DOMINANCE, AGE, AND REPRODUCTIVE SUCCESS IN A COMPLEX SOCIETY: A LONG-TERM STUDY OF THE MEXICAN JAY

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ABSTRACT.—Observations of mate guarding by males and robbing of nest material by females suggest the hypothesis that dominance should be related to reproductive success in the Mexican Jay (*Aphelocoma ultramarina*). We analyzed the probability of successful reproduction in this plural-breeding, group-territorial species with respect to variation in social rank, sex, age, flock territory, and year. We examined the correlates of dominance rank at two stages of nesting, early (before and during laying) and late (after laying). The correlates of rank differed between the sexes and nesting stages. In the early or prelaying stage, success in getting a mate and initiating laying was correlated with rank in males but not in females, and with age in both females and males. In the late stage, given that a bird had a nest with eggs, fledging success was not significantly related to rank overall. In females, however, a significant interaction was found between rank and age such that top rank was associated with greater success in older but not younger females. These effects of dominance at two stages of the nesting cycle (i.e. before and after egg laying) are consistent with the mate-guarding behavior of males and the nest-robbing behavior of females during nesting. *Received 30 January 1996, accepted 19 December 1996.*

LONG-TERM STUDIES of individual behavior are useful for understanding annual and lifetime reproductive success and are central to modern avian population biology (Blondel et al. 1990, Perrins et al. 1991). Studies of intragroup dominance have clarified the causation of reproductive success in a variety of avian species (Clutton-Brock 1988, Newton 1989). Observations of mate guarding by males and robbing of nest material by females (Brown 1963b, Trail et al. 1981) suggest the hypothesis that dominance should be related to reproduction in the Mexican Jay (*Aphelocoma ultramarina*). The goal of this study is to begin an assessment of the importance of intragroup dominance for individual annual reproductive success in this species.

The Mexican Jay is well suited for such studies. Most individuals live year-round in the same social group and the same territory (Brown 1963b, 1994) and come readily to bait, where dominance interactions may be observed. Unlike most avian species with helpers (Skutch 1935, 1961), the Mexican Jay has more than one

breeding female per group, a situation that is known as "plural" breeding (in contrast to singular breeding, in which only one female breeds in a territory or group; Brown 1978). The mating system of the Mexican Jay includes monogamy, polygyny, and polygynandry. Plural breeding provides an opportunity to study dominance relationships among breeders within the same group and their statistical association with the probability of breeding success.

Plural breeding is nearly universal in the population of Mexican Jays that we studied. In 179 group-years (1969 to 1994), group sizes in May ranged from 4 to 22 (Brown and Brown 1985; Brown 1994, unpubl. data). Average group sizes have varied across years from 7.6 to 13.3. The number of females per group that attempted nesting ranged from zero in a drought year to five. There were two or more nesting females in 106 of 124 (1975 to 1991) group-years. Successful nesting of two or more females in the same group has occurred in every year and in every flock (Brown 1985a, unpubl. data).

Information about dominance relative to fitness in plural breeders is sparse. There are few territorial, plural-breeding species in the first place, and for most of them no information exists about reproductive success in relation to social rank (based on behavioral data) determined prior to the breeding season. Ideally, dominance rank should be assessed independently of

breeding success before breeding begins. Perhaps the simplest *a priori* prediction is that the dominant bird (within each sex) should have higher reproductive success than its subordinates. In a more general form, reproductive success would be related to dominance rank at several or all ranks.

In this paper we examine components of age-specific annual reproductive success in each sex in relation to dominance rank and variance among territories and years. Our study is unique in its inclusion of many group-years of data and in its multivariate analysis, enabling estimation of the relative importance of age and rank within each sex while controlling for effects of year and flock. In future papers we plan to examine other components of fitness and to reach a more comprehensive evaluation of the role of dominance in this plural-breeding species.

METHODS

The population under study was located in the Chiricahua Mountains of southeastern Arizona, at the Southwestern Research Station of the American Museum of Natural History. The population was color-banded and observed every year, 1969 through 1995. Consequently, the histories of many individuals were known, allowing their ages to be determined accurately during the years of this study (1979 to 1994). During this period, the population varied in size between 63 and 141 jays. The birds lived in nine flocks, each occupying a stable group territory that varied little in location and size from year to year. The variable, "flock," allowed us to analyze variance among these flocks. Each flock lived on the same territory each year. Nearly all nestlings and older immigrants were banded each year, so the ages of most birds were known precisely. Further details on this population are available elsewhere (Brown and Brown 1990, Brown 1994).

