CONTRIBUTIONS TO FLEDGLING FEEDING IN THE FLORIDA SCRUB JAY

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SUMMARY

(1) The provisioning of fledgling Florida scrub jays was studied at the Archbold Biological Station, Florida for two breeding seasons. The amount of food provided by breeding and helper jays was quantified, and effects of helper contributions were examined.

(2) Feeding of Florida scrub jay fledglings by adult jays extended from fledging at about 18 days of age to nutritional independence at about 85 days of age. Fledglings were fed for a longer period of time and at a greater rate than were nestlings, indicating greater investment by all group members in this portion of the breeding cycle.

(3) Retention of young within the group may be responsible for the extended parental care seen in this population, which may be typical of cooperative-breeding bird species.

(4) In contrast to results for feeding nestlings reported in a previous study, no differences were found in contributions by the various status classes of adult jays. Furthermore, all Florida scrub jay group members fed all fledglings in their group; no brood division was found.

(5) Food received by each fledgling increased with increasing numbers of helpers. Neither male breeders nor female breeders decreased contributions when helpers were present.

(6) Helper enhancement of survival of fledglings and breeders may be related to predator detection and not to extra food provided.

INTRODUCTION

As defined by Skutch (1961), 'helping' includes providing food to individuals other than the direct descendants of the provisioner. This definition includes feeding all dependent young, not just nestlings. Because following recently fledged birds is difficult, nearly all studies of feeding contributions by members of cooperatively breeding groups have concentrated on the feeding of nestlings (e.g. Brown 1972; Gaston 1973; Parry 1973; Sappington 1977; Brown *et al.* 1978; Stallcup & Woolfenden 1978; Hegner *et al.* 1979; Reyer 1980; Emlen 1981; Lewis 1982; Wilkinson 1982; Mumme 1984; Rabenold 1984, 1985; Wilkinson & Brown 1984; Austad & Rabenold 1985). Few studies have investigated the feeding of fledglings, and most of these have used incidental observations, data from only part of the dependent fledgling period, or observations from only one or two groups (Brown 1970; Dow 1978; Brown & Brown 1980; King 1980; Joste *et al.* 1982; Clarke 1984; Zack 1986b). Data on fledgling feeding may be more important than data on nestling feeding (Royama 1966). In some species the period of dependence as fledglings is longer than as nestlings (e.g. Nice 1937; Blanchard 1941; Snow 1958; Morehouse & Brewer 1968;

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Morton, Orejuela & Budd 1972). Consequently, the 'parental' investment required may be greater after the young have left the nest. Information about this time in the life cycle is needed for a better understanding of helper contributions in cooperative-breeding birds.

Stallcup & Woolfenden (1978) examined the feeding of nestling Florida scrub jays (*Aphelocoma coerulescens coerulescens* (Bosc)) and found significant differences in contributions by adults. In this paper we follow up this work by examining the amount of food provided by group members to fledgling Florida scrub jays, and the effect of helpers on breeder contributions and total amount of food provided to the young.

METHODS

We collected fledgling feeding data in 1983 and 1984 for twenty-one family groups in a marked population of Florida scrub jays at the Archbold Biological Station in Highlands County, Florida. (For a detailed description of the study area and population, see Woolfenden & Fitzpatrick 1984, 1989.) We followed groups from fledging of the young at approximately day 18 after hatching (Woolfenden 1978) through nutritional independence, approximately 2 months later. We observed groups for 251 observation periods of approximately 2 hours each for a total of 480 hours. In addition, we observed nestling feeding by twelve groups in 1984 for a total of 66 hours.

During each observation period we followed a family group with fledged young as closely as was possible without being scolded by the adults. For most families this distance was within 10 m shortly after fledging and to within 1 m after the young could fly. Florida scrub jay fledglings make a distinctive sound when fed, apparently a combination of high intensity begging and swallowing. This sound attracts the other fledglings in the family, which tend to remain near each other. Dow (1978) noted similar behaviour for the noisy miner (*Manorina melanocephala* (Latham)). By remaining in the vicinity of the young jays we were able to detect nearly all feedings of fledglings occurring in the observation period. For each feeding event we recorded the identity of the fledgling, the adult doing the feeding and often the item fed. Many feeding events were detected only by sound. We quantified the relative amount of food delivered to a young jay at each feeding using the bolus method of Stallcup & Woolfenden (1978) in which size of the food bolus was recorded on a scale of 1–3. Small items that did not distend the throat were given a value of 1. Large prey items that distended the throat fully or protruded from the bill were assigned a value of 3. Intermediate bolus sizes were given a value of 2. We were able to estimate bolus size on 2099 (57·7%) of the 3636 feedings recorded.

We used feeding rates to compare groups rather than absolute numbers of feedings because not all groups were observed for the same amount of time. Because repeated observation periods with one group are not independent of each other, we summarized data by groups when considering total feedings by a group and helper effects, and by individual for group member contributions. Only for the comparison of fledgling age and feeding rate did we treat all observation periods as independent data points.

We examined the contributions of six classes of Florida scrub jay group members (after Stallcup & Woolfenden 1978): male and female breeders, male and female older helpers (2 years old or older), male and female yearling helpers. Sample sizes differed between classes; all groups had breeding males and females, and none had helpers of all types. We calculated mean seasonal feeding rates to analyse group member contributions. For these analyses we arbitrarily defined the end of nutritional dependency as the first observation period with a feeding rate of less than two feedings per hour. Any observation period with

less than two feedings per hour and all subsequent observation periods were excluded. Fifteen groups had more than 800 min of observation time within the limits defined above and were observed for a total of 331 hours.

