Helping-at-the-nest and group size in the Arabian Babbler
Turdoides squamiceps

Jonathan Wright

The effect of group size on the productivity of communally-breeding bird species has for many years been linked with the various adaptive explanations for helping-at-the-nest. This study examines the effect of group size on group provisioning effort and group productivity in the Arabian Babbler Turdoides squamiceps, a species in which helping behaviour is reported to have limited impact on parental reproduction, and has instead been uniquely proposed to operate as a signal within the group to gain social prestige. Contrary to these earlier reports, the present study showed a strong positive and linear effect of group size upon the total number of provisioning visits to the nest and the number of fledglings produced. Larger groups produced larger numbers of young, although individual fledging mass did not decrease with this increase in brood size. Fewer faecal sacs were removed per visit in nests with larger broods, and this was the only variable for which an initial positive effect of group size could be explained by the potentially confounding effect of brood size. In addition, individual provisioning effort was reduced in larger groups, both in terms of number of nest visits and the size of prey items delivered per visit. Although these data were collected over only three breeding seasons, the group sizes and breeding conditions involved are broadly representative of this population during the previous 25 years of records. These results therefore suggest that, under the majority of circumstances, helping-at-the-nest in Arabian Babblers has a positive and linear effect on the reproductive success of parents, as well as substantially reducing the provisioning effort required of other group members. Groups were nearly always made up of closely related individuals, and so these data are consistent with kin selection. Helpers gain indirect fitness benefits from the increased reproductive success of nests, as well as potentially reducing the survival costs of chick feeding for adult relatives. The possibility of direct fitness benefits from helping, especially regarding pseudo-reciprocity and adaptive group augmentation, is also discussed with reference to the evolution of helping behaviour and group-living in the Arabian Babbler.

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In over 200 species of birds, breeding pairs are assisted by 'helpers-at-the-nest' that contribute towards feeding chicks that are not their own (Brown 1987). A number of hypotheses have been proposed to explain why this apparently altruistic behaviour has evolved. These include: (a) direct or indirect fitness benefits derived from feeding related young via kin selection (Hamilton 1964, Maynard Smith 1964); (b) future increases in survivorship and/or reproduction of helpers through pseudo-reciprocity and augmenting group sizes (Woolfenden and Fitzpatrick 1978, 1984, Ligon 1981, Brown 1983, 1987, Connor 1986, 1995); and (c) enhancement of helper dominance rank, and therefore future breeding success, because chick feeding operates as a signal of 'social status' or 'social prestige' within the group (Zahavi 1974, 1977, 1990, 1995). The effect of helper number on group provisioning effort has always been an important component in any adaptive argument for helping-at-the-nest (see Brown 1987, Stacey and Koenig 1990, Emlen 1991). Additional helpers may increase group productivity, as well as reduce the provisioning effort required (and therefore
the magnitude of future survival and reproduction costs incurred) by the parents and other group members (e.g. Brown et al. 1978, Lewis 1982, Rabenold 1984, Reyer 1984, Austad and Rabenold 1985, Sydeman 1989, but see Mumme et al. 1989). The shape of the relationships between helper number, provisioning effort per bird, and group productivity can therefore indicate the marginal fitness returns experienced by both helpers and parents when provisioning nestlings in groups of different sizes (see Brown 1987, Emlen 1991). Group size effects on factors such as reproductive output are also important when considering the evolution and stability of cooperative groups of different sizes (see Emlen 1997).

According to kin selection theory (Hamilton 1964, Maynard Smith 1964), the shape of the relationship between helper number and group productivity is generally predicted to be a positive one. This would allow helpers to gain marginal increases in the indirect fitness benefits derived from investing effort in rearing related young. However, this is not necessarily a critical prediction. In larger groups or years of plentiful resources, when there are too many group members feeding one brood of nestlings, helpers may still obtain other indirect fitness benefits from easing the chick feeding effort required from other related group members (see Emlen 1991). For example, parents with more helpers may be more likely to survive and reproduce in the future (e.g. Rowley 1965, Reyer 1984, Mumme et al. 1989), or may just increase their chances of producing a second brood in the same season (e.g. Brown and Brown 1981, Lewis 1982). Additional kin-selected benefits may also be gained by the parents allowing older offspring, or other relatives, the safety of remaining within the group, despite their presence being superfluous to group productivity (i.e. ‘parental facilitation’, Brown 1987).