We observed 117,169 dominance interactions over 15 years (1979 to 1994, except 1992 when no dominance observations were made) involving 1,279 bird-years and 102 group-years. Observations were made in January, February, and early March. In preparation for observations the observer put out sunflower seeds and then blew a whistle to call in the jays. Little or no food was left at the end of the observations, and the birds were not otherwise provisioned by us. Six of the territories were uninhabited by people, and three territories were inhabited by a few people in winter. We requested the local residents not to feed the jays, but some people disregarded our requests. Flock sizes ranged from 5 to 23 birds. The results of interactions were spoken into a tape recorder in the field, played

back in the lab, and transcribed on paper. The data were then entered into a dominance matrix following the procedure of Brown (1975:86), which attempts to place the members of a group in the order that maximizes linearity (or transitivity) in the rank order and minimizes uncertainty in the case of nonlinear relationships. Altogether there were 7,418 dyads with an average of 15.8 interactions per dyad. For the analyses in this paper, birds were ranked within their sex based on the ranks for the entire flock. Our field methods and other results are described more fully elsewhere (Craig et al. 1982, Barkan et al. 1986).

We first created a data set that had a record of dominance rank for each color-banded individual recorded in each flock-hierarchy each year. Some individuals (28 cases) occurred in more than one flock-hierarchy in one year. For these "double memberships" we kept the record that was in the same flock in which that individual lived during the subsequent breeding season of the same year and eliminated the other record. If the individual was not recorded during the breeding season of the same year, we chose the record that had the largest number of interactions and eliminated the others. Thus, in any one year no individual appeared more than once in the data set used for this analysis. Each record also contained information about the individual (sex, age, past history) and its reproductive success in the same calendar year.

Most birds were banded initially as nestlings or at an age (≤ 2 years) when age could be determined reliably. Jays in their first two years were assigned an age using the methods of Pitelka (1945), which we have confirmed with birds banded as nestlings and trapped subsequently. A few birds were age three or older when initially banded (5–16% in different years). These were assigned the age of three at the time of banding and used in this analysis. Females were birds known to have incubated, and males were birds that built nests with a known female.

This paper is about banded birds of breeding age, which is arbitrarily set to begin at three years of age. One-year-olds never bred on our study area even though they often had a high rank in winter (Barkan et al. 1986, unpubl. data). To include them in the analysis would have obscured the analysis of breeding-age birds. About one-fifth of the two-year-olds of each sex breed. They were excluded for similar reasons. Age at first breeding is summarized by sex in Brown (1994). Unsexed birds of breeding age (2–4%) were not used in our analyses, nor were unbanded birds.

We observed the reproductive success of each member of a flock by finding all the nests in each territory each year. For each nest we determined the parents from behavioral observations. The mother was the bird that incubated the eggs and brooded the young. The putative father was the male that guarded the mother just before eggs were laid. We recorded a variety of nest variables including its most advanced stage (i.e. no eggs, eggs, nestlings, or fledglings). The

breeding success of each member of the winter hierarchy was estimated from these nest records.

We determined success at two stages of nest development. In the first, which reflects success in obtaining a mate, the criterion was the presence of eggs in any nest of the individual in that year. The presence of eggs was regarded as proof of having mated. Males or females with a nest but no eggs were not regarded as having a mate (some males build an incomplete nest, attempting to attract females, but are not successful). The second stage, which reflects the care of eggs and nestlings, was determined at the time of fledging, which is roughly 25 days of age.

