# SOME PROBLEMS AND APPROACHES IN AVIAN MATE CHOICE

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ABSTRACT.—Most studies of mate choice in birds consider questions such as the existence of mate choice, which traits are preferred, and how the preferences evolved. In order to answer these questions, it is necessary to distinguish between pairs of key processes such as dominance and choice, assortative mating and type preference, or male choice and female choice. We review these and other difficulties in the study of avian mate choice. As an illustration of methodological issues, we discuss our work on Pinyon Jays (*Gymnorhinus cyanocephalus*). Males that were successful in mate-choice experiments were more brightly colored and had large testes, but were not necessarily larger or dominant. Preferred females were large, dominant, and had thicker bills. In free-living populations, smaller than average males and larger than average females lived longer. Pairs composed of small males and large females had sons with higher fecundities and greater survivorship. We suggest that many ornithologists could combine their long-term field observations with controlled experiments to profitably study mate choice. *Received 27 January 1989, accepted 6 November 1989.*

THE AREA of sexual selection is currently one of the most controversial and rapidly developing in biology (Andersson and Bradbury 1987). There is a large body of theory on sexual selection; and an increasing number of empirical studies, particularly of mate choice, focus on birds (e.g. Komers and Dhindsa 1989, Zuk et al. in press a, b). Empirical studies often fail because they do not address important theoretical questions, their methodology does not allow discrimination of key processes, or both. Our discussion of the first problem is brief, as this topic is reviewed in detail elsewhere (Arnold 1985, Bradbury and Andersson 1987). We focus here on commonly encountered methodological difficulties in the empirical study of avian mate choice. We suggest approaches to these problems and provide an example from work with captive and free-living Pinyon Jays (*Gymnorhinus cyanocephalus*) that illustrates some of these methodological issues.

## DIFFICULTIES IN THE STUDY OF MATE CHOICE

A central theoretical question is how female choice can affect the evolution of secondary sex characteristics. Closely associated is the question of how the mating preferences themselves evolved. The considerable theory in this area offers numerous questions for empiricists to address (Heisler et al. 1987). Empirical studies of female choice usually begin with the question of whether female mating preferences for particular male traits exist.

*Identifying traits.*—The first difficulty in investigating mate choice is to decide which traits might be important. If there are field data for the species of interest, one can identify traits used in courtship displays, search for correlations between specific traits and mating or reproductive success, or look for assortative mating with respect to specific traits. These traits suggest a starting point for experimental study. If there are no relevant field data, theory and common sense can suggest traits for experimentation. Ideally, one should then go to the field to determine the fitness consequences for individuals with the preferred traits.

*Is mating nonrandom?*—Once appropriate traits have been identified, it is necessary to document nonrandom mating for the traits of interest. Standard statistical procedures can be applied to the results of laboratory experiments. In the field, however, it can be unclear whether an observed pattern is the result of preferences for a particular trait (type preference; Burley 1983) or prevalence of that trait in the pool of prospective mates at the time mating occurs (Cooke and Davies 1983). For example, in several bird species, the ages of partners are correlated (Reid 1988). Reid (1988) has shown that, with stable pair bonds, such correlations can

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occur in the absence of mate choice, through random mating alone.

To investigate apparent nonrandom mating patterns, it is not appropriate to apply standard statistical procedures (such as Chi-square approximations or correlation analyses) to the traits of a free-living population of existing pairs, because these tests require that different pair bonds form independently. Mate pools are finite, and once two individuals in a finite mate pool pair, the remaining individuals have reduced choices that depend on previous choices. In monogamous species, this continues until the last two individuals have no choice but to pair with one another. Such clearly dependent events cannot be analyzed with parametric or nonparametric tests of association.

Randomization procedures can avoid this problem by comparing all possible (random) pairings at a given time with the pairings actually observed (Marzluff and Balda 1988b, Johnston and Johnson 1989). For this approach, it is necessary to know which individuals were available in the mate pool at the beginning of the pairing period and calculate the N! possible patterns that can be formed between N males and N females. Nonrandomness of the observed pairing pattern is calculated by determining how rare that pattern is relative to all possible patterns.

*Factors confounding choice.*—To decide whether nonrandom mating patterns are the result of mate choice, it is necessary to rule out the process of intrasexual competition as a complicating factor. Consider female choice of males in a typical nonterritorial species in which males usually show behavioral dominance to females. If nonrandom mating occurs, it can be unclear whether the mating pattern is a result of female preference for certain male types or whether intra-male competition allows dominant males to monopolize access to females. Even when females appear to choose males, male-male competition can mediate female choice. For example, female American Wigeons (*Anas americana*) mate more often with larger, heavier adult males in full alternate plumage, but these males also tend to be dominant (Wishart 1983; see also West et al. 1981, for Brown-headed Cowbirds, *Molothrus ater*).