In contrast to kin selection, the direct fitness benefits gained by helpers from pseudo-reciprocity or group augmentation (Woolfenden and Fitzpatrick 1978, 1984, Ligon 1981, Brown 1983, 1987, Connor 1986, 1995) predict that there is always a positive effect of helper number on group productivity. For these explanations involving some form of mutualism between helper and offspring, we expect helpers to contribute only in groups where their efforts will result in useful increases in group size. There may also be limited reproductive advantages to helpers from enlarging groups beyond a certain point, because an overly-large group would not be of any extra use to helpers when they themselves become breeders in the future. However, additional benefits to helpers from producing more young group members may not necessarily involve enhanced future reproductive output of the group. For example, larger groups may be more effective for mutual protection from other groups of conspecifics (Zahavi 1989) or from predation (Caraco et al. 1980a, b).

The theory of helping-at-the-nest in order to gain social prestige within the group (Zahavi 1974, 1977, 1990, 1995) provides few explicit predictions regarding the shape of the relationship between helper number and group productivity. However, signalling for social prestige between group members means that chick-feeding effort does not necessarily have to be related to any fitness consequences for the brood. Therefore, if the altruism of chick-feeding functions only as a signal within the group, we might not expect to see group-wide reductions in chick-feeding effort per bird as group size increases (as predicted for kin selection and group augmentation hypotheses). Social prestige theory also predicts “interference” between helpers, which would have the effect that the number of helpers does not necessarily have a positive effect on the number of fledglings produced (Zahavi 1974). Evidence for such interference between helpers-at-the-nest in Arabian Babblers Turdoides squamiceps has been presented by Carlisle and Zahavi (1986). In line with this, group size was claimed to have little influence on the number of fledglings produced in this species (Zahavi 1974). However, Brown (1975) re-examined Zahavi’s (1974) data and showed that it was statistically consistent with an overall positive effect of group size on group productivity (although this result is itself brought into doubt, by the potentially incorrect use of a one-tailed test, and a P-value of 0.045). Zahavi (1990) presents additional data from the same population, indicating that the effect of group size may be restricted only to smaller groups and only in certain years. Further information and data concerning helping-at-the-nest and its effects on the fitness of the chicks are obviously required before any firm conclusions can be reached concerning the effect of group size in Arabian Babblers (see Brown 1987, p. 173).

This study uses three years of data from the communally nesting Arabian Babbler to examine the effect of group size on total group provisioning effort and the resulting productivity in terms of fledgling number. Observations include provisioning visit rates, the type and size of prey delivered, the removal of faecal sacs from the nest, and the number and mass of young prior to fledging.

Methods

The study population

The Arabian Babbler is a group-territorial, communally breeding thrush-like bird with open nests in thorn bushes, occurring in the Arabian and Sinai deserts. Groups range from 2 to 22 individuals, but more usually between 3 and 12 birds, of both sexes, with age-related linear dominance hierarchies within each sex class. Each group usually contains only one breed-
ing pair, although both behavioural and genetic data (Parker, Lundy, Perl and Zahavi, unpubl. data) have shown that subordinate individuals may obtain some reproduction if they are unrelated to the dominant breeder of the opposite sex (i.e. there is an 'incest taboo'). Young birds delay dispersal for one to three years whilst acting as helpers to their parents, although helpers in newly formed or restructured groups may be less closely related to the breeding pair (for more details see Zahavi 1988, 1989, 1990).

The study site at Hatzeva comprises a 25 km² area of desert, located 30 km south of the Dead Sea in the Arava rift valley in Israel. Twenty groups of Arabian Babblers have been continuously studied there since 1971 by Prof. Amotz Zahavi and students from Tel Aviv University. For at least the last seven years, up to 40 groups have been continuously monitored on a weekly basis and habituated to human observers. All birds are individually colour-ringed and their family histories known.

