The Auk 116(1):131–140, 1999

HOW WHITE-THROATED MAGPIE-JAY HELPERS CONTRIBUTE DURING BREEDING

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ABSTRACT.—We investigated the mechanisms by which helpers contribute to breeder reproduction in a Costa Rican population of White-throated Magpie-Jays (*Calocitta formosa*). Helpers provided a substantial proportion of all feedings to female breeders and their offspring, proportionately more than most species of cooperatively breeding New World jays. Breeding males typically fed breeding females and offspring less frequently than expected, however. There was little evidence of brood division in the sense of individual provisioners (breeders or helpers) preferentially feeding particular fledglings within a brood. The rate of provisioning per recipient increased as a function of group size only during the pre-incubation period (provisioning of the laying female). Provisioning rates per nestling and per fledgling were not correlated with group size, and the number of offspring fledged per successful nest did not increase with group size. Helpers did reduce the provisioning burden on breeders, however, and occasionally were the primary care-providers of fledglings, which allowed breeders to renest. More successful nests were produced in groups with many helpers than few, resulting in more fledged young per year. Mechanisms contributing to this "helper-effect" included more nesting attempts per year and a higher likelihood of renesting after a successful attempt. We conclude that the contributions of magpie- jay helpers increased breeder fitness, and the indirect and direct benefits gained by helping probably favored its expression by nonbreeding group members. *Received 30 October 1997, accepted 18 June 1998.*

FOR A FEW carefully studied species of cooperatively breeding birds, evidence suggests that helpers (individuals that feed and perform other parental-care activities for offspring that are not their own; Skutch 1961, Brown 1987) have no effect on, or may even reduce, the fitness of breeders whose offspring they help (Leonard et al. 1989, Marzluff and Balda 1992, Komdeur 1994, Magrath and Yezerinac 1997). For many other cooperatively breeding species, however, helpers do indeed appear to increase the survivorship and reproductive success of the breeders they help through a variety of specific mechanisms (Brown 1987, Stacey and Koenig 1990, Emlen 1991). For example, helpers can increase the number or viability of offspring in each brood by decreasing the risk of starvation and predation (e.g. Rabenold 1984, Strahl and Schmitz 1990, Emlen and Wrege 1992, Heinsohn 1992, Mumme 1992), or they can reduce the time and energy that the breeders devote to each bout of reproduction, resulting in higher breeder survivorship or more frequent renesting (e.g. Brown and Brown 1981, Rowley and Russell 1990, Komdeur 1994).

Groups of White-throated Magpie-Jays (*Calocitta formosa*) typically are composed of a primary breeding pair and three to four helpers (range one to nine; Innes and Johnston 1996, Langen 1996a, Langen and Vehrencamp 1998). Most females remain on their natal territory as helpers, but males disperse at about one year of age and become floaters (Langen 1996a, b). The primary breeding pair attempts to reproduce repeatedly during the long breeding season (greater than 200 days), and some female helpers also breed on occasion (Langen 1996a). Offspring are fed by helpers during the nestling period and after fledging until nutritional independence (Langen 1996b). Group members associate while foraging and give a variety of visual and auditory signals that alert others to the presence of food, predators, and conspecific intruders (Langen 1996b, c, unpubl. data).

In a recent paper (Langen and Vehrencamp 1998), we analyzed the effects of group size and territory size on the reproductive success of magpie-jay groups. In our sample of 14 territories, the number of offspring fledged per successful nest did not vary with group size,

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but a significant positive association existed between group size and the number of successful nests per year. As a result, large groups (i.e. groups with many helpers) fledged significantly more young per year than did small groups. This putative "helper effect" was independent of territory quality. Here, we examine in more detail how helpers contribute during breeding. We ask whether: (1) helpers increase nesting success by reducing the likelihood of nest failure or increasing the number of nesting attempts, (2) helpers reduce the rate of food provisioning by the breeders or increase the rate of food delivery to recipients, and (3) breeders and helpers divide reproductive tasks to increase efficiency during breeding.