The easiest way to eliminate the effects of male-male competition is to experimentally restrict males from competing (e.g. Burley 1981a, 1986). Males should be isolated visually and physically to prevent dominants from inhibiting subordinate display behavior (Komers and Dhindsa 1989).

Alternatively, it may be necessary to choose experimental design and analysis that allow separation of the effects of choice and competition, without physically separating competitors. Pinyon Jays are highly social and do not behave normally when isolated in captivity. Thus, mate-choice trials must be run without isolating males. Johnson (1988a) determined the males (and their traits) that were successful in male-male competition (i.e. male dominance) in the absence of females, and then females were allowed to choose among several males that were not separated physically. In these female choice experiments, female choice and male-male competition operated simultaneously. There are several possible outcomes with this type of design. First, the same males may be successful when male-male competition acts alone as when male competition and female choice occur simultaneously. This outcome indicates that male-male competition is the primary factor that determines male mating success. Second, when female choice is introduced, additional males or traits may be favored. This indicates that both competition and choice affect male mating success. Third, entirely different males or traits may be favored in the male-male competition and male competition-female choice trials. This result implies that female choice operates in the presence of male-male competition and that male-male competition does not override the operation of female choice. In Johnson's experiment, male competition alone appeared to favor different birds and male traits from male competition and female choice acting simultaneously. This suggested that female Pinyon Jays exercise their preferences, even in the presence of males, who are usually dominant to females. Similar logic was used by Komers and Dhindsa (1989) for Black-billed Magpies (*Pica pica*) in captive flocks. When either of the first two conditions occurs, however, the effects of choice and competition are indistinguishable. Whenever possible, it is simpler to separate competitors at the outset of the experiment.

We have suggested ways in which intrasexual competition can be distinguished from female choice; however, nonrandom patterns of mating may also result from female and male choice operating simultaneously. In species in which both males and females invest in offspring, both sexes should be selective (Trivers 1972). High-quality individuals should be more choosy than low-quality individuals (Burley 1977). High-quality birds should pair assortatively, which leaves low-quality birds to pair with each other. This can give the appearance of assortative mating with respect to the traits of interest, when in fact the pattern results from both sexes having type preferences for high-quality mates (Burley 1983). The best way to avoid this fallacy is with controlled experiments in which only one sex is allowed to choose at a time, to determine preferred traits and the strengths of preferences for both sexes (Burley 1981a, 1986; Johnson 1988a, b).

Whether examining naturally varying or artificial traits, there are two basic approaches to mate-choice experiments. Numerous studies have taken a univariate or bivariate approach, and examined only one (Yosef and Pinshow 1989) or two (Duncan and Bird 1989, Komers and Dhindsa 1989) traits. With this approach, it is best to match choice birds for all except the trait of interest (Burley 1981a, 1986). A potentially more informative approach is to select choice birds randomly, measure all traits that might be relevant, and analyze several measured traits simultaneously with multivariate procedures (Johnson 1988a, b; Johnston and Johnson 1989; Zuk et al. in press a).

Use of nonindependent observations is a common problem with experimental studies. If a subject (e.g. a choosing female) is used in more than one trial in the same experiment, her two choices should not be considered independent data points. Similarly, caution must be used in re-using stimulus birds within the same experiment. The details of experimental design in mate-choice experiments are beyond the scope of this paper, but workers should avoid faulty designs that could invalidate results (Hurlbert 1984, Kroodsma 1989).

In territorial or lekking species, female choice may operate independently, because females are free to move from one more or less stationary male to another. In territorial species choice for a male can be confused with choice for his territory.

*Why choose mates?*—Once it is clear that mate choice, and not simply intrasexual interaction, results in nonrandom mating, it is important to know how the preferences evolved. The nature of the preferred trait indicates whether or not choice is functional. Birds can make adaptive, or functional, choices on the basis of resources, parental investment, or genes. By definition, functional mate choice provides fitness benefits to the chooser. An alternative is that birds choose mates on the basis of aesthetic traits that confer no advantage on the chooser (Burley 1986, Brodsky 1988). Genetic models of runaway sexual selection have shown that nonfunctional preferences may evolve because of correlations that develop between the genes for the female's preference and the genes for the preferred male trait (Lande 1981, Kirkpatrick 1982).

