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INDIVIDUAL CONTRIBUTIONS TO COOPERATIVE NEST CARE IN THE ACORN WOODPECKER[1]

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Abstract. Acorn Woodpeckers (*Melanerpes formicivorus*) are cooperative breeders that live in permanently territorial family groups of two to 15 individuals. Groups typically contain one to four breeding males, one to two breeding females, and zero to 10 nonbreeding group offspring. In this paper we examine how reproductive status, sex, age, and group size affect individual contributions to four aspects of cooperative nest care: incubation of eggs, brooding of nestlings, feeding of nestlings, and nest sanitation. Breeding Acorn Woodpeckers make significantly greater investments in caring for eggs and nestlings than do nonbreeders. Furthermore, the differences between breeders and nonbreeders are attributable to differences in reproductive status per se and not age; analysis of variance reveals that age itself has no significant effect on any aspect of nest-care behavior. For all aspects of nest care except nest sanitation and nocturnal incubation and brooding, females invest more heavily than do males. Although several measures of the parental behavior of breeders are negatively correlated with group size, these relationships are generally weak and nonsignificant. We conclude that (1) the greater contributions of breeders to nest care relate to their direct gametic investment in offspring and to the frequent dispersal forays of nonbreeders, (2) first-year Acorn Woodpeckers are just as capable as older birds of comparable sex and breeding status in caring for eggs and nestlings, and (3) the burden of parental care on breeders is not substantially reduced by the presence of helpers.

Key words: Acorn Woodpecker; Melanerpes formicivorus; *cooperative breeding; helping behavior; parental care; alloparental care; group size.*

INTRODUCTION

Cooperative breeding in birds is defined by the presence of more than a single male-female pair cooperatively rearing the young of a single nest (Emlen 1984, Brown 1987). This phenomenon is of interest to evolutionary biologists because the rearing of nondescendant young (helping behavior) is generally difficult to explain via the classical concepts of individual natural selection. Despite considerable recent research, the evolutionary origins of helping behavior remain controversial and, in many cases, largely enigmatic (Brown 1987; Jamieson 1989; Ligon and Stacey 1989; Koenig and Mumme, in press).

The controversy surrounding the origins and functions of helping behavior focuses primarily on three questions: (1) Is helping behavior an evolved adaptation or merely an unselected consequence of group living (e.g., Jamieson and Craig 1987, Jamieson 1989)? (2) Does helping behavior provide significant adaptive benefits to the helper by increasing the indirect (kin) component of its inclusive fitness (e.g., Brown and Brown 1981, Clark 1984, Curry 1988, Emlen and Wrege 1988)? (3) Does helping behavior benefit helpers primarily by increasing their direct (individual) fitness (e.g., Woolfenden and Fitzpatrick 1978, Ligon 1983)? Data on the patterns of cooperative nest care, particularly the provisioning of dependent young, have been used frequently by researchers in developing and testing these hypotheses (e.g., Brown et al. 1978, Stallcup and Woolfenden 1978, Emlen and Wrege 1988, Jamieson 1988, Clark 1989).

The Acorn Woodpecker (*Melanerpes formicivorus*) is a cooperatively breeding bird whose complex social organization makes its parental and alloparental (helping) behavior of particular interest. In California, this species lives in permanently territorial family groups of two to 15 individuals. Group members participate in several forms of communal behavior, including

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storing acorns in centrally located storage trees (granaries) and cooperatively rearing the young of a single nest. Groups typically contain one to four breeding males, one to two breeding females, and zero to 10 nonbreeding group offspring of past reproductive seasons (MacRoberts and MacRoberts 1976, Koenig et al. 1984, Stacey and Koenig 1984, Koenig and Mumme 1987).