Because of the many feeding contributions of unknown size, we could not calculate directly the amount of food each jay provided in 'food units' as was done for nestlings by Stallcup & Woolfenden (1978). Instead, for comparison with their data we calculated a mean bolus size for those individuals observed bringing at least ten boluses. We multiplied this mean by the individual's mean feeding rate to obtain a measure of food provided during the year in food units.

Because many fledglings died during the study, fledgling number in some groups changed. For comparison of feeding rates and fledgling number we calculated a mean number of fledglings present during the study. Such a method gave fractional numbers of fledglings for the season.

RESULTS

Feeding rates

Total feeding rate by groups and by individuals in those groups increased with fledgling number (Fig. 1). Bolus size showed no discernible change with fledgling age, with bolus size 3 always the most common. For these reasons we consider feeding rates per fledgling to be the most important measure of food contributions for fledglings, but we also present feedings per hour for comparison with other studies, and food units delivered for comparison with nestling feeding data reported by Stallcup & Woolfenden (1978).

The amount of food delivered increases after fledging, reaching a peak when the young jays are about 5–7 weeks old (Fig. 2). The same pattern was evident using feeding rate and feeding rate per fledgling. The youngest fledglings not fed during an observation period were 72 days old, and the mean (± 1 S.D.) age of first period without a feeding for eight families was 83·75 ($\pm 10·61$). Age of last observed feeding in a family ranged from 76 to 110 days ($\bar{x} \pm 1$ S.D. $= 84·44 \pm 12·91$, $n=9$). From these results the average age of nutritional independence can be stated as approximately 85 days after hatching. We observed one young female jay 155 days old fed by her father. This case may differ from typical fledgling feeding, as no feedings had been seen in this family for over 1 month, and the feeding of nutritionally independent group members by adults may serve a social function (Woolfenden & Fitzpatrick 1978).

Only one of fifty-five adults, distributed in seventeen families, did not feed fledglings. This exception was an immigrant non-breeding female. Because her membership in the group was questionable and because she never fed the young, this individual was not considered a helper and was excluded from all analyses of helper behaviour. In the fifteen family groups where we recorded more than twenty feeding events with the identity of the adult and the young jay known, all adults fed all fledglings (Table 1). No brood division existed. In only four groups did any adult show a statistical preference for feeding any particular fledgling, and in those instances all adults continued to provide food for all the young throughout the period of fledgling dependence.

Feeding rates of all group-member classes peaked around day 45 and dropped to almost zero by day 85 (Fig. 3). Within families with helpers, feeding rate did not differ with provisioner status (Fig. 4a). When feeding rate per fledgling was considered, only yearling females and breeding males differed significantly (Fig. 4b). Mean bolus size did not vary with status (Kruskal–Wallis $H_5 = 2·89$, N.S.), and no class mean differed from the overall
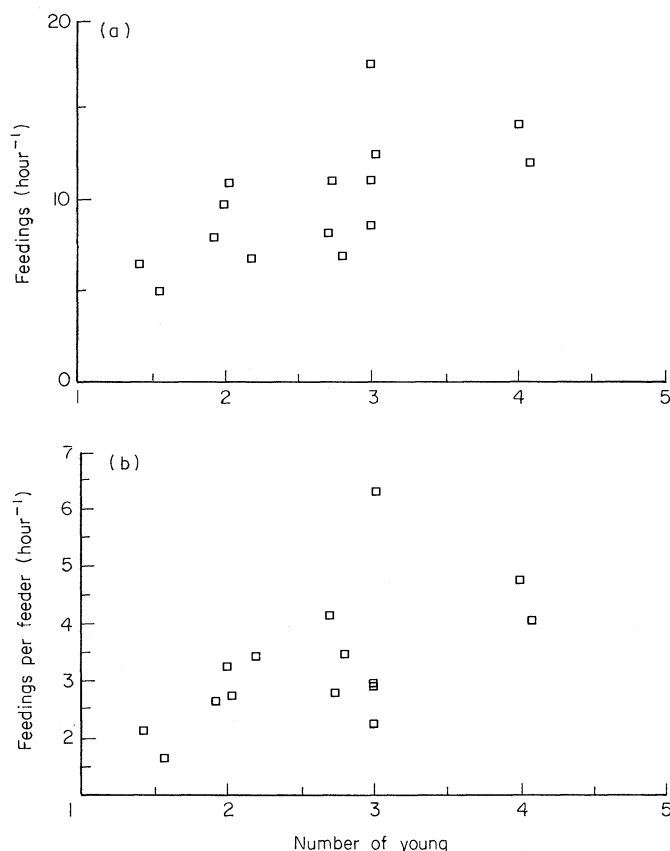
FIG. 1. Effect of fledgling number on (a) feeding rate per group, $r_s = 0.79$, $n = 15$, $P < 0.01$; and (b) feeding rate per group per adult, $r_s = 0.64$, $n = 15$, $P < 0.02$. Feeding rate and number of young shown are seasonal means for each family group.

mean bolus size of 2·70. When food units provided per hour per fledgling were considered, breeding males and yearling females no longer differed (Kruskal–Wallis $H_5 = 1.20$, N.S.).