It is reasonable to assume that females that pair with territorial males are free to choose. It can be difficult to determine what benefits females derive from being selective. In the many species that defend type A territories, females may simultaneously receive resources, parental care, and genes from males. It can be difficult to determine which, if any, is most important. In addition, features of the male and the territory are often correlated (e.g. Searcy and Yasukawa 1983, Alatalo et al. 1984, Price 1984).

Red-winged Blackbirds (*Agelaius phoeniceus*) represent a case in point. After several years and many careful studies (a partial list includes Searcy 1979; Lenington 1980; Yasukawa et al. 1980, 1987; Searcy and Yasukawa 1981, 1983; Yasukawa 1981), most workers agree that territory quality is an important criterion for female choice, but the influence of male attributes, especially parental care and genetic contribution, is still open to question (Weatherhead and Robertson 1979; Searcy and Yasukawa 1981, 1983; Searcy 1982; Eckert and Weatherhead 1987; Yasukawa et al. 1987). When male and territory qualities are not correlated, the two can be examined independently. For example, in Pied Flycatchers (*Ficedula hypoleuca*), nest boxes were manipulated to control male settling pattern. This disrupted the male-territory correlation that develops when the first-arriving, older males have access to the preferred boxes (Alatalo et al. 1986).

Another approach to the confounding problem of territory quality is to use each male, before his traits are altered, as his own control (Andersson 1982). An advantage of this approach is that an individual trait can be manipulated, which controls for correlated traits. With adequate sample sizes, territorial males can be manipulated randomly, which randomizes the effects of territory quality on female choice. Changes in mating success of manipulated males are then assumed to be due to the manipulation rather than territory quality. Where mate choice is resource-based, quality of resources on the territory can be manipulated (Yosef and Pinshow 1989).

In species where males provide parental care but do not defend resources on which females can base a choice, choice is based on male qualities. The problem is to distinguish among choice for parental qualities, good genes, and arbitrary attractiveness (Johnson 1988a). Several studies have shown that male parental investment increases female reproductive success (Patterson et al. 1980, Alatalo et al. 1981, Catchpole et al. 1985, Leonard and Picman 1988). To show functional female choice for male parental qualities requires also finding male traits that indicate in advance parental investment and showing that females prefer those traits (e.g. Eckert and Weatherhead 1987, Yasukawa et al. 1987).

In lekking species, the investigator must distinguish between mate choice for good genes and arbitrary (aesthetic) choice. To test good genes hypotheses, it is necessary to show that male attractiveness is correlated with viability of males or their offspring. For birds, this means that both mate-choice experiments and field studies may be required.

One criticism of the good-genes hypothesis is that sexual selection for good genes will eventually reduce heritable variation in the preferred traits until it becomes so low that no benefit results from choice for genes (Maynard Smith 1978, Searcy 1982). Showing heritable variation for the preferred traits would counter this criticism. Alternatively, it is possible that indicator traits such as secondary sex characteristics are facultatively influenced by environmental factors like disease (Hamilton and Zuk 1982). In this case, heritability of indicator traits is expected to be low, while phenotypes reflect physiological condition, and overall fitness remains heritable.

Some models of runaway sexual selection (arbitrary choice) require the development of a genetic correlation between females' preferences and males' traits in order for female preference to evolve (Lande 1981, Kirkpatrick 1982). To test hypotheses of the evolution of female mating preference, it is necessary to know if female preferences are heritable. Investigation of heritabilities and genetic correlations requires the techniques of quantitative genetics, which were not developed for use in natural populations. Environmental heterogeneity, genotype-environment interactions, positive assortative mating, and other factors can strongly affect the estimation of these quantities in natural populations (Van Noordwijk 1984, Hailman 1986). For breeding studies, samples usually must be sizable and relatedness between individuals known. For these reasons, genetic studies should be undertaken only after careful planning (Heisler et al. 1987).

Burley (1981b, 1986) has pointed out the potential for birds to choose mates and allocate reproductive effort based on aesthetic traits. With few exceptions (Watt 1982, Brodsky 1988, Hagan and Reed 1988), field-workers have not tested the effects of color bands on reproductive success. If band colors are applied randomly in the field, differential mating success or nonrandom mating by band color may indicate that the birds respond to artificial aesthetic markers. Laboratory experiments can be used to investigate this possibility (Burley 1986). Workers who experiment on mate choice for naturally varying traits should avoid the potential complications caused by color-marking experimental birds. Likewise, field-workers should either control for this confounding effect or use large sample sizes and take care to apply color bands randomly.