METHODS

Monitoring of breeding groups.—We collected data at Santa Rosa National Park, Guanacaste Conservation Area, Guanacaste Province, Costa Rica (10°50'N, 85°37'W) during 1992 and 1993. A detailed site description can be found in Langen and Vehrencamp (1998). The members of six groups containing individually marked birds were the primary focus of study, and an additional eight groups were monitored less intensively during the breeding season (details on marking and censusing in Langen 1996a, b). We include data from these additional groups where appropriate.

We visited all focal territories and nearby habitat at least weekly during the breeding season (January to August). Nests were detected by listening for the loud food-solicitation calls that are broadcast with monotonous regularity during the pre-incubation period by breeding females in the vicinity of their nest (Langen 1996a). Once a breeding episode had begun, we initiated intensive monitoring of the group (see below). In addition, group members were tallied during visits. Because the absence of a female might indicate nesting, we carefully searched territories for additional nests after detecting that a female was absent. Most nests (83%) were located during the pre-incubation period; the remainder were discovered shortly after the onset of incubation.

Feeding of the breeding female or offspring by other group members was quantified during each of three nesting stages: (1) pre-incubation, when the breeding female was laying but not yet incubating; (2) incubation, when the breeding female brooded the eggs; and (3) the nestling period. Nests were observed through spotting scopes at a distance of 20 to 75 m (depending on the tolerance of group members) for 90 min per morning throughout each monitored breeding attempt such that every instance that an individual brought food to the incubating female or nestlings was recorded (although we were not able to determine the distribution of feedings among nestlings). We also monitored the provisioning of each fledged offspring until nutritional independence via timed samples during which we recorded the number of feedings received and the identity of provisioners (see Langen 1996b). Samples were made once per week or more frequently (8 to 14 sample days per fledgling), each sample lasting 30 to 60 min (timed only when the animal was in sight). Magpie-jays are relatively tolerant of humans, so most observations could be made at distances of 10 to 25 m. We could not reliably quantify the quality and load size of the food brought by provisioners at any stage of breeding, however.

Classification of group members.—Group members comprised all individuals that repeatedly were found associated while foraging or resting and who ranged within the boundaries of a single territory (Langen and Vehrencamp 1998). The female that incubated the clutch and the male that consorted and copulated with her during the pre-incubation period are designated as the breeders during a nesting attempt; other birds that fed the incubating female or the offspring are called helpers. Within groups, the same female incubated during most of the nesting attempts; we refer to these birds as primary breeding females. A few female helpers also infrequently established their own nests in the group territory (19% of helpers and 17% of nesting attempts). The nests of these secondary breeders are analyzed separately from those of the primary breeders because the former generally received much less help from other group members (see Results).

The helper category of group members includes secondary breeding females because they helped at most of the nests of primary breeders. Young helpers are birds that were participating in their first full breeding season (under 19 months of age; 16% of helpers). Older helpers are those that had participated in at least one full breeding season. When comparing among species, we refer to nonbreeding group members collectively as auxiliaries, because helping behavior is not observed in all species in which nonbreeders are present during nesting (Brown 1987).

Statistical analysis.—To analyze the association between group size and provisioning rate, we calculated the median provisioning rate (feeding visits per hour) during each breeding stage for each group year. Nestling and fledgling provisioning rates used to calculate the median are adjusted for the age of the offspring (residuals of the regression of provisioning rate on age) because preliminary analyses indicated a significant effect of this variable on feeding rate (Langen 1996b). We analyzed provisioning rate from the perspective of a recipient and a donor. The recipient provisioning rate is defined as the number of feeding visits per hour to the female (pre-incubation and incubation stages), a nestling (nestling stage), or a focal fledgling (fledgling stage). The rate per nestling is estimated by dividing the number of feeding visits to the nest per hour by the number of nestlings present at banding (around 10 days posthatching). We calculated the donor provisioning rate by dividing the total rate of feeding to all recipients by the number of group members (i.e. feeding visits per hour per provisioner). We estimated the total rate of provisioning during the fledgling stage by multiplying the number of feeding visits per hour to a focal fledgling by the number of fledglings in the brood. We present analyses using total helper number (group size − 2); the conclusions did not differ when the same analyses were performed while excluding young helpers, presumably because the two measures of group size are highly correlated ($r = 0.86$).