Feeding rates of groups with helpers was not greater than simple pairs (Table 2). However, the group feeding rate increased significantly with increasing numbers of helpers (Fig. 5a). Feeding rate per fledgling gave an even stronger association (Fig. 5b).

Contributions made by male breeders in families with helpers did not differ from those made by males in pairs alone (Table 2), and group size did not affect feeding rate (Fig. 6). Female breeders with helpers fed at a lower rate than females in pairs alone, but this difference was not significant for feeding rate per fledgling (Table 2). Group size had no effect on female breeder feeding rate (Fig. 7).

Fledgling behaviour

From fledging to day 35 post-hatching, young Florida scrub jays generally sat on concealed perches and waited to be fed. Although they moved toward a calling adult or the sound of other fledglings being fed, not until day 28 was a fledgling observed moving toward a silent incoming adult. Starting at day 32, fledglings flew after the adults and
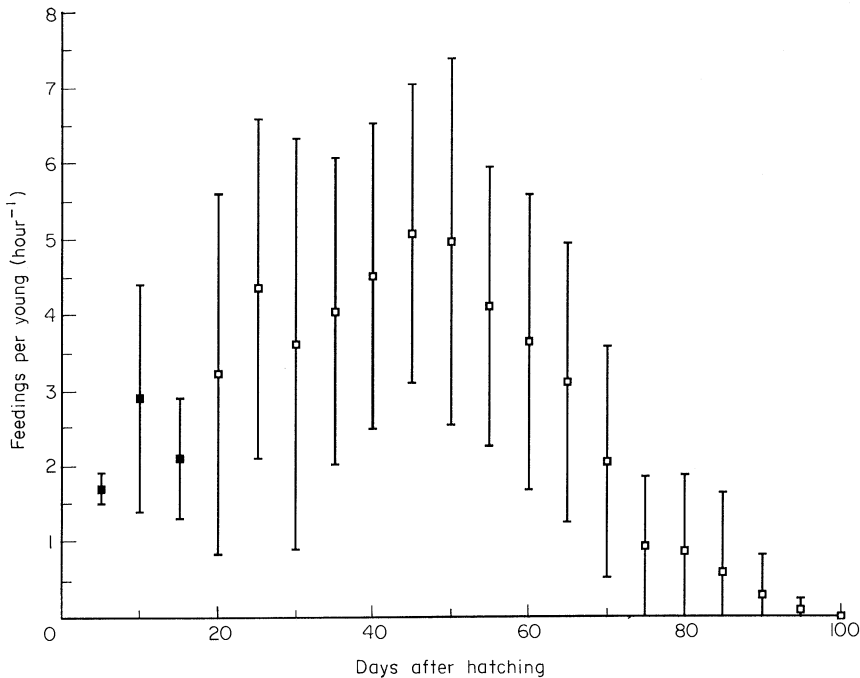
Fig. 2. Effect of offspring age on feeding rate per offspring by groups. Points are means for all young of that age (±1 S.D.). Values are for nestlings (■) and fledglings (□).

followed them as they foraged. Beginning by day 44 the young were more aggressive in begging to the adults and started to steal items from them. The fledglings followed the adults closely as the adults foraged and snatched insects caught and subdued by the older jays. Around day 65 these thefts began to take the form of prolonged chases of the adults by begging fledglings. Chases could last nearly a minute, and usually resulted in the young jay gaining the item.

At fledging the jays pecked at inedible objects in an explorative manner. Until around day 40 they often pecked, pulled, carried and swallowed non-food items such as sand, twigs, pieces of leaves, or moss. The first successful capture of a live arthropod from the ground was observed on day 33, but the next earliest was on day 38. After day 38 the fledglings often were successful in catching arthropods. They caught them on the ground, plucked them from vegetation, or jumped up and caught hovering insects. Most prey caught by the young were slow-moving arthropods that are easily captured, but are usually ignored by adults. Examples include hemipterans, spiders (Araneida), ants (Formicidae) and love bugs (Diptera: Bibionidae: *Plecia nearctica* Hardy). The first attempt to capture flying insects by aerial pursuit was observed on day 45, with the first successful capture observed on day 50. By day 55 the young consistently were successful in foraging. By day 60 they were spending most of each observation period foraging on their own.

Beginning around day 40 the fledglings began to pluck and eat berries, such as blueberries (*Vaccinium* spp.) and hairy huckleberries (*Gaylussacia dumosa* Torrey & Gray). The young frequently had been fed these berries by the adults. Virtually no other

TABLE 1. The distribution of observed feeding events by adult Florida scrub jays among dependent fledglings

| Family	Fledgling number	Male breeder	Female breeder	Helper 1	Helper 2	Helper 3	Helper 4	G score (d.f.)
BEND83	1	35	22	20				0·81
	2	27	24	17				(2)
LINS83	1	28	45					0·11
	2	38	58					(2)
	3	30	43					
NRID83	1	5	6	1				2·52
	2	5	10	1				(6)
	3	11	9	2				
	4	5	10	1				
PLAZ83	1	17	19	21				16·73**
	2	12	18	11				(6)
	3	18	21	11				
	4	21	10	31				
ROSE83	1	13	36					8·28**
	2	27	22					(1)
SAND83	1	13	18	17				0·61
	2	18	17	20				(2)
SSAN83	1	23	33	17	22			2·55
	2	28	35	15	18			(3)
	3	31	29	14	18			
BEND84	1	20	10	20				11·93*
	2	20	18	11				(2)
	3	26	17	6				
CABS84	1	11	13	7				0·83
	2	18	14	7				(2)
EBAY84	1	17	10					6·98*
	2	10	24					(2)
	3	13	17					
FIRE84	1	10	13					0·37
	2	11	13					(2)
	3	7	6					
PLAZ84	1	17	14	15	10	8	8	2·99
	2	19	13	16	5	6	6	(10)
	3	16	13	10	7	6	5	
ROSE84	1	5	43	16	6			5·79
	2	3	33	25	12			(3)
SAND84	1	21	8	25	22	13		6·24
	2	14	10	13	15	10		(8)
	3	16	11	26	12	14		
SORA84	1	13	1	4				10·88
	2	10	1	7				(6)
	3	12	5	5				
	4	13	9	4				

