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Does Group Size Affect Field Metabolic Rate of Arabian Babbler (*Turdoides squamiceps*) Nestlings?

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ABSTRACT.—Arabian Babblers (*Turdoides squamiceps*) are territorial, cooperative breeding passerines in which groups consist of parents and helpers. All members of the group feed nestlings in a single nest and all group members provision at similar rates. We hypothesized that the field metabolic rate (FMR) of Arabian Babbler nestlings is related to group feeding; that is, FMR would be greater in nestlings of larger rather than smaller sized groups. To test that hypothesis, we measured FMR of 10 day old nestlings from small (2 and 3 individuals), medium (4 and 5 individuals), and large (6 or more individuals) groups. We also determined number of hatchlings and fledglings produced per group. There was an increase in body mass and FMR from small to medium-sized groups, but there was a levelling off or decrease in those parameters in large groups. That suggests that there is an optimum group number for provisioning nestlings, above which there may be a negative effect. The relationship between group size and annual number of eggs was not significant, but there was a positive and linear relationship between group size and annual fledglings production. Thus, more eggs reached the fledgling stage with an increase in group size, suggesting that larger groups are better able to defend the nest against predators.

There are over 200 species of cooperative breeding birds in which parents and helpers feed nestlings (Brown 1987). Group size varies within species, and the significance of the number of individuals has been researched and discussed extensively (Wright 1998, Shaw and Shewry 2000). It has been suggested that because helpers provision nestlings, they can increase the productivity of the group. Helpers can reduce the onus placed on parents to provision nestlings and reduce the parents' reproduction costs (Rabenold 1990, Sydeman 1989), which can allow the parents to nest more frequently and produce more offspring.

The Old World genus *Turdoides* includes 29 species. Of these babbler species, 14 are known to be cooperative breeders and 12 are likely to be so (see Shaw and Shewry 2000). Territories are usually passed through the males, whereas the females disperse more readily (Gaston 1978a, Shaw and Shewry 2000). The Arabian Babbler (*T. squamiceps*) inhabits extreme deserts and is the only bird species in Israel that lives in groups year round. Those groups are territorial, with number of birds per group generally between 3 and 5 individuals, but can range between 2 and 22. Each group usually contains one breeding pair; young birds do not disperse for one to three years, during which time they act as helpers (Zahavi 1989, 1990). Zahavi (1974, 1990) found either no relationship between group size and number of fledglings produced or, when there was a relationship, it was restricted to smaller groups and to certain years. Wright (1998), studying babblers at the same site over a three year period, found that larger groups produced more fledglings.

Arabian Babbler helpers and parents provision nestlings at similar rates, irrespective of sex or dominance rank within the group (Wright 1997, 1998). Consequently, nestlings from large groups should receive more food than nestlings from small groups. We hypothesized, therefore, that group size has an effect on the field metabolic rate (FMR) of nestlings; that is, field metabolic rate would be greater with an increase in group size. To test that hypothesis, we determined FMR and body mass of nestlings from different sized Arabian Babbler groups. We also determined the number of nestlings and fledglings produced by the groups.

Materials and Methods.—Study species and study site.—We divided the groups of babblers into three size categories: *small* included 2 and 3 individuals, *medium* included 4 and 5 individuals, and *large* included 6 or more individuals. The study was done from January 1994 to December 1995 at the Nature Reserve at Hatzeva (30°45′N, 35°15′E) in the Arava, ~30 km south of the Dead Sea. The Arabian Babbler and the site have been described (Anava et al. 2001).

Doubly labelled water measurements.—Measurements of FMR and water flux on 10 day old Arabian Babbler nestlings were done as described by Anava et al. (2001). Only one nestling, chosen at random, was measured per nest.

Treatment of data.—The study was done over two breeding seasons on 36 groups. We collected data on

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TABLE 1. Water efflux, field metabolic rate and body mass of 10 day old nestling babblers from small (2–3 adults), medium (4–5 adults) and large (6–9 adults) groups. Values are means ± SD. Values within rows with different superscripts are different from each other ($P < 0.05$).

Group size	Small	Medium	Large
Sample size	14	24	20
Body mass (g)	35.9 ± 1.54[a]	39.8 ± 1.24[b]	38.7 ± 2.18[ab]
Water efflux (ml/d)	13.6 ± 1.18[a]	15.9 ± 0.95[b]	14.5 ± 0.90[ab]
Field metabolic rate (kJ/d)	43.3 ± 6.53[a]	59.6 ± 5.6[b]	46.1 ± 5.13[a]

each group each year and treated the data on groups as statistically independent ($n = 72$). That seemed justified because the helpers and composition of some of the groups as well as the group size changed between years. There were 20 small, 31 medium, and 21 large groups. We used a two-way analysis of covariance (ANCOVA) to analyze for difference of body mass among group sizes, taking brood size as a covariate factor. In that way, the effect of brood size on body mass of the nestlings was removed. In addition, we used a two-way ANCOVA to analyze for difference of FMR and water flux among group sizes, taking body mass and brood sizes as covariate factors. Thus, the effects of body mass and brood size on water flux and FMR were removed. Least squares difference (LSD) was used to separate means where significance was found. Data are presented as means ±1 SD, and $P < 0.05$ was chosen as the lowest acceptable level of significance.