For all comparisons between helper number and a dependent variable, we use group year as the unit of replication. We initially performed ANCOVA that included year as a factor, because helper effects may be limited to particular years. If the interaction term was not near significance ($P > 0.1$) it was removed from the model, and if year was subsequently not near significance, it was also removed. Before making tests of linear associations, we examined plots for evidence of nonlinear effects. For parametric tests, variables were transformed as needed. All statistical probabilities are two-tailed.

RESULTS

Nesting success and group size.—The number of successful nests per year, and hence the number of young fledged, increased with group size (Langen and Vehrencamp 1998). Large groups may have had more successful nests than small groups because: (1) the probability of success per nesting attempt was higher, (2) primary breeders attempted more nests, or (3) more females bred.

We were confident that we detected all of the nesting attempts in a total of 12 group years during the study. The proportion of nesting attempts that failed covaried with the number of helpers differently between years (helper number × year interaction, slope = 0.197, $F = 6.6$, $P = 0.03$) and varied significantly between years (1992, $\bar{x} = 0.82 \pm$ SE of 0.046 nests failed; 1993, $\bar{x} = 0.76 \pm 0.063$; $F = 6.2$, $P = 0.04$). Nest predation was implicated in virtually all failures whose cause could be determined, but wind damage may have caused a few of the failures. Confirmed diurnal nest predators included white-faced capuchin monkeys (*Cebus capucinus*; six nests), Crested Caracaras (*Polyborus plancus*; one nest), and black iguanas (*Ctenosaur similis*; one nest); several other instances of nest predation may have been caused by nocturnal mammals.

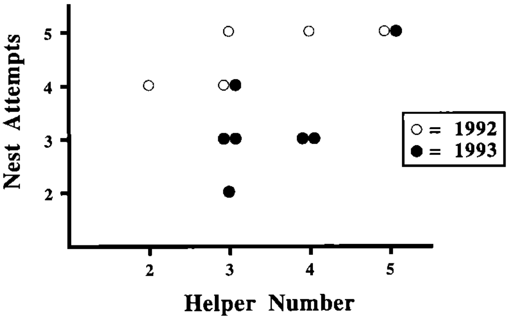

FIG 1. Relationship between the number of nesting attempts by White-throated Magpie-Jays per year and number of helpers during the two years of this study. Each circle represents one group year; all groups from 1992 were also present in 1993.

The total number of nesting attempts increased with helper number and differed between years (helper number, $F = 5.2$, $P = 0.05$; year, $F = 12.2$, $P = 0.007$; Fig. 1). The number of nesting attempts per year by the primary breeding female was predicted by year only (helper number, $F = 0.8$, $P = 0.4$; year, $F = 15.4$, $P = 0.004$; 1992, $\bar{x} = 4.2 \pm 0.37$ nesting attempts, 1993, $\bar{x} = 2.7 \pm 0.18$). The time between the termination of one failed nest and the start of the next was not predicted by helper number ($\bar{x} = 12.0 \pm 2.08$ days, $n = 9$, $F = 0.2$, $P = 0.7$), perhaps because the breeding pair performed most of the nest construction within groups (e.g. delivered 94.7% of the nesting material, $n = 133$ deliveries among four breeding pairs). However, primary breeders with many helpers were more likely to renest after having fledged offspring than breeders with few helpers (Mann-Whitney $U = 27$, $n_1 = 4$, $n_2 = 7$, $P = 0.02$). Renesting typically began before fledglings had attained nutritional independence; two instances were 16 and 31 days after offspring had fledged. This corresponded with the period of peak offspring provisioning (Langen 1996b: figure 1).