Previous research on this species has shown that all group members usually participate in at least some aspects of nest care (MacRoberts and MacRoberts 1976, Joste et al. 1982, Koenig et al. 1983). In this paper, we extend these earlier works and examine in detail the individual contributions made by breeding and nonbreeding Acorn Woodpeckers to four aspects of cooperative nest care: incubation of eggs, brooding of nestlings, feeding of nestlings, and nest sanitation. Our primary objective is to examine how individual contributions to nest care vary with reproductive status, sex, age, and group size. Unfortunately, because of the complex breeding structure within Acorn Woodpecker groups, parentage and relatedness within groups have yet to be determined with any degree of certainty (Joste et al. 1982, 1985; Mumme et al. 1985; Koenig and Mumme 1987). An analysis of the effects of relatedness on patterns of nest care therefore must be deferred until a later time.

METHODS

The study was conducted at Hastings Natural History Reservation, Monterey County, California, where a color-banded population of Acorn Woodpeckers has been under continuous observation since 1971 (MacRoberts and MacRoberts 1976, Koenig and Mumme 1987).

Data on individual contributions of Acorn Woodpeckers to nest care were collected at 59 different woodpecker nests between 1979 and 1982. A total of 765 individual nest watches of 1- to 4-hr duration were performed at these nests. Mean group size was 4.2 birds (range = 2–11). We attempted to obtain representative samples of nest-care behavior by conducting nest watches at all times of the day throughout the 11-day incubation period and the 32-day nestling period. Most nest watches were 3 hr in length, and a total sample of 2,198 hr of behavioral data was available for analysis. Because we did not consider separate nest watches conducted on the same nest to be independent samples of an individual's behavior (Mumme 1984), all data collected on the same individual at a single nest were grouped together and treated as a single sample prior to statistical analysis.

During the 11-day incubation period, 678 hr of daytime incubation data were collected during 234 separate nest watches at 51 nests. Forty-three of these nests were attended by groups larger than a single breeding pair. At least 8 hr of daytime incubation data were collected at each of these 51 nests. As in most species of woodpeckers (e.g., Red-cockaded Woodpeckers *Picoides borealis*; Lennartz and Harlow 1979), nocturnal incubation is performed almost exclusively by breeding males and is discussed elsewhere (Koenig et al. 1983).

After hatching, Acorn Woodpecker nestlings are brooded sporadically until they are about 12 days old (Mumme 1984). A total of 674 hr of data on individual contributions to brooding of young was gathered during 234 separate nest watches. A minimum of 8 hr of data was obtained at each of the 45 nests used in the analysis of brooding behavior. Five of the 45 nests were attended by only a single breeding pair that lacked breeding or nonbreeding helpers.

Data on adult contributions to the feeding of nestlings and removal of fecal matter from nests were collected from 50 nests during 531 separate nest watches totalling 1,520 hr in duration. Observations were conducted throughout the 32-day nestling period, and at least 8 hr of data were collected at each nest used in these analyses. Data were obtained from five nests attended by only a single breeding pair; 45 nests were attended by cooperative groups.

Methods of data collection were similar to those described by Joste et al. (1982). Nest watches were conducted with tripod-mounted 20–45× spotting scopes from observation blinds, or from vantage points far enough away from nests so that the behavior of birds was not affected. During the incubation and brooding periods, we recorded the amount of time individual birds spent inside the nest cavity. While inside the nest, Acorn Woodpeckers frequently climb to the nest entrance and look out. Because birds looking out of the nest cavity are not actively warming eggs or young, time spent looking out of the nest cavity was subtracted from the total time in the nest cavity to better reflect the actual time individuals spent incubating eggs or brooding young. For both incubation and brooding, the data for individual birds were summarized as percent at-

TABLE 1. Individual contributions of Acorn Woodpeckers to cooperative nest care in relation to reproductive status, sex, and age. Values are $\bar{x} \pm$ SD (n).