Results.—Nestling development, growth, water flux and field metabolic rate.—At 10 days of age, nestlings from medium-sized groups had a greater body mass ($P < 0.04$) than nestlings from small groups; large groups did not differ from either small or medium-sized groups (Table 1). FMR of 10 day old nestlings from medium-sized groups was higher ($P < 0.05$) than that of small and large groups (Table 1). Water efflux of 10 day old nestlings from medium-sized groups tended to be higher ($P < 0.07$) than that of small and large groups (Table 1).

Reproductive success.—Group size did not have a significant relationship with annual number of eggs (Table 2). However, the relationship between the annual number of fledglings (N_f) and group size (GS) was significant and took the form (Fig. 1):

$$N_f = 0.316 + 0.0.805\ GS$$

($n = 72$; $S_a = 0.89$ $S_b = 0.18$; $S_{y.x} = 2.69$; $F = 19.7$, df = 1 and 70; $r^2 = 0.22$ and $P < 0.001$).

Of 169 total nesting attempts, 34.9% (59 of 169) failed to produce fledglings. Small groups failed in 43% (20 of 46), medium-sized groups in 37% (30 of 81), and large groups in 21% (9 of 42) of nest attempts.

Discussion.—Body mass and field metabolic rate.—In some species of cooperative breeding birds, growth rate of nestlings is higher with more helpers (Bennun 1994), but that was not found for all communal birds (Brown 1987, Dow and Wilmore 1990). Wright (1998) found no relationship between group size and body mass in 10 day old Arabian Babbler nestlings. However, in this study, body mass of 10 day old nestlings from medium-sized groups was greater than that of small groups and, therefore, group size had an effect on body mass. But body mass did not increase with group size in large groups. In fact, nestlings from the medium-sized groups tended to have the greatest body mass.

FMR in 10 day old nestlings basically followed the same relationship to group size as did body mass; that is, FMR was highest in nestlings attended by medium-sized groups. That indicates that the nestlings from the medium-sized groups received the most food and energy and explains the difference in body

TABLE 2. Annual reproductive characteristics and success in Arabian Babblers of different group sizes. Values are means ±SD. Values within columns with different superscripts are different from each other (ANOVA, $P < 0.05$).

Group size	n	Number of nesting attempts	Eggs	Hatchlings	Nestlings	Fledglings	Fledglings/eggs
2	7	1.6 ± 0.5	5.2 ± 1.8	3.6 ± 1.5[a]	3.2 ± 1.1[a]	2.4 ± 0.5[a]	0.50 ± 0.18[ab]
3	13	2.2 ± 1.1	8.3 ± 3.9	5.6 ± 2.8[ab]	4.8 ± 2.2[ab]	3.0 ± 2.0[ab]	0.36 ± 0.20[a]
4	22	2.4 ± 0.9	8.6 ± 3.3	5.2 ± 1.9[ab]	5.0 ± 2.0[abc]	4.0 ± 2.2[ab]	0.51 ± 0.31[ab]
5	9	2.2 ± 1.0	9.1 ± 3.7	6.8 ± 2.3[bc]	6.0 ± 2.3[bd]	5.0 ± 2.7[abc]	0.60 ± 0.29[ab]
6	8	2.3 ± 1.0	7.8 ± 2.6	7.3 ± 2.5[bc]	5.8 ± 3.9[abcd]	5.5 ± 4.1[abc]	0.68 ± 0.39[ab]
7	4	2.7 ± 1.2	9.7 ± 3.8	8.3 ± 4.1[c]	8.3 ± 4.1[d]	6.7 ± 4.9[c]	0.59 ± 0.37[ab]
8	6	2.3 ± 0.6	9.3 ± 2.3	7.7 ± 0.6[bc]	7.3 ± 1.2[cd]	7.3 ± 1.2[c]	0.81 ± 0.17[b]
9	3	2.7 ± 1.2	10.3 ± 4.0	8.0 ± 0.0[bc]	7.7 ± 0.6[bc]	6.3 ± 1.5[abc]	0.68 ± 0.30[ab]