The number of nesting attempts per year by secondary breeding females was not associated with helper number ($F = 2.5$, $P = 0.1$; $\bar{x} = 0.5 \pm 0.20$ nests). The failure rate of nests of secondary breeders was not significantly higher than that of primary breeders (Langen 1996a),

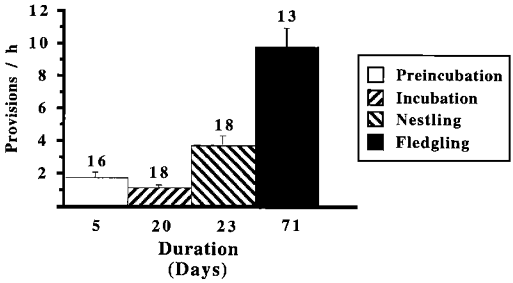

FIG. 2. Total rate of provisioning (number of feeding visits per hour) to female or all offspring White-throated Magpie-Jays combined during each stage of breeding ($F = 41.1$, df = 3 and 61, $P < 0.0001$; Scheffé post-hoc test, pre-incubation = incubation < nestling < fledgling). Each sample is a mean rate per group year; above each bar is the number of group years sampled among 10 groups. The mean duration in days of each breeding stage is shown below the bar. The fledgling stage only includes feedings through the mean age of nutritional independence.

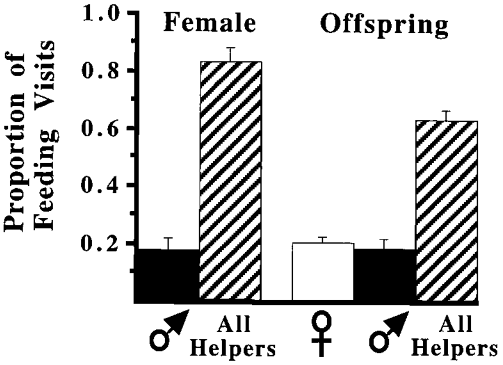

FIG. 3. Proportion of feeding visits made by breeding male White-throated Magpie-Jays and all helpers to the female, and by the breeding female, breeding male, and all helpers to offspring (n = nine group years from five groups).

but because these nesting attempts were infrequent, only 1 of 10 successful nests was by a secondary breeder.

Rate of provisioning.—The rate of provisioning varied greatly among the different stages of breeding, with the highest levels occurring after offspring had fledged (Fig. 2). Primary breeding females were fed at significantly higher rates than were secondary females in the pre-incubation and incubation stages (mean provisioning rate compared with t-tests separately for each group; trend among groups tested using Fisher's combined probability; pre-incubation, $\chi^2 = 13.9$, $n = 2$ groups, $P < 0.01$, secondary rates 61 ± 11.3% lower; incubation, $\chi^2 = 24.6$, $n = 5$, $P < 0.01$, secondary rates 66 ± 12.7% lower; nestling, $\chi^2 = 3.9$, $n = 2$, $P > 0.1$). For nests of primary breeders, the rate of provisioning increased significantly with helper number during pre-incubation from the point of view of the recipient and possibly of the donor (per recipient, $F = 8.8$, $P = 0.02$, slope = 0.046; per donor, $F = 3.9$, $P = 0.07$, slope = 0.006, $n = 14$). There was no significant effect of helper number on either donor or recipient provisioning rates during the incubation and nestling stages (incubation, $Fs < 0.03$, $n = 14$, $Ps > 0.8$; nestling, $Fs < 0.1$, $n = 12$, $Ps > 0.7$). During the fledgling stage, there was a trend for provisioning per donor to decline with helper number, particularly in 1993 when provisioning rates were higher (helper number × year interaction, slope = 0.043, $F = 3.7$, $P = 0.09$; helper number, slope = -0.043, $F = 3.8$, $P = 0.08$; year, slope = -0.270, $F = 4.0$, $P = 0.08$; per recipient helper number, $F = 0.4$, $n = 13$, $P = 0.5$; $n = 13$). Sample sizes were too small to perform the same analyses for secondary breeders.

