billed jays survived longer than short-billed jays.

Relative age (a measure of breeding experience) was correlated with reproductive success as follows: (1) similar-aged partners produced more young over the duration of their pair bond than did disparate-aged partners, and (2) young of similar-aged partners survived longer than young of disparate-aged pairs.

AGGRESSION BETWEEN MATES

Adult males consistently dominated adult females throughout the year. Adult females lost 77.5% of 324 encounters with adult males during the breeding season, but lost 88.9% of 316 encounters during the late breeding/molting season, and lost 89.5% of 669 encounters during the nonbreeding season. Adult females fared significantly better against adult males during the breeding season than at other times of the year ($\chi^2 = 34.01$, df = 1, $P < 0.01$).

Encounters typically occurred during the nonbreeding season between adult males and adult females that were not mated. We observed 1,309 encounters between adult males and adult females; only 38 (2.9%) were between mates. Pairs consisting of heavier than average females and lighter than average males rarely interacted (Table 2). Pairs consisting of females with long bills and males with short bills interacted frequently on average; however, six interactions by one pair inflated this average. Excluding this pair, partners only averaged 0.75 interactions over a 2.5-year period. Over half (51.1%) of all encounters occurred during the 5 months of the nonbreeding season.

DISCUSSION

Choice of a mate is an important decision for Pinyon Jays for at least three reasons: (1) breeding success is correlated with parental behaviors (Gabaldon 1978; Marzluff 1983, 1985, 1988; Marzluff and Balda in press a, in press b), (2) mate fidelity is strong even after several years of poor breeding performance (Marzluff and Balda, in press a), and (3) most Pinyon Jays (57.1% of males, 65.0% of females) only have one mate during their lifetimes (Marzluff and Balda, in press a). Here we do not document mate choice. Pairing patterns and their relationship to fitness only enable us to generate hypotheses about which characters should be used by jays in their choice of mates.

ASSORTATIVE PAIRING FOR AGE

The strongest nonrandom pairing pattern evident in this flock of jays was assortative mating for age, or some correlate of age. Breeding experience is directly related to age (Marzluff and Balda, in press a). Thus, assortment for age equates to assortment for experience. This nonrandom pattern was evident among birds forming initial pair bonds, in pairs forming subsequent bonds, and within yearly mate pools. Experimental evidence is needed to conclude that even-aged mates are actively selected (Cooke and Davies 1983).

Mating of similar-aged individuals is not unique to Pinyon Jays. Coulson and Thomas (1983) noted a similar trend in young kittiwakes but believed old individuals made no attempt to select mates of similar age or breeding experience. Young Arctic Terns, *Sterna paradisaea* (Coulson and Horobin 1976), Shags, *Phalacrocorax aristotelis,* Herring Gulls, *Larus argentatus* (Chabryzk and Coulson 1976), and Red-billed Gulls, *Larus novaehollandiae scopulinus* (Mills 1973), also show assortment for age. Canada Geese (*Branta canadensis*), at least up to age four, also tend to mate with similar-aged individuals (Raveling 1981). Two yearlings or two adults pair more frequently than one yearling and one adult in Eurasian Sparrowhawks, *Accipiter nisus* (Newton et al. 1981); however, assortment may result because of different arrival times on the breeding grounds (Village 1985).

PAIRING WITH RESPECT TO BODY SIZE

Pairing with respect to body weight and bill size, or correlates of them, was not strongly assortative nor disassortative. This does not mean mates were chosen at random for size; nonrandom, but opposing, choices within a population could produce a random pattern. Such a process may have produced bimodal pairing patterns for size in our population (Figs. 3, 4).