If no relationship exists between male traits and male mating success, it is reasonable to reject the existence of female choice of males (Lightbody and Weatherhead 1987, Leonard and Picman 1988). There are several potential problems with the conclusion that mate choice does not occur. First, it is difficult to be certain that all relevant traits were measured. Second, females may have preferences but may exercise them only when appropriate choices are offered (Zuk et al. in press b), or when male competition does not constrain female choice.

We believe that measuring male traits vs. mating success in a free-living population of a typical territorial, monogamous species is unlikely to produce new insights into avian mate choice. A combination of laboratory experiments to distinguish among confounding influences and field measurements to allow meaningful interpretation of experimental data will usually prove productive.

## A CASE STUDY

*Mate choice in Pinyon Jays.*—Pinyon Jays maintain large flocks and nest in loose colonies. There is ample potential for individuals to compare prospective mates (Balda and Bateman 1971, 1972). Pinyon Jays form monogamous, lifelong pair bonds and separation is almost nonexistent (Marzluff and Balda 1988a). Because both males and females make large parental investments, both sexes should be selective about their mates. Mate choice is not confounded by territory quality because Pinyon Jays do not defend a breeding territory (Balda and Bateman 1971, Bateman and Balda 1973). Males are ca. 13% heavier than females and have larger bills (Ligon and White 1974). Male plumage is generally brighter than female plumage, although there is considerable overlap. The sexual dimorphism, male-biased sex ratio (60 : 40, Marzluff and Balda 1988c) and some results of mate-choice experiments suggest that sexual selection may operate more strongly on males than on females (Johnson 1988b).

We discuss results of two separate studies of Pinyon Jays. One was a long-term field study performed by R. Balda and his colleagues, the other a laboratory mate-choice study conducted by K. Johnson. Most of the data discussed are presented in detail elsewhere. We present summaries of those analyses, along with some new data. We discuss general conclusions from both studies to illustrate methodological issues.

## METHODS

*Mate-choice experiments.*—Wild-caught Pinyon Jays were housed in large aviaries on the roof of the University of New Mexico biology building. Johnson captured males and females at different localities, to ensure that males and females would be unfamiliar with one another, and housed them in separate aviaries. Forty-one female choice trials were conducted, in which each female was allowed to choose among three (1986) or two (1985) males and to perform courtship. A similar male choice experiment ($n = 26$) in which males chose among three (1986) females was performed. Choice experiments were done in a smaller experimental aviary, and dominance rankings of choice birds were determined before the trials began. These rankings agreed with dominance rankings of birds when they were in the large aviaries. Choice birds all wore two yellow bands (two on the right leg, two on the left, or one on each leg), and choosers were unbanded. Desirability scores were computed for each individual, based on the number of times each bird performed courtship and was chosen in the experiments. Each bird was measured for weight, tarsus, wing length, bill length, and bill thickness and compared with museum specimens to score it for brightness of head and malar feathers and size of the white throat patch. Laparotomies were performed to confirm sex and allow measurement of testes (see Johnson [1988a, b] for details of methods and statistics).

*Observations of free-living birds.*—A flock of color-banded, known-aged Pinyon Jays near Flagstaff, Arizona, was monitored from 1972 to 1986 as it visited feeding stations. Reproductive success of pairs and their offspring was determined each breeding season (details in Marzluff and Balda 1988b). We used these data to investigate reproductive success of pairs with traits shown to be preferred in the lab. Pairs were classified according to whether partners were *heavy*, meaning heavier than the mean for individuals of that sex in the Flagstaff population, or *light*, meaning equal to or lighter than the mean.

## RESULTS

*Female choice of males.*—Male desirability scores fell into three clear groups: males that were never successful with females, males that were sometimes successful, and those that were highly successful. Univariate and multivariate analyses of variance were used to determine which traits were preferred by females. Malar feather brightness and testis length differed among the three groups of males by the univariate tests, and the MANOVA for all measured traits indicated that the three groups differed in a linear combination of all variables. All possible contrasts were significant at the $P < 0.05$ level. Females preferred males with brighter plumage and larger testes, but they did not prefer larger males nor males having the traits important in male-male competition (Johnson 1988a). Testis size was not correlated with overall body size.