Age (years)	Breeders		Nonbreeders	
	Males	Females	Males	Females
Incubation (% attendance)				
1	11.6 ± 14.1 (3)	34.0 ± 16.5 (4)	3.4 ± 4.8 (25)	4.7 ± 7.2 (18)
2+	21.6 ± 13.7 (79)	26.0 ± 14.6 (46)	4.6 ± 7.8 (7)	1.1 ± 1.6 (3)
Brooding (% attendance)				
1	13.9 ± 12.0 (3)	11.6 ± 14.2 (4)	2.1 ± 3.8 (23)	10.2 ± 10.1 (16)
2+	13.6 ± 8.9 (73)	17.7 ± 11.0 (41)	3.5 ± 5.6 (7)	8.0 ± 13.9 (3)
Hourly feeding rate (per nest)				
1	4.7 ± 3.0 (3)	4.3 ± 2.6 (4)	2.1 ± 2.2 (28)	2.3 ± 1.7 (17)
2+	3.0 ± 2.1 (86)	4.4 ± 2.7 (46)	1.6 ± 1.4 (7)	2.4 ± 2.8 (5)
Hourly feeding rate (per nestling)				
1	1.3 ± 0.7 (3)	1.0 ± 0.4 (4)	0.6 ± 0.6 (28)	0.8 ± 0.5 (17)
2+	0.9 ± 0.6 (86)	1.3 ± 1.0 (46)	0.4 ± 0.4 (7)	0.7 ± 0.7 (5)
Fecal sacs removed (% of feedings)				
1	3.9 ± 6.7 (3)	0.3 ± 0.4 (4)	1.4 ± 3.5 (28)	1.2 ± 2.7 (17)
2+	9.0 ± 11.1 (86)	1.5 ± 2.0 (46)	3.0 ± 7.1 (7)	0.0 ± 0.0 (5)

tendance (percentage of total observation time that each bird was inside the nest cavity and not looking out).

After the eggs hatched, we recorded all feeding visits made to the nest by individual group members. We also estimated the relative amount of food delivered to the nestlings on each visit using the method of Joste et al. (1982), modified from Stallcup and Woolfenden (1978). Although estimates of the size of food items delivered to nestlings have proved to be important in analyses of nest care in other cooperatively breeding birds (e.g., Stallcup and Woolfenden 1978, Hunter 1987), we found virtually no interindividual variation in the amount of food delivered to nestlings per feeding visit (Joste et al. 1982, Mumme 1984). We thus used the total number of feeding visits made to the nest per hour as the measure of individual contributions to the feeding of nestlings.

Nest-sanitation behavior was documented by recording the percentage of an individual's total feeding visits following which it removed fecal matter from the nest cavity. Nest contents, hatching dates, and brood size were determined by regular nest inspections. Group size and composition were determined from periodic censuses (Koenig and Mumme 1987). Acorn Woodpeckers were classified as potential breeders or nonbreeders based on criteria discussed in detail by Koenig et al. (1984) and Koenig and Mumme (1987, p. 25–28). A few individuals of unknown age or of ambiguous breeding status were excluded from analyses that required these data. Incubation, brooding, and nest-sanitation data were summarized as percentages, but converted to proportions and normalized by the arcsine transformation (Sokal and Rohlf 1981) prior to statistical analysis.

RESULTS

Contributions of Acorn Woodpeckers to cooperative nest care are summarized in relation to sex, breeding status, and age in Table 1. Despite

TABLE 2. Results of a three-way analysis of variance of the effect of sex (male vs. female), reproductive status (breeder vs. nonbreeder), and age (1 year old vs. older) on individual contributions to cooperative nest care in the Acorn Woodpecker, based on data summarized in Table 1. Percentages (in parentheses) reflect the relative contributions of each factor to the total sum-of-squares.

	F-values[1]			
	Sex	Status	Age	df
Incubation (% attendance)[2]	2.25 (0.7%)	48.96** (16.0%)	0.00 (0.0%)	1, 177
Brooding (% attendance)[2]	9.50** (4.1%)	19.63** (8.4%)	0.37 (0.1%)	1, 162
Hourly feeding rate (per nest)	9.46** (4.4%)	10.53** (4.9%)	0.77 (0.2%)	1, 188
Hourly feeding rate (per nestling)	9.09** (4.2%)	8.39** (3.9%)	0.18 (0.0%)	1, 188
Fecal sacs removed (% of feedings)[2]	23.17** (9.4%)	6.33* (2.6%)	0.79 (0.3%)	1, 188

[1] * $P < 0.05$; ** $P < 0.01$; Two-way and three-way interaction terms were nonsignificant in all five ANOVAs.
[2] Based on arcsine-transformed proportional data (Sokal and Rohlf 1981).

considerable interindividual variability (Tables 1, 2), breeders generally make greater investments in nest care than do nonbreeders (Table 1, Figs. 1–3). In addition, females generally invest more in nest care than do males (Figs. 1, 2); the only aspect of cooperative nest care in which males play a greater role than females is nest sanitation (Fig. 3). A three-way analysis of variance that employs sex, age, and breeding status as factors indicates that except for the nonsignificant effect of sex on incubation attendance, sex and breeding status significantly influence all aspects of nest care (Table 2).