Dominance among males was slightly size dependent; nine of 13 dominant males in 1972 to 1974 had average or greater weights and bill lengths. Dominant, large males may prevail over less dominant males in the selection process and pair with large, long-lived females. Large females, however, also had high fitness when mated with small males and hence may prefer them even when large males are available (Table 2). Small males paired with large females would result in disassortative mating for size, and a preponderance of small differences in bill size (1.7 mm or less in our sample) and body weight (8.18 g or less in our sample). Large males paired with large females would result in assortative mating patterns, and a preponderance of intermediate differences in bill size (2.78 to 3.39 mm) and body weight (12.43 to 14.80 g). Larger differences in size result when small males pair with small females and the largest occur when large males pair with small females. Qualitatively, the size differences between large males and large females, and between small males and large females match modes in observed pairing patterns

(Figs. 3, 4). Thus, conflicting assortative and disassortative pairing for size may have produced the overall nonrandom pattern we have documented. Conflicting pairing patterns may reflect sexual differences in mate preference. Aviary mate choice experiments suggest that large, dominant males prefer large females but large, dominant females do not prefer large males (Johnson, in press a, in press b).

ARE PAIRING PATTERNS RELATED TO FITNESS?

Mated jays may influence each other's fitness in a variety of ways. They may affect each other's longevity and fecundity, and the fitness of their offspring. Choosing a mate with characters that enhance pair-bond duration may also be important in this population for two reasons: (1) breeding success in the first year of initial pair bonds is low (Marzluff and Balda, in press a), and (2) annual reproductive success is very low because of high levels of predation and variably harsh spring weather (Marzluff 1988).

Assortative pairing for age may be favored by natural selection because pairs of similar-aged individuals had higher fecundity and produced longer-living offspring than pairs of dissimilar-aged individuals. Similarity in age may promote increased fecundity by insuring compatibility of partners. Partners of similar age have had similar experiences and have similar demographic expectations (e_x, residual reproductive value, etc.). Thus similar-aged mates may have been favored by natural selection because they solve problems encountered during the breeding season in compatible ways. How much to invest in feeding offspring is one such problem. Behavioral observations indicate that males contribute more time to the feeding of offspring than females when partners are of dissimilar age. Similar-aged partners, in contrast, more equally divide the work load which reduces the time parents spend at the nest, thus possibly lowering predation risks (Marzluff 1983). More data are needed to imply that age difference is causally related to fitness because, in our sample, another correlate of fitness (lineage of descent) was related to age difference. Our data do not allow us to determine if H-lineage pairs were successful because of their slight age differences, or if pairs assorting for age were successful because they were descendents of H-lineage families.

We hypothesize that mate choice with respect

to body size should depend on the size of the chooser. Large males should prefer to mate with large females because male fecundity is, on average, highest in such pairs. Small males should also prefer to mate with large females because male longevity is highest and fecundity is relatively high in such pairs (Table 2). Pair-bond duration is also highest when males pair with large females (Marzluff and Balda, in press a). Large females have high fitness regardless of the size of their mate (Table 2); however, pair-bond duration is consistently longer (Marzluff and Balda, in press a), and their offspring are more fit when they pair with small males. Thus, all males should prefer large females and large females may prefer small males. Male preference for large females and lack of female preference for large males has been observed in laboratory mate choice tests (Johnson, in press a, in press b).

High fitness by pairs of large females and small males may be related to intrapair dominance. Aggressive encounters were rare between such partners (Table 2), perhaps because small males did not completely dominate large females. Aggressive encounters were more frequent when males were mated to small females. Relative domination of the female by the male may affect pair-bond duration (Marzluff and Balda, in press a), and hence fitness of the pair.

USE OF CHARACTERS IN MATE CHOICE

In order to decrease the chances of choosing an inferior mate, selection may favor individuals choosing mates on the basis of many characteristics that indicate fitness. Female Red-winged Blackbirds (*Agelaius phoeniceus*) in Indiana appear to use both male and territory quality in their choice of mates (Yasukawa 1981). Similarly, experiments conducted on Rock Doves indicate that mates are selected by a combination of plumage characteristics, age, experience, and dominance (Burley 1981).

Pinyon Jays might also use multiple criteria when selecting mates; however, our results suggest that there is a hierarchy to this use. We base this hierarchy on our documentation of nonrandom pairing and on the effects that choice for one character may have on choice for other characters.