Mexican Jays tend to be monogamous in a given year in that typically a single pair builds a nest and only the female builder incubates. Studies with allozymes (Bowen et al. 1995) and DNA microsatellites (Li and Brown unpubl. data) have not revealed any cases of conspecific brood parasitism or joint nesting, so behavioral observations are a reasonable estimate of female reproductive success. For males the picture is complicated. Extrapair paternity has been found for about 40% of broods and 25% of young in the population (Bowen et al. 1995, Li and Brown unpubl. data). The role of dominance in extrapair fertilizations is under study, but preliminary indications are that dominants are likely to achieve more fertilizations, and subordinates fewer, than behavioral observations reveal. Nevertheless, behavioral observations of social pairing do seem to be useful for males, and they constitute the data that are analyzed in this paper. Our criterion of success was conservative in the sense that a male was considered successful if only one young fledged. Thus, even if some but not all of his brood were fertilized by others, he would still achieve success.

We used logistic regression to supply maximum-likelihood ANOVA tables and point estimates (CATMOD procedure in SAS). Significance level was set at $P \leq 0.05$. In some analyses, ages or ranks were combined to satisfy assumptions of the method.

RESULTS

Egg stage.—First, we examined the effects of sex and rank on the fraction of individuals that reach the egg stage in a given year using logistic regression and the levels of rank and age shown in Table 1. The interaction between sex and rank was significant ($P = 0.024$). Therefore, we examined each sex separately. Next, we considered the effect of age on reaching the egg stage and found that the interaction of age and rank was not significant in males ($P = 0.510$) or females ($P = 0.704$). Therefore, age and rank were examined together in each sex. In males there was a significant effect of rank ($P < 0.001$)

TABLE 1. Proportions of jays over all years (1979 to 1994) that successfully reached the egg stage as a function of rank and age (e.g. at age 3, 39% of 65 males reached the egg stage and 61% did not).

	Males		Females	
	n	Frequency	*n*	Frequency
Age (years)				
3	65	0.39	71	0.51
4	63	0.44	61	0.71
5 to 7	149	0.55	129	0.67
≥8	132	0.64	92	0.79
Dominance rank				
1	94	0.80	81	0.72
2	91	0.58	85	0.69
3	77	0.42	74	0.65
4	57	0.40	51	0.71
5	42	0.45	32	0.59
≥6	48	0.38	30	0.60

but not age ($P = 0.222$). In females there was a significant effect of age ($P = 0.002$) but not rank ($P = 0.732$). Higher-ranking males and older females were more successful (Table 1).

Because there was considerable variation in the fraction of individuals that reached the egg stage among years (males: 0.42 to 0.69; females: 0.43 to 0.85) and among flocks or territories (males: 0.35 to 0.68; females: 0.53 to 0.90), we repeated the above analysis for each sex including these variables. Doing this permitted us to explore the effects of year of observation and flock, and also to sharpen the analysis for the other variables, age and rank. For males rank had a significant effect on reaching the egg stage ($P < 0.001$), along with age ($P = 0.018$) and flock ($P = 0.045$), but not year ($P = 0.194$). For females age had a strong effect ($P = 0.002$), along with flock ($P = 0.004$) and year ($P = 0.023$), but not rank ($P = 0.935$).

We examined the relative importance of the different levels of rank, age, flock, and year by an analysis of maximum-likelihood estimates of the regression parameters in the logistic regression, which correspond to slopes in a multiple regression. These provide estimates of the incremental effect of each age or rank from a logistic regression model. For example, was a particular rank or age more influential than others? The results, shown for age and rank in Table 2, reveal that rank 1 had a large positive effect for males (estimate = 1.26), whereas the other ranks had smaller and progressively more negative effects (values from 0.36 to −0.64), indicating a decrease in success in reaching the egg stage as

TABLE 2. Analysis of maximum-likelihood estimates for obtaining a nest and eggs in a given year for the model including age, rank, year, and flock. NA = not applicable for mathematical reasons.

	Males		Females	
	Estimate	SE	Estimate	SE
Intercept	−0.04	0.15	1.18	0.21
Age (years)				
3	−0.51	0.24	−0.78	0.25
4	−0.24	0.24	−0.08	0.27
5 to 7	0.13	0.19	0.04	0.20
≥8	0.63	NA	0.82	NA
Dominance rank				
1	1.26	0.27	0.17	0.27
2	0.36	0.22	0.08	0.26
3	−0.19	0.24	−0.13	0.26
4	−0.40	0.27	0.21	0.31
5	−0.39	0.30	−0.20	0.35
≥6	−0.64	NA	−0.12	NA