* $P < 0.05$; ** $P < 0.01$.
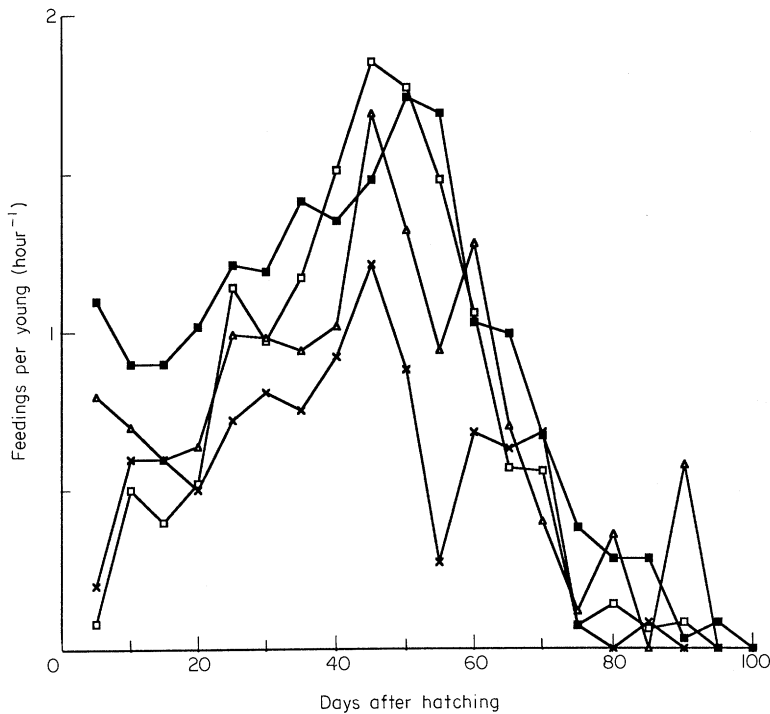
FIG. 3. Effect of offspring age on feeding rate per offspring by adults. Points represent mean feeding rate per offspring for all individuals of that class in families with helpers: male breeder (■); female breeder (□); older helper (△); yearling helper (×).

plant food was eaten by fledglings until acorns became available in late summer and were eaten in great numbers (DeGange *et al.* 1989).

DISCUSSION

Period of dependency

Investment by adult Florida scrub jays in young appears to be greater for fledglings than for nestlings: food is provided for a longer amount of time and at a greater rate. Increased feeding rates post-fledging also have been found for European robins (*Erithacus rubecula* (L.)) (East 1981), song sparrows (*Melospiza melodia* (Wilson)) (Smith 1978), northern wheatears (*Oenanthe oenanthe* L.) (Moreno 1984), and black-billed magpies (*Pica pica* (L.)) (Buitron 1988). In contrast, Morehouse & Brewer (1968) found the feeding rate of fledgling eastern kingbirds (*Tyrannus tyrannus* (L.)) was equal to or even less than rates during their last few days as nestlings, and Harper (1985) reported a constant decrease after fledging in the European robin. Royama (1966) suggested that although great tit (*Parus major* L.) fledglings required more food than nestlings, the energy parents expended did not increase because the young tits followed the foraging adults, eliminating the parents' cost of returning to the nest. Energetic demands on adult Florida scrub jays probably increase after fledging, in part because young jays do not follow foraging adults until 2–3 weeks after fledging. The period of fledgling dependence corresponds to the yearly peak of adult breeder mortality (Woolfenden & Fitzpatrick 1984).
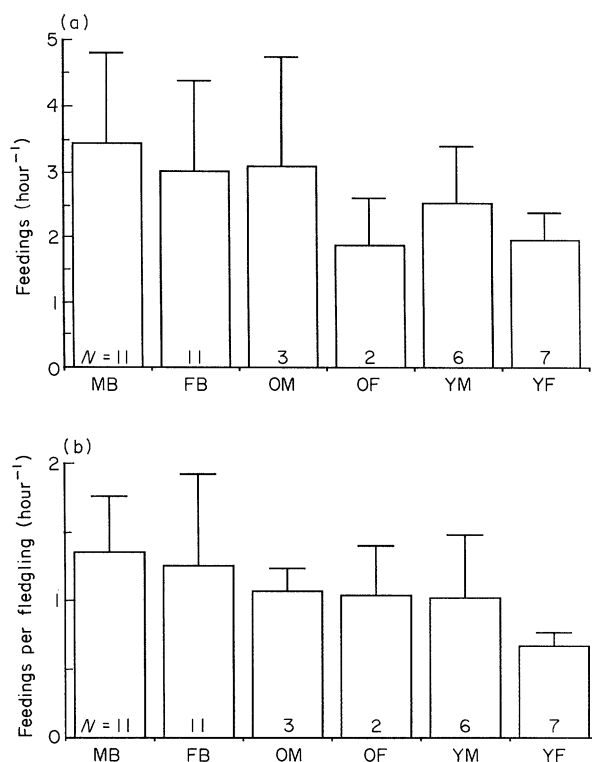
FIG. 4. (a) Fledgling feeding rate and (b) feeding rate per fledgling by adult status class. Bars are means of all individuals (± 1 S.D.). MB, male breeder; FB, female breeder; OM, older male helper; OF, older female helper; YM, yearling male helper; YF, yearling female helper. In (a), no means differed significantly from another (Kruskal–Wallis $H_5 = 9\cdot01$, N.S.). In (b), only MB and YF differed (Kruskal–Wallis $H_5 = 11\cdot12$, $P < 0\cdot05$, Dunn's test (Dunn 1964), $P = 0\cdot05$).