Provisioning and group membership class.—A majority of all feeding visits to the breeding female or offspring were made by helpers (Fig. 3). Half of the young helpers made significantly fewer visits than other group members, however (25 ± 11.5% fewer feeding visits than older group members, $n = 7$ young helpers; see Langen 1996b). Slight differences existed in provisioning effort among older helpers within a group (CV of older helper feeding visits = 0.36 ± 0.053, $n = 7$ group years). Breeding females made relatively smaller contributions to offspring feeding in groups with many helpers (Fig. 4), but their efforts typically were not different from those of the average older helpers (Table 1). Breeding males, however, made fewer feeding visits than expected (Table 1); five of six males provisioned less than expected during some period. Surprisingly, one of these males (group Comedor) made significantly more feeding visits to offspring than expected during one year and significantly fewer the following year. Apparently, both the breeding female and helpers compensated for a group's breeding male.

Division of fledged broods.—We examined

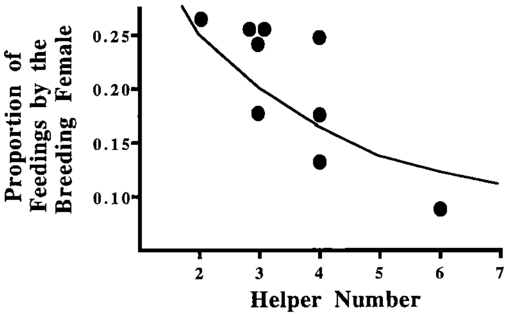

FIG. 4. Effect of total helper number on the proportion of White-throated Magpie-Jay offspring feedings (including nestling and fledgling stages) provided by the primary breeding female (r_s = −0.82, $P < 0.02$). The line represents the expected proportion of feedings if all individuals contributed equally (n = nine group-years among five groups).

whether each provisioner randomly distributed feedings within a fledgling cohort. The allocation of feedings to fledglings was significantly nonrandom during one group year out of seven (plus one trend; Table 2). In the one significant group year (Comedor 92), the breeding male fed one fledgling disproportionately, and one helper fed a second fledgling disproportionately, but the other group members displayed no bias among the three fledglings.

Survivorship of offspring.—Clutch size was significantly higher in large groups than in small groups (Langen 1996a), but the number of nestlings at the day of banding (10 days post-hatching) did not covary with group size (r_s = −0.07, n = 27, $P > 0.5$; $\bar{x}$ = 3.2 ± 0.18 nestlings). Although in larger groups a lower proportion of eggs produced nestlings at day 10, as expected from the previous results, the relationship was not significant (r_s = −0.11, n = 17, $P > 0.5$; $\bar{x}$ = 0.61 ± 0.061). For nests that fledged young, nestling survival from banding to fledging did not differ significantly between small groups (1 to 3 helpers, 38.1% disappeared, n = 21) and large groups (4 to 7 helpers, 45.5% disappeared, n = 11; Fisher's exact test, P = 0.5). Disappearances between fledging and six months of age, which is the period of transition to nutritional independence (Langen 1996b), did not differ significantly between small groups (37.5%, n = 8) and large groups (11.7%, n = 17; Fisher's exact test, P = 0.3).

TABLE 1. Results of goodness-of-fit tests comparing the total number of feeding visits made by older classes of White-throated Magpie-Jay group members with the null expectation that all members provision equally. For significant results, we also include the χ^2 cell contribution and the direction of deviation for each provisioner class.