The data presented in Table 1 suggest that age has no consistent influence on patterns of nest care: the contributions made by first-year birds are generally comparable to those made by older birds of equivalent sex and reproductive status (Table 1). This conclusion is further supported by an analysis of variance that reveals that age has no significant effect on any aspect of nest care (Table 2).

The influence of group size and group composition on the nest-care behavior of breeders is summarized in Table 3. Breeder contributions to incubation of eggs, brooding of nestlings, and feeding of nestlings are generally negatively correlated with group size and the total number of breeders in the group (Table 3). This suggests that the presence of additional group members may "lighten the load" on individual breeders (Figs. 4, 5). These negative relationships, however, are generally weak, and only a few of the correlations (those relating to incubation and brooding behavior) shown in Table 3 are statistically significant. Thus, the presence of additional group members appears to reduce only slightly the individual contributions that breeders make to nest care.

DISCUSSION

EFFECTS OF REPRODUCTIVE STATUS AND SEX

Breeding Acorn Woodpeckers make significantly greater contributions to nest care than do nonbreeding nest helpers. This result holds for all aspects of nest care measured during this study, including incubation of eggs, brooding of nestlings, feeding of nestlings, and nest sanitation (Table 1, Figs. 1–3). Furthermore, the differences between breeders and nonbreeders in nest-care behavior appear to be attributable to differences in reproductive status per se and not to age. Even though most breeders in this study were 2 years old or older and most nonbreeders were first-year birds, age itself had no significant effect on the patterns of nest care (Tables 1, 2).

Two nonexclusive hypotheses can be suggested to explain why breeders contribute more to cooperative nest care than do nonbreeders: (1) Acorn Woodpeckers provide care for eggs and young in proportion to the probability of their direct gametic contribution and overall opportunity of parentage (see Stacey 1979, Joste et al. 1982, Hannon et al. 1985). Thus, breeders, with relatively high opportunity for parentage, make considerable investments in nest care from which they profit directly. In contrast, the benefits nonbreeders receive from nest care, if any, are tenuous and primarily indirect (Koenig and Mumme

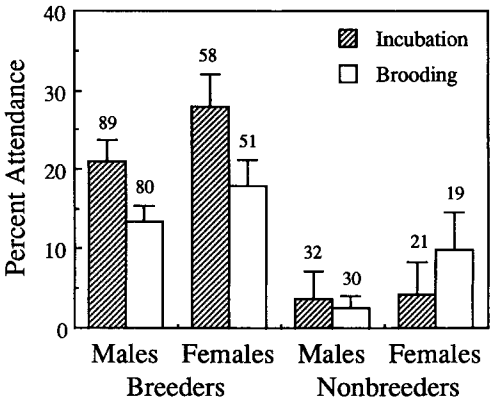

FIGURE 1. Individual contributions of Acorn Woodpeckers to incubation of eggs and brooding of young in relation to reproductive status and sex. Means of incubation or brooding attendance, upper 95% confidence limits, and sample sizes are shown for birds of each category.

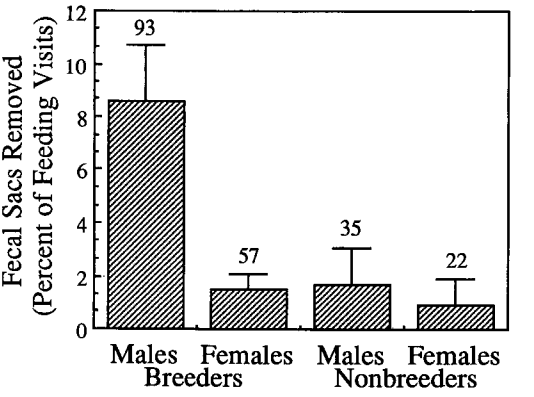

FIGURE 3. Individual contributions of Acorn Woodpeckers to removal of fecal sacs from nests in relation to reproductive status. The mean percentage of feeding visits after which fecal sacs were removed, upper 95% confidence limits, and sample sizes are shown for birds of each category.