TABLE 2. Effect of helper presence on Florida scrub jay fledgling provisioning rates

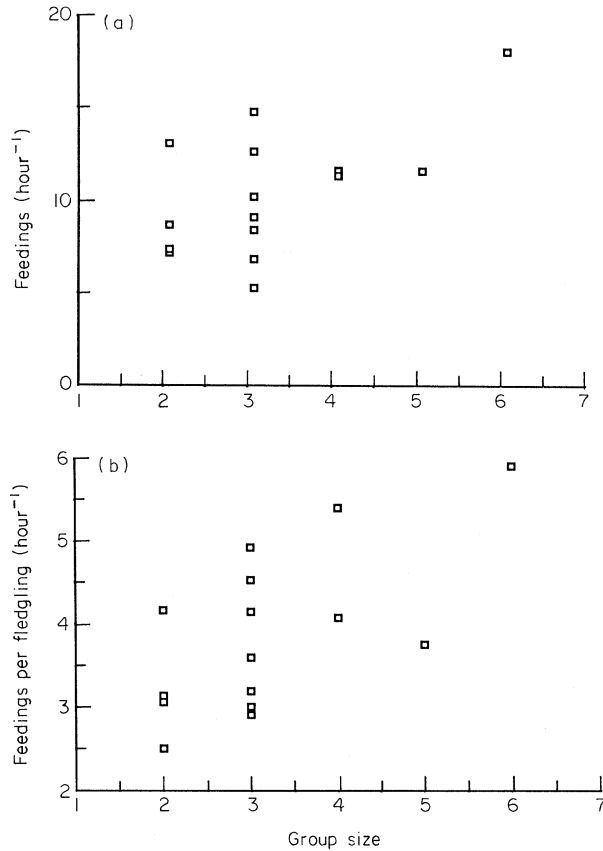|	Families with helpers Mean ± 1 S.D. (n)	Families without helpers Mean ± 1 S.D. (n)	Student's t
Feedings (h^{-1})			
Male breeder	$3\cdot43 \pm 1\cdot37$ (11)	$3\cdot82 \pm 0\cdot88$ (4)	$0\cdot52$
Female breeder	$3\cdot01 \pm 1\cdot36$ (11)	$4\cdot98 \pm 2\cdot21$ (4)	$2\cdot11^*$
Total group	$10\cdot51 \pm 3\cdot58$ (11)	$8\cdot69 \pm 2\cdot72$ (4)	$0\cdot92$
Feedings per fledgling (h^{-1})			
Male breeder	$1\cdot35 \pm 0\cdot41$ (11)	$1\cdot42 \pm 0\cdot16$ (4)	$0\cdot33$
Female breeder	$1\cdot25 \pm 0\cdot67$ (11)	$1\cdot80 \pm 0\cdot64$ (4)	$1\cdot42$
Total group	$4\cdot13 \pm 0\cdot98$ (11)	$3\cdot22 \pm 0\cdot70$ (4)	$1\cdot69$

* $P < 0\cdot05$; one-tailed.

Fig. 5. Effect of group size on (a) fledgling feeding rates of broods, $r_s = 0.47$, $n = 15$, $P < 0.05$ one-tailed; and (b) feeding rate per fledgling, $r_s = 0.56$, $n = 15$, $P < 0.025$ one-tailed.

The 85-day dependent period of Florida scrub jays is long for a passerine. In general, small and medium-sized passerines are dependent from 30 to 50 days after hatching, e.g. eastern kingbird, 50 days (Morehouse & Brewer 1968); northern wheatear, 31 days (Moreno 1984); European blackbird, *Turdus merula* L. 29–39 days (Edwards 1985); spotted flycatcher, *Muscicapa striata* (Pallas) 30 days (Davies 1976); song sparrow, 31 days (Smith 1978). However, corvids in general have longer periods of dependence, ranging from less than 50 days in *Pica*, *Garrulus*, and *Cyanocitta stelleri* (Gmelin) (Goodwin 1976) to over 100 days in the brown jay (*Cyanocorax morio* (Wagler)) (Lawton & Lawton 1985) and possibly in the Eurasian nutcracker (*Nucifraga caryocatactes* (L.)) (Swanberg 1956). The Santa Cruz Island subspecies of scrub jay (*A. c. insularis* Henshaw) has a dependent period similar to Florida birds at around 80 days (Atwood 1980), while *A. c. superciliosa* (Strickland) from the mainland of California is shorter at around 60 days (Ritter 1983).