rank increased in number. For females rank had no effect on success. With regard to age, the youngest age considered, age 3, had a large negative effect (−0.78 in females, −0.51 in males), and the oldest ages had large positive estimates (0.82 in females, 0.63 in males). Older ages had progressively more positive effects, especially for the oldest females. These considerations led us to repeat the analysis using only two levels of rank, namely rank 1 vs. all others. The results were similar except that a significant interaction occurred between age and rank for males ($P = 0.030$; females $P = 0.072$). For males high rank was not sufficient to overcome the negative effect of young age (3–4 years), but in both categories of older males, rank–1 males did considerably better than lower-ranking ones (Table 3). In females the effect of rank was slight; the increase with age was apparent only for females below the dominant.

For the full analysis (Tables 1 and 2) there is an overall effect due to age (for females), espe-

cially for age 8+ years (summarized above). When we collapsed ranks to compare ranks 1 versus 2+, the effect of age was somewhat different, i.e. it held only for rank 2+ females. These results are consistent because there are many more females of rank 2+ than of rank 1. The overall effects are thus similar to those for females of rank 2+.

Fledging success.—Given that a bird had achieved the stage of having a nest with eggs, would its chances of raising young to fledging be influenced by dominance rank? For this analysis we first used the levels of rank, 1 to 5 and 6+. Because there was no significant interaction between sex and rank ($P = 0.675$), we would have analyzed the sexes together but did not because doing so would create artificially large sample sizes (success values of the mother and father at the same nest are not independent). The frequencies of success for rank and age are shown in Table 4 for each sex.

For males, the assumptions of logistic regression (no cells with all successes or all failures) forced us to combine age categories at the outset, leaving two age groups (i.e. 3–6 and 7+). Using six levels of rank (as in Table 4), we then found no significant effects of rank, age, and flock and a significant effect of year ($P = 0.018$).

Because of a large effect of the top-ranking male (maximum likelihood estimate of 0.62), we repeated the analysis using only two levels of rank, namely 1 and 2+ (Table 5). In this case, there were no significant effects of age and flock, but year was significant ($P = 0.020$). The P-value corresponding to rank, 0.058, was just above the criterion of 0.05, suggesting an effect due to males of rank 1.

For females, we began the analysis with five levels of rank (1, 2, 3, 4, 5+) and three levels of age (3–4, 5–7, and 8+). The only significant effect was year ($P = 0.011$). When we compared

TABLE 3. Proportion of each sex that obtained a mate with eggs, as a function of rank and age (lower ranks combined); n in parentheses.

	Age (years)			
Dominance rank	3 to 4	5 to 7	≥8	Total
		Males		
1	0.40 (10)	0.89 (35)	0.82 (49)	0.80 (94)
≥2	0.42 (118)	0.45 (114)	0.54 (83)	0.46 (315)
		Females		
1	0.71 (28)	0.75 (32)	0.67 (21)	0.72 (81)
≥2	0.57 (104)	0.64 (97)	0.83 (71)	0.66 (272)

TABLE 4. Frequency with which a parent jay had one or more nests that reached the stage of fledging, given that the parent had at least one nest with eggs in the same year. The numbers of males and females are not equal because for some nests one parent was either unknown or unbanded.

	Males		Females	
	n	Frequency[a]	n	Frequency
Age (years)				
3 to 6	107	0.59	135	0.57
≥ 7	113	0.63	103	0.60
Total	220	0.61	238	0.58
Dominance rank				
1	75	0.67	58	0.67
2	53	0.59	59	0.51
3	32	0.47	48	0.60
4	23	0.61	36	0.56
5	19	0.63	19	0.63
≥6	18	0.67	18	0.50
Total	220	0.61	238	0.58

[a] Proportion of n that fledged young that year.

the top-ranking females versus all others, there was a significant interaction with rank and age ($P = 0.034$), precluding simple inference about rank and age. The pattern in Table 5 for females mimics the pattern depicted in Table 3 for males; i.e. at young ages, high rank was not sufficient to overcome the negative effect of young age, but in both categories of older ages, rank–1 females did considerably better than lower-ranking ones (two-sided test of proportions, $z = 2.75$, $P = 0.006$).