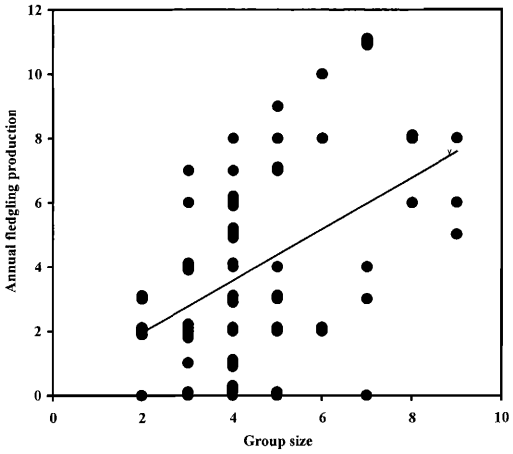

FIG. 1. The relationship between group size and the annual production of Arabian Babbler fledglings.

mass of nestlings among group sizes. FMR is composed of maintenance heat production and the heat increment of feeding for growth, but does not include energy retained in the body (Kam and Degen 1997a, b). Because the nestlings of medium-sized groups were largest, then those nestlings had a higher heat increment of feeding for growth than nestlings from small and large groups, and that could explain, at least in part, the higher FMR in those nestlings.

Reproductive success: Group size effect.—The effect of helpers on reproductive success has been discussed widely, and several theories in relation to nestling survival and body size have emerged: (1) more helpers improve the survival of nestlings by antipredator behavior (Mumme 1992, Woolfenden 1980); (2) more helpers bring more food, and therefore chick mortality due to starvation will be reduced, and growth rate will increase (Bennun 1994); and (3) allofeeding with more helpers will put less onus on the parents to provide food allowing the parents to reduce the interval between broods and produce more offspring per year.

In general, groups with helpers are more successful in reproduction than just pairs, and there is an increase in reproductive success with an increase in number of helpers. For example, Colonial Bee-eaters (*Merops bullockoides*) with helpers have more clutches and lower nestling mortality than just pairs (Dyer and Fry 1980). In addition, pairs with two to three helpers are twice as successful as pairs without helpers (Emlen et al. 1980). Florida Scrub Jays (*Aphelocoma coerulescens*) with one to four helpers have 2.1 offspring, whereas pairs without helpers have only 1.2 offspring per year (Woolfenden 1980). Similar results were found for *Campylorhynchus* wrens. Groups of those wrens usually range between two to eight individuals (pair plus zero to six helpers). Without helpers, reproductive success is extremely low; however, with two helpers (four individuals), there is a dramatic increase in reproductive success. Increases in number of helpers above that number results in only moderate increases in reproductive success (Rabenold 1990). However, benefits have not always been reported for cooperative breeders (Brown 1987). No effect on breeding success per nest because of helpers was found in the Superb Fairy-wren (*Malurus cyaneus*), in that groups (pair plus helpers) and pairs did not differ in nestlings hatched per egg laid, fledglings produced per hatchlings, number of nesting attempts, and number of fledglings produced per season (Nias and Ford 1992).

Babblers.—No relationship between group size and breeding success was found in the Common Babbler (*Turdoides caudatus*; Gaston 1978a), Jungle Babbler (*Turdoides striatus*; Gaston 1978b), Arrow-marked Babbler (*Turdoides jardinei*; Monadjem et al. 1995) and Bare-cheeked Babbler (*Turdoides gymnogenys*; Shaw and Shewry 2000). Results for the Arabian Babbler have been equivocal. Zahavi (1974), observing Arabian Babblers at Hazeva, first reported no relationship between group size and the number of fledglings produced; however, in a later study (Zahavi 1990), he found that a relationship between group size and fledglings occurred, but it was restricted to small group sizes and only to certain years. Wright (1998), studying Arabian Babblers at the same site as Zahavi, found a positive and linear relationship between group size and the reproductive success of the parents.

Zahavi (1974) theorized that chick feeding by Arabian Babbler helpers acts as a signal by the helper to gain social prestige within the group. Competition for social prestige can cause interference among helpers and can actually have a negative effect on productivity of the group (Carlisle and Zahavi 1986). In this study, there was an increase in body mass and FMR from small to medium-sized groups, but there was a levelling off or decrease in these parameters in large groups. Those results suggest that there is an optimum group number for provisioning nestlings, above which there may be a negative effect. That may be due to interference among the helpers. The relationship between group size and annual egg production was not significant, but there was a positive and linear relationship between group size and annual fledglings production. Highest percentage of nests that did not produce nestlings was in the small groups whereas the lowest percentage was in the large groups. That would indicate more eggs reached the fledgling stage with an increase in group size, suggesting that larger groups are better able to defend the nest against predators.

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