Group	No. of older helpers	Provisioning of female[a] χ^2	n	(Male, Older helper)	Provisioning of offspring[b] χ^2	n	(Male, Female, Older helper)
Aviary 92	3	4.3*	65	(−3.2, +1.1)	7.1*	239	(−3.4, +3.6, 0.0)
Aviary 93	5	0.5	33		3.0	122	
Caja 92	1	0.4	44		1.8	145	
Caja 93	1	—	—		9.2*	32	(−4.2, 0.0, +5.0)
Camp 92	4	0.4	70		1.5	23	
Casona 92	2	23.1***	93	(−15.6, +7.5)	1.5	136	
Casona 93	3	13.0***	39	(−9.8, +3.2)	10.0**	153	(−8.0, +0.2, +1.9)
Chirigon 92	1	7.9**	15	(−4.0, +4.0)	—	—	
Comedor 92	3	2.2	102		78.2***	351	(+61.7, −8.3, −8.2)
Comedor 93	2	0.9	21		19.0***	165	(−14.3, +1.5, +3.3)

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

[a] Feeding visits by breeding male and older helpers (pre-incubation and incubation stages combined).

[b] Feeding visits by breeding male, breeding female, and older helpers (nestling and fledging stages combined).

TABLE 2. Results of contingency tests examining whether individual White-throated Magpie-Jays preferentially provision particular fledglings within a brood.

Group	χ^2	(df)	No. of fledglings[a]	Provisioners[b]
Aviary 92	6.1	5	2 (56, 62)	M, F, 4H
Caja 92	3.5	3	2 (45, 52)	M, F, 2H
Caja 93	3.6	6	3 (30, 34, 49)	F, 3H
Casona 92	8.6*	4	2 (62, 66)	M, F, 3H
Casona 93	4.5	5	2 (63, 89)	M, F, 4H
Comedor 92	22.3**	8	3 (83, 109, 115)	M, F, 3H
Comedor 93	9.3	12	5 (38, 32, 39, 23, 27)	F, 3H

*, $P < 0.10$; **, $P < 0.01$.

[a] Number of observed feedings for each fledgling in parentheses.

[b] Group members that provisioned fledglings frequently enough to be included in statistical tests. M = breeding male; F = breeding female; H = helper.

DISCUSSION

Effects of helpers on breeding success.—Magpie-jay helpers engaged in much provisioning of breeding females and offspring. Compared with other New World jays (a monophyletic group within which cooperative breeding is widespread; Edwards and Naeem 1993, Espinosa de los Monteros and Cracraft 1997), magpie-jays provided a higher proportion of feedings to nestlings than 12 of 13 species that have auxiliaries (Table 3). The large contribution by nonbreeders was a consequence of four factors: (1) a large number of auxiliaries per breeding group; (2) each auxiliary was a helper; (3) most of the helpers were older, experienced group members; and (4) the average older helper provisioned at least as frequently as each breeder. However, as observed in a number of cooperatively breeding species (Brown et al. 1978, Brown and Brown 1981, Raitt et al. 1984, Russell and Rowley 1988, Woolfenden and Fitzpatrick 1990), the rate of provisioning did not appear to increase significantly with the number of helpers, nor did the number of offspring fledged per successful nest increase with group size. It is possible, however, that the quality or quantity of food brought during feeding visits varied with membership class, as is true of some other species (Stallcup and Woolfenden 1978, Hunter 1987). We could not estimate load size accurately, but for the subset of feeding visits in which food items were visible, young helpers did not provide qualitatively different

TABLE 3. Proportion of feeding visits to nestlings made by group members other than the presumed parents for species of New World jays. Only groups with potential helpers are included; *n* is the number of group years. Expected is the proportion of feeding visits provided by auxiliaries if all group members provisioned equally.

Species	Group size	Feedings		*n*	Source
		Observed	Expected		
Aphelocoma californica	4.0	0.01	0.50	1	Burt and Peterson 1993
Aphelocoma coerulescens	3.7	0.44	0.46	10	Stallcup and Woolfenden 1978
Aphelocoma ultramarina	13.3[a]	0.58	0.85	7	Brown 1972
Aphelocoma unicolor	4.0	0.77	0.50	2	Webber and Brown 1994
Calocitta colliei	5.7	0.49	0.65	12	Winterstein 1985
Calocitta formosa	5.6[b]	0.61	0.64	9	This study
Cyanocorax beecheii	4.5	0.47	0.56	8	Raitt et al. 1984
Cyanocorax melanocyaneus	11.0	0.60	0.82	1	Hardy 1976
Cyanocorax morio	5.3	0.54	0.62	3	Skutch 1960
Cyanocorax sanblasianus nelsoni	6.0	0.45	0.67	1	Hardy 1976
Cyanocorax s. sanblasianus	20.5[a]	0.40	0.90	8	Hardy et al. 1981
Cyanocorax yncas cyanodorsalis	4.0	0.43	0.50	2	Alvarez 1975
Cyanocorax yncas glaucescens	4.7	0.00	0.57	9?	Gayou 1986
Gymnorhinus cyanocephalus	3.0	0.26	0.33	4	Marzluff and Balda 1990