*Male choice of females.*—A stepwise multiple regression of the female traits on female desirability gave five significant regression models. The best one-variable model was body weight, the best two-variable model included weight plus dominance rank, and the best three-variable model was weight plus rank plus bill thickness. All three partial regression coefficients were significant for the three-variable model and step 3 contributed a significant increment to the total $R^2$. Significance decreased beyond the three-variable model to become nonsignificant for steps 6-9. Thus, body weight, dominance rank, and bill thickness were related to the likelihood of females being chosen by males (Johnson 1988b).

*Reproductive success of free-living pairs.*—The data of Marzluff and Balda (1988b) suggest that the pairs that remained together longest were light (male)-heavy (female) pairs (Table 1; trends are evident, but sample sizes did not allow hypothesis testing). Because of slight sexual dimorphism, a male that is much lighter than average and a female that is heavier than average will be close to the same weight. In contrast, a

TABLE 1. Fitness measures ($\bar{x} \pm$ SE) of four types of Pinyon Jay pairs, classified according to mass. H = heavier than the mean for that sex; L = lighter than the mean for that sex. Sample sizes are in parentheses.[a]

| Body mass | | Life span | | Fitness of sons | |
|---|---|---|---|---|---|
| Male | Female | Male | Female | Fecundity | Longevity |
| H | H | 5.75 ± 0.48 (4) | 6.44 ± 1.24 (9) | 0.00 (1) | 4.00 ± 0.00 (1) |
| H | L | 3.50 ± 1.50 (2) | 5.33 ± 1.76 (3) | 0.67 ± 0.33 (3) | 5.00 ± 1.41 (4) |
| L | H | 8.44 ± 1.30 (9) | 7.75 ± 0.65 (8) | 2.00 ± 0.63 (5) | 5.33 ± 1.05 (9) |
| L | L | 6.44 ± 0.50 (9) | 6.50 ± 0.48 (6) | 0.88 ± 0.30 (8) | 4.07 ± 0.55 (14) |

[a] Descriptive statistics are given without hypothesis testing because of small and unequal sample sizes (excerpt from Marzluff and Balda 1988a); birds with incomplete life histories account for discrepancies in number of birds in different weight classes.

heavy (male)-light (female) pair will have a large weight difference. Over all pair types, male lifespan was significantly negatively correlated with weight differences (male-female) between partners ($r = -0.28$, $P = 0.043$, $n = 24$). Light males appeared to live longer than heavy males, and regardless of weight, males mated to heavy females appeared to live longer (Table 1).

In contrast to the situation for males, life span appeared to be slightly greater for heavy females. Regardless of female weight, females mated to light males had greater survivorship than females mated to heavy males, although the effect of the mate is not as pronounced on females as on males.

The light-heavy pairs did not appear to rear more young than other pairs (Marzluff and Balda 1988b), but their sons (data are not available for daughters because of female-biased emigration, Marzluff and Balda 1989) apparently produced more sons themselves (Table 1). The correlation between differences in parental weights (male-female) and the fecundity of their sons is negative and significant for all pair types ($r = -0.41$, $P = 0.05$, $n = 17$). Weight differences between parents were negatively correlated with sons' lifespans (Marzluff and Balda 1988b). Therefore, the pairs with the smallest weight differences, the light-heavy pairs, had greater longevity themselves and had sons with higher fecundities and greater survivorship.

## DISCUSSION

The mate-choice experiments suggest that the ideal Pinyon Jay pair would be composed of a brightly colored male, not particularly large or necessarily dominant, paired to a large, aggressive female with a thick bill. If Pinyon Jays choose mates on the basis of genetic or parental quality, pairs with these traits should have greater reproductive success, survivorship, or both, than pairs with other attributes (for a discussion of the possible implications of preferences for the above traits, see Johnson 1988a, b).

Light males and males mated to heavy females lived longer. This may mean that there is a survival advantage for a male that is mated to a heavy female. For example, a male with a relatively large, aggressive mate might have to expend less energy assisting the smaller, subordinate female in winter competition for food. Observations of pairs at feeding stations would indicate if the status of a bird's mate affected individual energy budgets at winter food sources. However, it is also possible that males mated to heavy females live longer because they are higher quality males themselves and also have access to the preferred, heavy females. That is, a male's survivorship may be independent of the characteristics of his mate.

Unlike males, heavy females and females mated to light males survived slightly better. It is not entirely clear how light males could enhance their mates' survivorship. The mate-choice experiments did not show small males to be preferred (only that they were not discriminated against). Thus we cannot attribute the enhanced survival of females mated to small males to the fact that those quality females had access to better males.