1987). Although this hypothesis has been criticized by Craig and Jamieson (1985), Burke et al. (1989) have demonstrated that nest care and parentage are highly correlated in the cooperatively polyandrous Dunnock (*Prunella modularis*). (2) Nonbreeding Acorn Woodpeckers frequently engage in "dispersal forays" in which they wander over wide areas searching for breeding vacancies on other territories (Mumme and de Queiroz 1985; P. N. Hooge, unpubl. data). Established breeders only rarely engage in such behavior. At Hastings Reservation, almost 85% of identified territorial intruders are nonbreeders (Mumme and de Queiroz 1985, p. 305–306), even though nonbreeders comprise only 39% of the population as a whole (Koenig and Mumme 1987, table 3.6). Because such dispersal forays are most frequent during the breeding season, nonbreeders spend less time on their territories and thus have fewer opportunities to provide care to eggs and young. Nonbreeders thus appear to subordinate their contributions to alloparental care in order to improve their chances of finding and securing a suitable breeding territory in an ecologically saturated population (Hannon et al. 1985, Koenig and Mumme 1987). This hypothesis may also explain, at least in part, why the contributions of nonbreeders are less than those of breeders for several other aspects of cooperative behavior, including maintenance of acorn storage facilities and intra- and interspecific territory defense (Mumme and de Quieroz 1985).

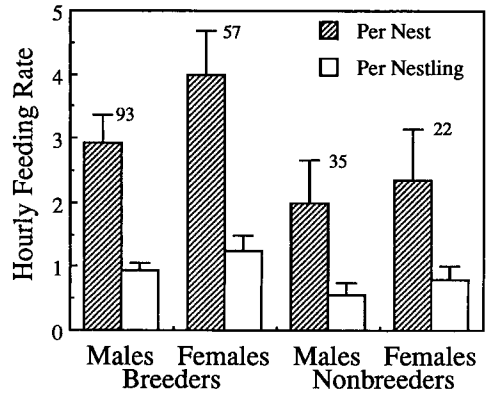

FIGURE 2. Individual contributions of Acorn Woodpeckers to feeding of nestlings in relation to reproductive status and sex. Means of per-nest and per-nestling feeding rates, upper 95% confidence limits, and sample sizes are shown for birds of each category.

Sexual differences in contributions to nest care in Acorn Woodpeckers are also pronounced. Compared to males, females make significantly greater investments in brooding and feeding nestlings (Figs. 1, 2), and slightly but not significantly greater contributions to incubation of eggs (Tables 1, 2). Although the ecological and phylogenetic factors that might be responsible for these sexual asymmetries are unclear (Koenig et al. 1983), greater female investment in incubation of eggs and brooding and feeding of nestlings

TABLE 3. Spearman's rank correlation coefficients between breeder contributions to nest care and group size and number of breeders.

	Sex	*n*	Group size	Number of breeders
Incubation (% attendance)	Males	89	−0.10	−0.25**
	Females	58	−0.27*	−0.13
Brooding (% attendance)	Males	80	−0.12	−0.13
	Females	51	−0.32*	−0.26*
Hourly feeding rate (per nest)	Males	93	−0.02	0.01
	Females	57	−0.02	0.02
Hourly feeding rate (per nestling)	Males	93	−0.13	−0.06
	Females	57	−0.18	−0.20
Fecal sacs removed (% of feedings)	Males	93	0.03	−0.02
	Females	57	0.10	0.13

* $P < 0.05$ (one-tailed).
** $P < 0.01$ (one-tailed).

may be a partial cause of the very high rate of nesting-season mortality among breeding females (Koenig and Mumme 1987, p. 183–186).