Ashmole & Tovar (1968) concluded that prolonged parental care in birds relates to the attainment of specialized feeding skills needed to catch active prey or large prey at infrequent intervals. Fogden (1972) found that many, unrelated species of insectivorous birds in forests in Sarawak, Indonesia, had long periods of dependence. He suggested that
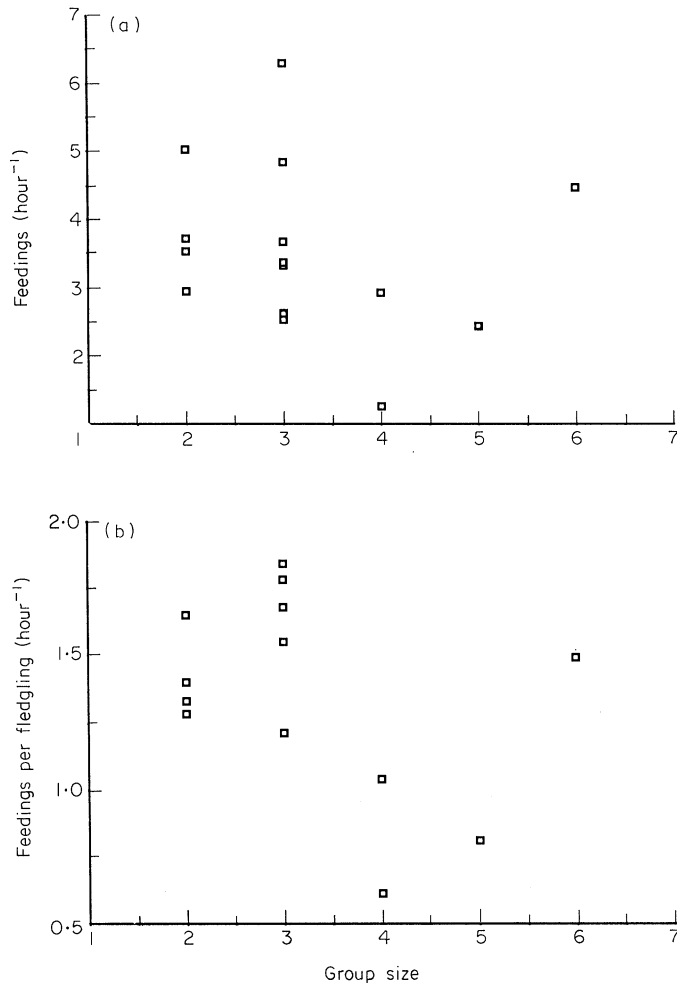
FIG. 6. Effect of group size on (a) fledgling feeding rates per brood by male breeders, $r_s = -0.29$, $n = 15$, N.S.; and (b) feeding rate per fledgling, $r_s = -0.23$, $n = 15$, N.S.

although the skills necessary to catch insects were not difficult to learn, learning to recognize edible insects among the many species represented by few individuals may require a long period of learning. Within corvids, the specialized feeding methods of nutcrackers may account for their long dependent period, but scrub jays are omnivorous and seem to have few specialized foraging skills.

Cooperative breeding also may be responsible for long dependent periods. The cooperatively breeding red-cockaded woodpecker (*Picoides borealis* (Vicillot)) has a dependent period of 180 days (Ligon 1970), longer than those of the non-social congeneric hairy and downy woodpeckers (*P. villosus* (L.), 44 days; *P. pubescens* (L.), 41 days) (Lawrence 1966). The fledglings of common fiscal shrikes (*Lanius collaris* L.) attain independence at around 50 days after fledging (Zack 1986a), while young of the sympatric cooperatively breeding grey-backed fiscal shrike (*L. excubitorius* Prévost and Des Murs) are fed by adults for twice as long (S. Zack, personal communication). The cooperative-
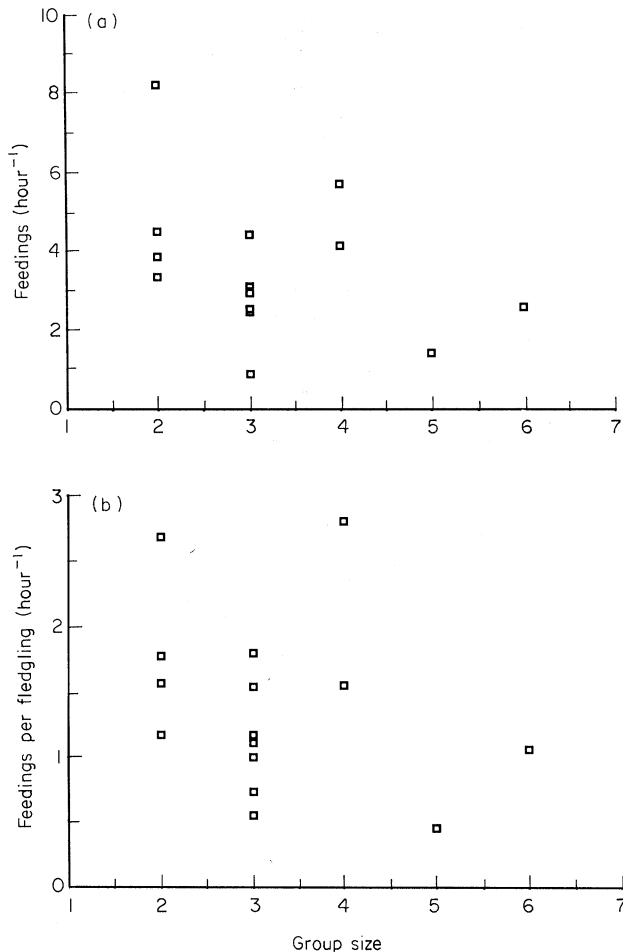
Fig. 7. Effect of group size on (a) fledgling feeding rates per brood by female breeders, $r_s = -0.29$, $n = 15$, N.S.; and (b) feeding rate per fledgling, $r_s = -0.26$, $n = 15$, N.S.