DISCUSSION

Our primary objective was to evaluate the importance of dominance relations for the likelihood of successful reproduction each year in the Mexican Jay. We suspected that the disruptive visits of birds to nests of others that we had reported earlier (Brown 1963b, Trail et al. 1981)

might reflect underlying dominance relationships in the social group. Also, after watching individually color-banded Mexican Jays in the early years of this long-term study, we suspected that the success of males in guarding females might also be better understood using the general concept of dominance relationships. Therefore, we initiated studies of dominance in 1979 (Barkan et al. 1986).

After a few years we were able to demonstrate advantages of high rank in competition for food (Craig et al. 1982), but it was more difficult to evaluate general demographic correlates of rank. Although after a few years we could have shown that dominance rank was correlated with reproductive success within each of a few flocks, we realized that such data would not allow generalization across flocks and years because important variation existed among flocks and years. Furthermore, the statistical effects of rank could not be properly estimated without considering age, which was known to be correlated with reproduction in this species. Therefore, we decided to accumulate more data before performing the present analysis. We believe that our sample of 102 group-years from 1979 to 1994 allows us to generalize about the role of dominance in reproductive success.

Our finding that mating success was statistically associated with dominance in males helps to explain the conspicuous aggressive competition among males within flocks for females. Competition among males may be overt or covert. Overt competition occurs when a dominant male takes over a fertile female from her previous mate and guards her. We assigned parentage in such cases to the male that guarded the female just before laying, not necessarily to the nest builder. Covert competition took the form of extrapair copulations. We have not seen enough extrapair copulations to warrant discus-

TABLE 5. Proportion of each sex that fledged ≥ 1 young given a nest with eggs, as a function of rank and age (lower ranks combined); n in parentheses.

	Age (years)			
Dominance rank	3 to 4	5 to 7	≥8	Total
	Males			
1	1.00 (4)	0.61 (31)	0.68 (40)	0.68 (75)
≥2	0.45 (49)	0.59 (51)	0.71 (45)	0.58 (145)
	Females			
1	0.40 (20)	0.88 (24)	0.71 (14)	0.67 (58)
≥2	0.53 (59)	0.55 (62)	0.59 (59)	0.55 (180)

sion here, and the relationship between ex-trapair fertilizations and dominance is under study using molecular methods (Li and Brown unpubl. data).

The correlation of pairing success and egg lay-ing with age in females was surprising in its ex-tent. Of particular interest is the relatively large maximum-likelihood estimate (Table 2) for fe-males of age 8 and older. It is well known that reproductive success improves with age in rela-tively young birds, such as the Galapagos Mock-ingbird (*Nesomimus parvulus*; Curry and Grant 1989), but to find improvement at ages of 8 and above is unprecedented in a passerine.

We were also surprised at first by the lack of a statistically significant overall effect of rank in females in early or late stages. Certain indi-vidual females were conspicuous in their inter-ference in the nests of others, and we expected this would show up in our overall analysis. Dominant females accompanied by their males sometimes usurped a nest from another pair, es-pecially if their own nest failed before egg lay-ing. There also was a high frequency of robbery of nest lining (Brown 1963b) that we now know was done mainly by dominants from subordi-nates (pers. obs.). In addition, dominants of both sexes often stand on the nests of subordinates and seem to harass them before, during, and af-ter egg laying by the dominant. This sometimes caused subordinates to renest elsewhere in the same territory or to cease nesting altogether. In these activities the female seemed to take the leading role. In short, a variety of aggressive and harassing behaviors by dominant females, often accompanied by their males, appeared to reduce the nesting success of subordinates. These ef-fects of harassment on subordinate females were sometimes ameliorated by the fact that the lat-ter were able to fledge young anyway by per-sisting and waiting until after the dominant had settled down to incubation. Those individual dominant females that were known to harass subordinate females that were trying to nest were in the older age categories. In these older ages, the top-ranking females were more likely to fledge young in a given year (Table 5), giv-ing rise to a significant statistical interaction be-tween age and sex.