The use of age as a cue appears to be secondary to the use of prior breeding performance. Prior breeding performance would be a very reliable cue because past and future breeding success are significantly positively correlated (Marzluff and Balda, in press a). Jays appear to forgo pairing with similar-aged mates in order to pair with previously successful jays. Age differences were more variable among pairs including previously successful jays than among pairs of formerly unsuccessful jays.

If a conflict between using age or size as a cue in mate choice occurs, it is only functional in subsequent bonds. Pairing between individuals similar in age does not appear to restrict their ability to use body size as a secondary cue in initial bonds. As a result, age and size can be used simultaneously in the choice of initial mates. This may occur because many jays of similar age are initially available in the mate pool. In subsequent bonds, however, fewer jays of similar age are alive and/or unmated. Pairing with a similar-aged mate appears to be more important than pairing with respect to size in subsequent bonds because jays with mates similar to their own age had more variable size differences than pairs of dissimilar-aged jays. This may result because jays obtaining similar-aged mates tolerate variability in size differences, or because similar-aged jays represent a biased sample of sizes. Pairs of similar-aged birds had more similar bill lengths than did pairs of dissimilar-aged birds.

We propose that jays choose mates by using cues in the following hierarchy. Jays prefer, first, to mate with proven breeders. If successful breeders are not available, or not obtainable, mates similar in age are preferred. Assortment may result from older, more dominant, jays choosing each other and, by default, leaving younger individuals to mate with one another. If similar-aged mates are not available, body size is used as a cue. Pairing may be assortative or disassortative for size depending on the size of the chooser. Body weight should be used before bill size as a cue in subsequent bonds because weight differences of partners were more closely correlated with fitness than were bill differences. Our data are consistent with this scenario, but it is provided only as a testable hypothesis. We have not considered the presence of close relatives as a factor affecting mate choice in this scenario because in our population it is very rare (five cases over 12 years) that two close relatives ($r \geq 0.25$) of opposite sex are alive and unmated in the same year.

Selection should favor the careful choice of an initial mate because that is likely to be the only

mate a jay obtains (Marzluff and Balda, in press a). A very telling cue, previous success, however, is obviously not available to jays making initial choices. Perhaps the ability to simultaneously, rather than sequentially, use age and size as cues is important in initial bonds for this reason. Experimental studies of mate choice need to account for possibly different use of cues by experienced and inexperienced breeders.

HOW IS OFFSPRING FITNESS AFFECTED BY CHARACTERS OF THEIR PARENTS?

We were surprised to find that partners similar in age and weight not only had high fecundity, but that their offspring also had high fitness. Why do these parents produce successful young? Several alternative hypotheses may provide the answer. (1) The relationship could be spurious; our sample sizes are small. (2) These offspring may select mates according to the cues used by their parents. We only have data on seven parents and their sons to appraise this possibility. Offspring may follow their parents' example for weight, but parental bill differences were inversely related to bill differences between their sons and their sons' mates. (3) Similar mates could produce higher quality young by providing them with better parental care or better genes than those provided by dissimilar mates. Both may occur. Similar mates care for nestlings differently than dissimilar pairs do (see above and Marzluff 1983), but how this affects nestlings' lifespan and fecundity as breeders is unknown. Body size is heritable and correlated with fitness, thus large males and females may provide genes correlated with long lifespan to their offspring in addition to caring differently for them.

Our results are interesting in light of current debate over whether mates are chosen for their genotypic or phenotypic properties (e.g., Weatherhead 1984). Our results suggest that large birds may be of highest genetic quality, but this quality may be negated if their phenotype does not match their mates' phenotype. For example, although long-billed males lived longer than short-billed ones and body size was heritable, long-billed males mated with short-billed females (large bill size difference) only produced one third as many yearlings while paired together as were produced by short-billed males mated with long-billed females (small bill size difference) (Table 2). Thus, the genetic quality of a mate does not guarantee success; phenotypic properties of mates also must be compatible.

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