breeding black tit (*Parus niger* Vicillot) is dependent for 40–50 days after fledging (Tarboton 1981), while the non-social great tit is dependent only for about 2 weeks after fledging (Lack 1966). As mentioned, the cooperatively breeding Florida race of the scrub jay also has a longer dependent period than other non-social races, although it is similar to *A. c. insularis*, a race with limited juvenile dispersal (Atwood 1980).

Retention of young in the home territory by cooperative breeders necessitates a decrease in aggressive actions by parents towards those young. A decrease in aggression in turn may decrease the drive to make the young independent and result in an extended period of feeding. Considered slightly differently, the failure of young to disperse may be responsible for the long duration of feeding rather than any change in parental drives. Contrary to theoretical predictions that parents force young to leave (Trivers 1974), in some bird species fledgling independence results from the young leaving before the adults' drive to feed them has extinguished (Burger 1981). By remaining at home, young Florida

scrub jays may give parents the opportunity to feed them until the drive to do so disappears.

Brood division

Several studies of the feeding of fledglings by passerines that do not breed cooperatively have found that brood division, specifically adults tending to feed different young, is commonplace (Cowdy 1962; Nolan 1978; Smith 1978; Smith & Merkt 1980; Moreno 1984; Edwards 1985; Harper 1985; McLaughlin & Montgomerie 1985; Price & Gibbs 1987). Snow (1958) and Smith (1978) suggested that brood division is a common arrangement often overlooked because of the difficulties in following fledglings and the paucity of studies on the post-fledgling period. McLaughlin & Montgomerie (1985) even suggested that division of fledgling broods may be the more common situation in birds. We found no evidence of brood division in Florida scrub jays, nor did Buitron (1988) in her study of black-billed magpies. Although in a few families a significant trend existed for one adult to feed one young more than another, in no case did this approach the extent of feeding preference seen by other studies. Within a single observation period one or several young could be fed predominantly or exclusively by one adult, but such an observation was probably the result of an adult returning repeatedly to the same location after foraging, rather than a real preference for certain young. These young were not fed preferentially during the next observation period that followed. Smith (1978) mentioned that in nearly all song sparrow broods he observed, each parent showed an exclusive preference for feeding certain individuals (but see Hailman 1978). McLaughlin & Montgomerie (1985) found that forty-four of forty-seven fledgling Lapland longspurs (*Calcarius lapponicus* (L.)) were fed exclusively by one parent. Edwards (1985) found that after division of the brood, a parent European blackbird would feed only those young in its subgroup, and would not feed the others even if they begged to that parent. Compared to these other species, Florida scrub jays do not divide their broods of fledglings.

Similar benefits have been proposed for brood division and having helpers, in that both may allow females to decrease their work load with a first brood, renest earlier, and raise more broods in a season (Snow 1958; Rowley 1965; Smith 1978; Brown *et al.* 1978). Both may function to decrease the work load of the parents, or insure that each young gets an appropriate amount of food (Smith 1978; Brown 1978). Possibly the presence of helpers diminishes the need for brood division. One could predict that in a cooperatively breeding species, if brood division existed it should be more likely in pairs or small groups with large numbers of young than in large groups or groups with few young. However, in Florida scrub jays neither pairs nor groups divided their broods. Florida scrub jays rarely attempt second broods after a successful first nesting (Woolfenden & Fitzpatrick 1984), and food for fledglings may not be limiting (see below), so brood division may offer few benefits for this species. Although no brood division was found in this study, other investigators should look for this phenomenon with other species of cooperative breeders.

Helper contributions

The contributions of Florida scrub jay group members differ between the fledgling and nestling stages. Stallcup & Woolfenden (1978) found that nestlings were fed most by older male helpers, and slightly less by breeding males. All other adults fed the nestlings even less, with breeding females feeding them the least. Our results show that contributions change after the young fledge; no classes differ in feeding rate and all contribute substantial amounts. Yearling male helpers and females of all status classes increase their

feeding rates to approximately the rates of the breeding male and older male helpers. The increase in female breeder feeding rate follows the trend evident near the end of the nestling period (Stallcup & Woolfenden 1978). As nestlings grow older and the female breeder broods them less, she is freed to forage and find food for the young. When the young fledge the nest is abandoned and the female can contribute at the same level as does the male.