In studies such as ours, the question often arises as to whether dominance in one context or season carries over to dominance in another. We gathered data on dominance from mid-January through mid-March. Thus, our observa-tion period overlapped with the period of pair-ing and construction of nests, which can begin in late February. Except for reproduction, deaths, and occasional movements of individuals among flocks, the composition of flocks of Mexican Jays does not change through the year (Brown 1963b, Brown 1994), and the same individuals are present on the same territories year-round. Simi-larly, dominance relationships between indi-viduals are stable from month to month and even year to year (unpubl. data). Furthermore, our ob-servations of dominance interactions among fe-males at nests and among males guarding fe-males (unpubl. data) were in good agreement with those observed at feeding stations.

Formally, we report in this paper statistical re-lationships between two sets of data on the same individuals. However, our observations show that these relationships are biologically caused by the aggressive behavior of males competing for females and females competing over nests. There is no evidence to suggest a different bio-logical causation.

Comparing the early and late stage of nesting, it is interesting that the effects of yearly varia-tion on nesting success were evident mainly in the post-laying stage. This may be because cli-matic variables, which are known to affect re-production in the Mexican Jay (Brown and Li 1996), have a relatively larger effect on rearing young than on obtaining a mate.

A correlation between dominance rank and reproductive success may be expected in jays for several reasons. The most straightforward is complete suppression of breeding by subordi-nates in the dominion (Brown 1963a) or territory (Woolfenden and Fitzpatrick 1977), as in the Steller's Jay (*Cyanocitta stelleri*) and Florida Scrub-Jay (*Aphelocoma coerulescens*), respectively. In contrast, in the Pinyon Jay (*Gymnorhinus cya-nocephalus*), which lacks a traditional breeding territory, the cause of superior reproductive suc-cess of dominants may be more subtle, because subordinates are not prevented from breeding on the home range (Marzluff and Balda 1992). The superiority of dominants in these more-tolerant species might be due partly to priority of access to contested resources and partly to su-perior vigor and disease resistance.

In the first systematic study of the fitness cor-relates of status in a plural-breeding territorial species, a small but significant advantage was observed for the last female to begin laying in the joint-nesting Groove-billed Ani (*Crotophaga*

sulcirostris; Koford et al. 1990). If being last is indicative of higher social status, then these results are similar to ours. The meaning of order of initiation of laying in respect to social status generally, however, remains to be clarified.

Three other studies on plural-breeding, territorial species have studied correlates of dominance. In the Galapagos Mockingbird, dominance was examined in relation to reproductive success using estimates of dominance that were derived independently from behavior at the nest (Curry 1988, Curry and Grant 1991). As in the Mexican Jay, dominant males obtained females more frequently than did subordinate males, at least in dry years. Similarly, dominants harassed subordinates at and away from nests. As in many singular breeders, age was closely linked to rank. In the Mexican Jay, however, age was not closely tied to dominance rank in the first year of life (Barkan et al. 1986). In the Dunnock (*Prunella modularis*), which often is polyandrous, the alpha male had slightly higher reproductive success than the beta male (Burke et al. 1989). One report rejects an association between dominance and reproductive success in a plural-breeding bird. In the Pukeko (*Porphyrio porphyrio melanotus*), Lambert et al (1994) studied two groups with more than one male. In one group, the dominant male sired no offspring despite being involved in 39% of the copulations, and the lowest-ranked of three males sired the most offspring. In this population, however, inbreeding is intense, and irregularities of sperm are possible. In any case, two groups in one year do not provide enough data on this matter for generalization.

In each of the above cases, the average difference in reproductive success between dominant and subordinate birds (if any) was not large. This result is consistent with the observed regular occurrence of plural breeding in these species and with the logic that subordinates would not regularly nest in the presence of dominants if such attempts were generally unsuccessful. These relationships agree with various models that represent conflict between dominants and subordinates (e.g. Vehrencamp 1983, Brown 1985b, Koenig et al. 1992), but they are not confirmation of the models.

Our study has provided new insights into the complex social system of the Mexican Jay and helped us to understand individual variation in reproductive success that we can directly observe. We can now state that there is a general advantage of dominance in males and that it arises primarily in the prelaying period, rather than after laying. Because the males we have seen mate guarding and taking over females from other males were the top-ranking males in their groups, this behavior very likely mediates the reproductive advantage of dominant males. The situation is different in females, however. A strong relationship with age, especially in older females, was revealed. A significant age-rank interaction in females is consistent with the harassing behavior that we have observed frequently among top-ranking females.

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