[a] Plural breeders in which breeders also help at other nests; group size includes all territory members.

[b] Primary breeders' nests only; includes young helpers.

food than did older group members (Langen 1996b).

Although not affecting the number of offspring fledged per nest, groups with many helpers had more successful nests per breeding season. This was not a result of higher rates of successful nesting or increased numbers of secondary nests in larger groups, but arose because breeders attempted more nests. Helpers provided a type of "load-lightening" (sensu Brown 1987) such that after producing fledglings, primary breeders were more likely to renest in large than small groups while helpers continued to care for offspring of the previous brood. Renesting even coincided with the peak period of offspring provisioning. Load-lightening that facilitates renesting by breeders or increases breeder survivorship is the most frequently documented benefit provided by helpers (Crick 1992).

Using data from this study and from previous publications (Langen 1996a, Langen and Vehrencamp 1998), we estimated the direct and inclusive fitness of primary breeding females in groups having one and six helpers (the range in our data). We assume that the only result of the helpers' contributions is to increase the number of successful nests, and we have estimated the proportion of successful nests that result from secondary breeders. We also assume that the number of offspring that result from egg dumping by nonbreeders is negligible, and that secondary breeders are full sisters or daughters of the primary breeder (coefficient of relatedness = 0.5). We estimated the difference in offspring production by primary breeders in groups with one versus six helpers to be 4.91 fledglings. Thus, each helper augments the offspring production of the primary breeder by 0.98 offspring within this range. Including the indirect component owing to secondary breeders changes this estimate slightly: the difference in production of offspring equivalents is 5.08, or 1.02 per helper.

Brood division.—After fledging, male and female parents care for a different subset of the brood in some pair- breeding birds (e.g. Moreno 1984, Edwards 1985, McLaughlin and Montgomerie 1985, Byle 1990). Offspring of different broods join after fledging in two cooperatively breeding, plural-nesting jays, and begging offspring are fed almost indiscriminately by all group members (Brown and Brown 1980), or principally by the parents and some male helpers (Marzluff and Balda 1992). Similar to another study of a cooperatively breeding jay (McGowan and Woolfenden 1990), brood division appears to be rare in magpie-jays. A relatively high risk of attracting Collared Forest-Falcons (*Micrastur torquatus*) because of offspring begging (Langen 1996b) may select for flexible responses to offspring demand by provisioners, as has been suggested for related species (Caraco and Brown 1986, Marzluff and Balda 1992).

In some pair-breeding birds, a reproductive division of labor exists after fledging in which males continue to care for the offspring while females prepare to renest (e.g. Zaias and Breitwisch 1989, With and Balda 1990, Weatherhead and McRae 1990, Verhulst and Hut 1996). A similar division of labor occurs between breeding magpie-jays and helpers: breeders renest and leave the helpers to continue feeding the fledglings until the latter reach nutritional independence. This division of labor has been observed in other cooperatively breeding birds (e.g. Brown and Brown 1981, Carlisle and Zahavi 1986, Rowley and Russell 1990) and may significantly increase both the reproductive rate of breeders and the duration of offspring care, which is typically longer than in species that lack helpers (McGowan and Woolfenden 1990, Heinsohn 1991).