For two aspects of nest care, however, the contributions of males (particularly breeding males) are greater than those of females. These are nest sanitation (Tables 1, 2, Fig. 3) and nocturnal incubation and brooding (Koenig et al. 1983). Male-biased asymmetries in these aspects of nest care appear to be general among woodpeckers (e.g., Johnson 1947, Kendeigh 1952, Crockett and Hansley 1977, Lennartz and Harlow 1979) and thus probably reflect a phylogenetic feature of the family Picidae and not ecological factors unique to the Acorn Woodpecker or its cooperative social system (Koenig et al. 1983).

EFFECTS OF AGE: SKILL AND LEARNING

The ability of young birds to care for dependent offspring is the focus of two related hypotheses concerned with the evolution of delayed breeding and helping behavior in cooperatively breeding birds. First, young birds may delay their own reproduction because they lack the foraging skills necessary for nesting and raising young successfully. This proposal has been dubbed the "skill hypothesis" by Brown (1987). Second, naive nonbreeders may learn these skills by acting as helpers and performing alloparental care, thereby enhancing their ability to provision their own offspring later in life (Lawton and Guindon 1981). We will call this the "learning hypothesis."

Results reported here provide no direct support for either of these related hypotheses. Age of Acorn Woodpeckers has virtually no effect on the quality or quantity of nest care that they provide to eggs or nestlings (Tables 1, 2). First-year Acorn Woodpeckers appear to be just as effective as older individuals of equivalent sex and breeding status in incubating eggs, brooding nestlings, provisioning nestlings, and removing fecal matter.

Our results, however, do not completely reject the skill and learning hypotheses. Young Acorn Woodpeckers could lack other important skills (e.g., proficiency in territory defense) that are unrelated to nest-care behavior but nonetheless necessary for successful reproduction. In fact, one-year-old male breeders have significantly lower reproductive success than do older birds (W. D. Koenig and M. T. Stanback, unpubl. data), and these data are consistent with the skill and learning hypotheses. The data presented in this paper demonstrate only that no lack of proficiency is evident from the individual contributions that first-year birds make to cooperative nest care.

The skill and learning hypotheses have received mixed support in other studies of cooperatively breeding birds as well. For example, age and experience of helpers have been found to have a significant effect on helper contributions to care of young in the Scrub Jay (*Aphelocoma coerulescens*; Stallcup and Woolfenden 1978), Brown Jay (*Cyanocorax morio*; Lawton and Guindon 1981), White-winged Chough (*Corcorax melanorhamphos*; Heinsohn et al. 1988), and Bell Miner (*Manorina melanophrys*; Clark 1989), but not in the Grey-crowned Babbler (*Pomatostomus temporalis*; Brown et al. 1978) or White-fronted Bee-Eater (*Merops bullockoides*; Emlen and Wrege 1989). However, as discussed by Koenig and Mumme (in press), unequivocal tests of

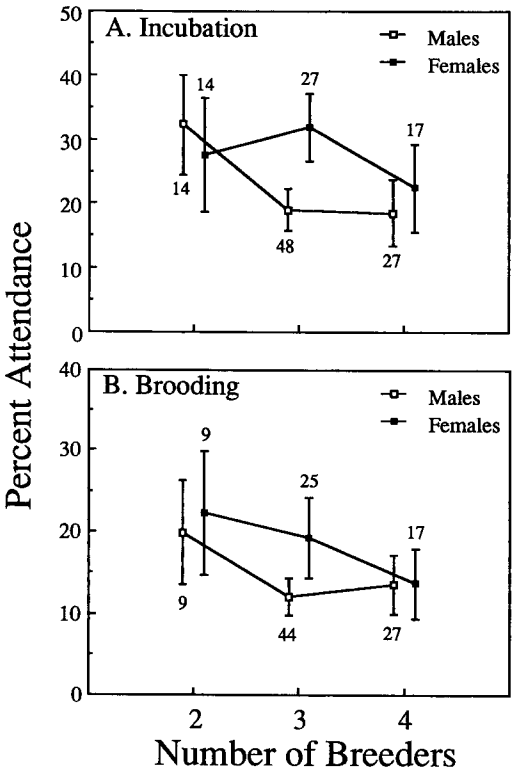

FIGURE 4. Individual contributions of breeding male and female Acorn Woodpeckers to (A) incubation of eggs and (B) brooding of young in relation to the total number of breeders present in the group. Means and 95% confidence limits of incubation or brooding attendance are shown.