There may be an optimal body size, somewhere between the average for males and females, that maximizes autumn or winter survival in Pinyon Jays. Very small birds may not be able to store sufficient fat reserves, whereas very large birds may require larger absolute amounts to survive. Large females and small males would most closely approach this optimum.

Differential allocation of reproductive effort is relevant to the question of functional mate choice for body size. Pinyon Jays may allocate reproductive effort to maximize either self-survivorship or pair-survivorship (Burley 1985, 1986). For example, in a species with long-term pair bonds in which survival greatly affects lifetime reproductive success, a high-quality bird paired with another high-quality bird may attempt to maximize the survivorship of both partners. A high-quality individual paired with a low-quality bird may instead opt to extract as much parental investment as possible from the poorer quality mate and hope to outlive it. In the case of Pinyon Jays, members of a pair are more likely than expected by chance to have similar survivorship (Marzluff and Balda 1988a). This is consistent with the hypothesis that they allocate reproductive effort so as to maximize pair survivorship, assuming that disappearances of "widowed" birds are due to death, rather than dispersal. Regardless of which of the above strategies birds use, allocation of reproductive effort on the basis of mate quality could mean that survivorship is a *result* of a bird's desirability as a mate, and not the reverse. If researchers use survivorship to define mate quality, but birds allocate reproductive effort such that desirability affects survivorship, circularity results. By using mate-choice experiments to define quality, it is possible to avoid this problem.

Light-heavy pairs had sons with higher fecundities and greater survival. It is troubling that these light-heavy pairs do not appear to produce *more* sons than other pairs (we assume this means that they produce fewer offspring altogether). The possibility that Pinyon Jays might bias sex ratios based on parental weights is intriguing. If so, heavy-heavy pairs should produce more daughters and light-light pairs more sons, but we cannot test this prediction with our data.

Wild Pinyon Jays do not mate assortatively with respect to weight (Marzluff and Balda 1988b), probably because other traits not correlated with weight are also important indicators of mate quality. However, Pinyon Jays do appear to mate assortatively with respect to age (Marzluff and Balda 1988b). This pattern could occur by positive assortative mating with respect to age. Alternatively, a preference by both sexes for older, more experienced individuals could result in older, more desirable birds mating with one another, and so on (Burley 1983, Reid 1988). With very stable pairs, even random mating can result in age correlations between partners (Reid 1988). However, the randomization procedure used by Marzluff and Balda (1988b) eliminates this as a possibility in the case of Pinyon Jays. The best way to distinguish among the first two possibilities would be to conduct controlled mate-choice trials using birds of known ages. We expect that such trials would reveal a type preference for experienced individuals, although jays may actively avoid previously unsuccessful birds, regardless of their experience (Marzluff and Balda 1988a).

This is the first attempt we know of to understand avian mate choice by combining controlled laboratory experiments with long-term field data. Our approach enabled us to circumvent several of the methodological problems mentioned in the first section of the paper. Laboratory mate-choice experiments have allowed us to identify preferences for morphological and color traits. Nonrandom mate choice with respect to these traits occurs in the laboratory. We have found type preference for body weight in the laboratory without assortative mating in the field and assortative mating for age in the field that probably indicates type preference.

Comparison of the results of mate-choice experiments and data on male dominance showed that male dominance does not override or mask female choice. It also appeared that female and male choice operated simultaneously. We have avoided the complication of territory quality by choosing a species that does not defend a territory.

We have attempted to determine whether body size is a functional trait (i.e. whether males gain by mating with heavy females). Although the data suggest that there may be a survival advantage to males mated to heavy females, it is not clear whether that advantage is actually conferred by the male's mate or is a quality intrinsic to the male himself.

We have not attempted to determine whether feather color, important in female choice, is an aesthetic or functional trait. To look for a relationship between reproductive success and feather color would involve further fieldwork. Laboratory experiments using artificial aesthetic markers (Burley 1986) would also be necessary to determine potential for mate choice for aesthetic traits.

Although we have learned much about Pinyon Jay mate choice, there are still many gaps in our understanding. One difficulty with combining results of two separate studies is that we chose to investigate different traits. If the experiments had been conducted before the fieldwork, feather brightness could have been measured in the field and related to reproductive histories.

Sample sizes for lifetime reproductive success are small, as with many long-term studies. This is perhaps the most difficult aspect of an investigation of functional mate choice. However, for ornithologists who have such data available, they may be combined with choice experiments to offer potentially important insights.

Clearly, the study of avian mate choice is complicated and requires careful thought and planning. Our hope is that other researchers who study birds will profit from the successes, as well as the shortcomings, of this study.

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