Conclusions about helper contributions.—Many uncertainties remain about the form and extent of helper contributions to breeder fitness in White-throated Magpie-Jays. The small sample of groups and the few years of study make it unlikely that we would have detected relatively small contributions by helpers, or contributions that were limited to exceptional years. The experience of breeders was unknown and conceivably may have been correlated with the number of helpers. Our study was conducted in a national park in which the density of jays and nest predators appeared to be much higher than is typical elsewhere within the species' current range (pers. obs.). Habitat and predator densities in the park were undergoing rapid changes (e.g. nesting habitat was declining because of succession after fire suppression [Janzen 1988], and the population of capuchin monkeys had grown by 33% in a decade [Fedigan et al. 1996]). Finally, we observed an unmanipulated range of group sizes; only a subset of groups had few helpers, and no group lacked a helper. It is possible that the presence of helpers had a positive effect on some undetected aspects of breeding relative to an unaided pair, but a ceiling was reached at a smaller helper number than existed in most groups (such ceiling effects are common; Emlen 1991).

Two aspects of helper behavior could modify the conclusions that we present. First, we have assumed that helper reproduction was negligible except via secondary nesting attempts. However, helpers occasionally attempted to lay eggs in the nests of primary breeders (Langen 1996a). If such attempts were regularly successful, then our estimate of helper contributions to breeder fitness is too high. Second, by associating with helpers during the transition to nutritional independence, offspring may have acquired foraging and other skills more quickly and reliably, potentially resulting in lifelong benefits (Langen 1996b). Skill acquisition may have improved because exploratory behavior and practice of skills were facilitated by supplemental feeding and vigilance against predators provided by helpers, or because helpers were exploited as sources of information about predators, appropriate food items, or foraging tactics (Langen 1996b, c). Indeed, young birds (i.e. less than 500 days of age) were more successful at harvesting arthropods in groups with many helpers than in groups with few helpers (Langen and Vehrencamp 1998).

Innes and Johnston (1996), who studied White-throated Magpie-Jays at the same location 10 years before us, came to somewhat different conclusions about the mechanisms by which helpers contribute during breeding. The main difference between the two studies appears to lie in the social classification of jays. For example, Innes and Johnston (1996) included among group members a class called "part-time helpers" that appears analogous to some of the birds that we called "floaters" (i.e. males in the process of natal dispersal; Langen 1996a, b). More important, Innes and Johnston (1996) included all females that attempted nests when investigating the effects of helpers on reproductive success. Their data appear to have included females that we would have classified as secondary breeders. If so, the variation in reproductive success that they associate with the number of helpers may be the result of differences in status and experience between primary and secondary breeders.

We conclude that the main contribution of magpie-jay helpers during our study was to lighten the burden of offspring care on breeders, resulting in rapid renesting after a brood had fledged. Although we probably failed to document some of the helper contributions during breeding, our data suggest that helpers provide a substantial reproductive benefit to breeders, a conclusion similar to that of Innes and Johnston (1996). Helpers probably benefit, too, because they are closely related to the offspring that are produced because of their efforts. However, some putative "helping" actually may be offspring care that results from egg dumping by the putative "helper." In part, helping may allow nonbreeders to gain access to nests and also may make it easier to become a breeder on the natal territory (Langen 1996a). Thus, it appears that helping behavior is selectively favored from the point of view of both the breeders and the helpers.

ACKNOWLEDGMENTS

We thank the staff of the Area de Conservacion Guanacaste in Costa Rica, especially R. Tiffer and R. Blanco, for permission to work in the park and for the many courtesies they performed during our stay. G. Barker, W. Fonseca, G. Birch, S. Villarino, D. Hoffmann, K. Schoonmaker, K. Ward, and J. Schalley worked extremely hard to help gather these data. Comments by three reviewers improved the paper. Financial support was provided by an NIH Genetics Training Grant, the Tinker Foundation, Sigma Xi, the T.C. Schneirla Comparative Psychology Award, the American Ornithologists' Union, and NSF Research Grant IBN 9120789 to S.L.V. This paper was prepared while T.A.L. was supported by an NIH National Service Research Fellowship.

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Associate Editor: K. Martin