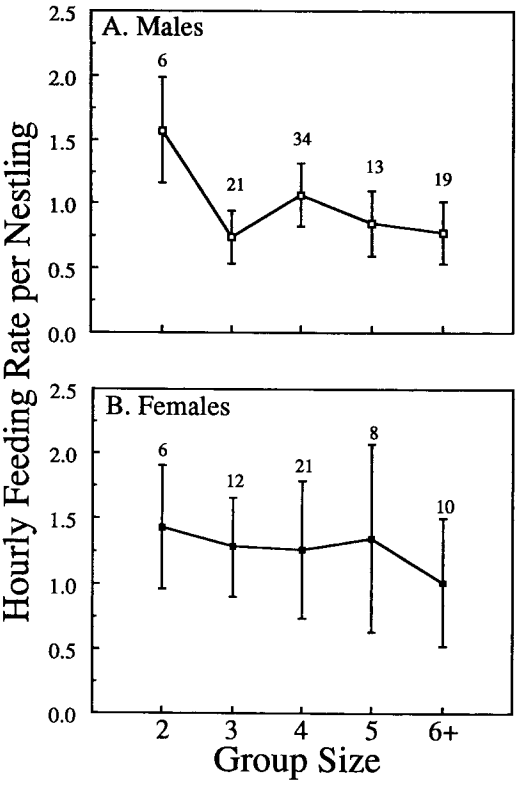

FIGURE 5. Individual contributions of breeding (A) male and (B) female Acorn Woodpeckers to feeding of nestlings in relation to total group size. Means and 95% confidence limits of hourly feeding rate per nestling are shown.

the skill and learning hypotheses are yet to be performed.

EFFECTS OF GROUP SIZE

In many cooperatively breeding birds, the alloparental behavior of helpers may allow breeders to reduce their levels of parental care (e.g., Brown et al. 1978, Lewis 1982, Rabenold 1984, Reyer 1984, Austad and Rabenold 1985, Sydeman 1989). This "lightening of the load" can benefit breeders by either promoting a higher incidence of renesting (e.g., Brown and Brown 1981, Lewis 1982) or by potentially increasing breeder survival and residual reproductive value (e.g., Reyer 1984, Mumme et al. 1989). Such cost sharing may be an important factor contributing to the evolution of group territoriality and helping behavior (Brown 1987), and could potentially explain why the annual survivorship of breeding male Acorn Woodpeckers increases dramatically with group size (Koenig and Mumme 1987).

In the Acorn Woodpecker, however, the presence of additional cobreeders and nonbreeding helpers appears to result in only modest reductions in the level of parental care performed by breeders (Table 3, Figs. 4, 5). Neither total group size nor the number of breeders was significantly negatively correlated with the provisioning rate of breeders, measured either on a per-nest or per-nestling basis (Table 3). This is consistent with data showing that both total provisioning rate and fledging success increase with group size in this species (Mumme 1984, Koenig and Mumme 1987).

The only significant negative relationships that we found between group size and breeder contributions to nest care concern incubation of eggs and brooding of nestlings. These negative cor-

relations, however, were weak (Table 3) and not unexpected: because total group incubation and brooding attendance cannot exceed 100%, and because all group members can participate in incubation and brooding (Fig. 1), increased group size will generally lead a priori to reduced individual contributions.

Our analysis therefore indicates that the presence of nonbreeding helpers and additional cobreeders in the Acorn Woodpecker does not result in a substantial reduction of the parental care burden on breeders. This in turn suggests that the enhanced survival of breeding males in larger groups is most likely to be a result of the benefits of group living rather than a result of alloparental (helping) behavior per se (Koenig and Mumme 1987, p. 189–190).

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