Female helpers may increase their feeding contributions for the same reasons that female breeders do. Female helpers appear to be attracted to the nest similarly to breeding females. They often come to the nest without food and attempt to sit on the nest (Stallcup & Woolfenden 1978, this study). Once the young fledge, this drive should disappear and female helpers could increase their feeding contributions. Also, female helpers often are chased from the nest vicinity by the male breeder or male helpers (Stallcup & Woolfenden 1978, this study), as also has been observed in the chestnut-bellied starling (*Spreo pulcher* (Müller)) (Wilkinson 1982). This action may prevent disruption of the nest by helpers' inexperienced brooding behaviour, prevent egg-dumping by potentially breeding females, or prevent egg-tossing or predation as has been observed in the grey-breasted (Mexican) jay (*Aphelocoma ultramarina* (Bonaparte)) (Trail, Strahl & Brown 1981). By guarding the nest against female helpers, males may effectively reduce female helper contributions to nestling feeding, as has been suggested for the Galapagos mockingbird (*Nesomimus parvulus* (Gould) (Kinnaird & Grant 1982). Once the young have fledged neither nest disruption nor egg dumping would be possible. Female helpers are not kept from the vicinity of the fledglings and their contributions rise accordingly. Carlisle & Zahavi (1986) reported that dominant Arabian babbler (*Turdoides squamiceps* (Cretzschmar)) helpers often interfered with subordinates bringing food to fledglings. No instances of aggression towards female Florida scrub jay helpers were noted after the young fledged.

Yearling Florida scrub jay helpers of both sexes show an apparent tendency to increase their food contributions to nestlings over time (Fig. 3; Stallcup & Woolfenden 1978). It is possible that inexperience with feeding young is the cause of low nestling feeding rates by first-year helpers. Lack (1968) suggested that experience in learning parental activities is a possible benefit of helping behaviour. Lawton & Guindon (1981) studying the brown jay found that the effectiveness of nest attendants increased with age, and that young birds significantly improved in effectiveness over one breeding season. Young Florida scrub jays may learn to feed young efficiently during the first nest cycle, with yearling helpers reaching adult proficiency by the time the young fledge or shortly thereafter.

In other cooperatively breeding species group members of different status also feed fledglings differently than they feed nestlings. In the cooperatively breeding grey-backed fiscal shrike, Zack (1986b) found that male breeders fed nestlings the most and male helpers fed more than female helpers. However, in the one family where he examined the feeding of fledglings, he found no significant differences between flock members, even though the female breeder tended to contribute the most. In one family of grey-breasted jays, Brown (1970) found that the lone female helper present increased the amount of food she provided to fledglings relative to that which she fed nestlings. In addition, while parents fed their own nestlings preferentially over young in the other nests in the communal territory, no such preference was evident after all had fledged (Brown 1970; Brown & Brown 1980). In the grey-crowned babbler (*Pomatostomus temporalis* (Vigors and Horsfield)), King (1980) found that the female breeder fed at the nest the least and the male breeder the most, but in four groups with fledglings the female breeder did the most feeding. Unlike these studies, Joste *et al.* (1982) found no change after fledging in

percentage of feedings by adult acorn woodpeckers (*Melanerpes formicivorus* (Swainson)) in the one group studied, and Tidemann (1980) stated that the white-winged fairy-wrens (*Malurus leucopterus* Dumont) that fed nestlings the most also fed the fledglings the most.

Effects of helper actions

Helpers positively influence the survival of fledgling Florida scrub jays (McGowan 1987), but how they do so is not clear. Food delivered to each fledgling increases with group size, and increased food could decrease the starvation of fledglings. Mumme (1984) attributed the decreased starvation of acorn woodpecker nestlings in groups with helpers to the additional food provided by the helpers, and food is also the important contribution provided by helper pied kingfishers (*Ceryle rudis* (L.)) (Reyer 1980). However, starvation is rare in Florida scrub jays. Few nestlings starve, and we have no evidence of fledgling starvation. The increased amount of food provided to young in families with helpers may have no direct effect on survival of those young. Unlike most species of passerines, the young are not evicted from the natal territory and do not need to build reserves for the period following independence. In addition, shortly after the young reach nutritional independence in late summer, an abundance of acorns becomes available to all jays, easily providing all the energy, if not all the nutrients needed. Most fledgling loss, like most egg and nestling loss is from predation: census data show that healthy young present one day are gone the next, and the loss of healthy young can be attributed to predation (Woolfenden & Fitzpatrick 1984). Protecting young from predators may be the way helpers help during this time. Protection may take the form of sentinel behaviour or increased vigilance (McGowan & Woolfenden 1989), or simply may be a function of attendance by the adults. With an increased feeding rate, an adult is likely to be near the fledglings more often. In this way predators can be detected more readily, even without the presence of formal sentinels. A similar explanation of the effect of helpers has been suggested for purple gallinules (*Porphyrula martinica* (L.)) (Hunter 1987).

In addition to increasing fledgling survival, helper presence may enhance breeder survival, possibly the most important benefit of helping. The length of breeding lifespan is the most important component of total lifetime reproductive success for the Florida scrub jay, more important than offspring survival at any stage (Fitzpatrick, Woolfenden & McGowan 1989). Increased breeder survival could result from decreased parental effort at this time. With more individuals feeding, the adults could decrease their efforts and theoretically decrease the risk incurred in foraging. Such adjustments in feeding nestlings have been found in other cooperative breeders (Gaston 1973; Brown *et al.* 1978; Hardy, Webber & Raitt 1981; Kinnaird & Grant 1982; Lewis 1982; Rabenold 1984; Austad & Rabenold 1985; Tidemann 1986), but were not found in this study. It is likely that helpers positively affect the survival of adults in much the same way that they do juveniles, by helping to detect predators. In this way the actual benefit of helping for breeder survival may be simply the benefit of group living rather than any direct effect of 'helping' behaviour *sensu stricto* (i.e. delivering food to dependent young).

ACKNOWLEDGMENTS

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