Data collection

Provisioning data were taken from 27 nesting attempts by 17 different groups during three consecutive breeding seasons, between 1 March 1993 and 30 June 1995. Observations were made for three hours in the morning (starting within an hour of sunrise) and for two hours in the afternoon (finishing within an hour of sunset). Observers sat between 30 and 3 m from the nest, using either telescopes or binoculars where necessary. Previous work on this population has confirmed that provisioning behaviour appears unaffected by these methods of observation (Wright 1997). Provisioning data included: (i) individual bird feeding-visit rate; (ii) prey delivered by size (classed 0–4) and type (larval or adult invertebrate, vertebrate or plant material); and (iii) the removal of faecal sacs from the nest. The mass of each chick was taken using a Pesola balance (to the nearest 0.1 g) on or around chick age 10 days.

Analysis

Provisioning effort was calculated as the mean visit rate to the nest per bird per hour. Prey size was reduced to a mean per bird per visit, and the type of prey delivered and faecal sac removal are presented as mean proportions per bird per visit. Each chick age was divided into two according to whether the observation session was in the morning (as whole number of days) and evening (as number of days plus 0.5).

Sample sizes for the provisioning data over the three breeding seasons were 27 broods on 17 different group territories, involving data on 139 individual birds and 7990 provisioning events. Chick mass data were obtained from only 25 of these broods. The unit of analysis was either chick age, individual bird or brood as appropriate. Some groups appear twice in the data set, because observations were made on two broods in different seasons. However, treating each nesting attempt as statistically independent seems justified since it is the effect of helper number on group productivity that is of interest here. In addition, when two broods from the same group territory were observed it was usually because there had been changes in group size, structure and individual composition between the different breeding seasons. The strict use of group as the unit of analysis would simply reduce the amount of usable data and sample sizes (i.e. 17 groups containing only 87 birds), and has no effect on the significance of any of the P-values or the direction of any of the main results presented here. Estimates of size and type of prey delivered were not available for four broods, and degrees of freedom in these tests have been reduced accordingly. Two-tailed P-values are given throughout.

Results

Provisioning behaviour

In order to test for an effect of group size on each of the provisioning behaviours, stepwise multiple regression procedures were used that tested for the linear effect of group size, and then added the effect of group size squared (i.e. any non-linearity in the group size effect) to the model, but only if it explained a significant additional part of the variance. As Table 1A shows, the total number of visits per hour received by broods increased linearly with group size (Fig. 1), whilst the contribution of each individual group member decreased linearly with group size. Average prey size also decreased with group size, again in a linear fashion (Fig. 2). There was no clear effect of group size on the
type of prey delivered to the nest, although the proportion of vegetable matter decreased with group size and with a decreasing slope (Table 1A). Table 1A also shows that faecal sacs were removed less often per visit as group size increased, but not significantly so. Importantly, there was a clear linear effect of group size on the size of broods (Table 1B, Fig. 3).

To separate out the potentially confounding effect of brood size from the main effect of group size, further multiple regression analyses were performed. As Table 2A shows, none of the significant effects of group size on total visit rate, visit rate per bird and mean size of prey delivered per visit were due to covariation with brood size. Changes in the type of prey delivered with the size of the group were somewhat clarified by this analysis. Larger groups provided less larval prey and more adult invertebrate prey, but neither of these effects was quite significant. Significantly fewer vertebrate prey were delivered to broods of larger groups, which may serve to explain the parallel reduction in mean prey size delivered in these groups, whilst the complex effect of group size on the delivery of vegetable matter disappeared once brood size was controlled for. However, the reduction in faecal sac removal per visit with increasing group size was the result of covariation with a negative effect of brood size, although this only approached significance (Table 2A).

**Mass and survival of young**

The larger brood sizes in larger groups were reflected in the number of fledglings that survived to independence, which was significantly greater for groups with more helpers (Table 1B). Surprisingly, mean chick mass was not significantly affected by group size. All of these group size effects were linear (Table 1B). Such group size effects on chick mass could again be confounded by the larger brood sizes in larger groups, so multiple regressions were carried out with both group size and brood size in the model. As Table 2B shows, mean chick mass was not significantly affected by group size or brood size.

**Discussion**

The present study shows that group size had a positive linear effect on the total amount of provisioning behaviour, and that this was associated with a positive linear increase in the number of fledglings produced per nest, with no reduction in the individual mass of fledglings. This suggests that, at least for the three years of data shown here, helping-at-the-nest in Arabian Babblers had a clear and positive effect on group productivity. Hence, in terms of chick-feeding and its effect on reproductive output, all groups in the present study would have benefitted from a greater number of helpers. Both parents and helpers in all groups would have benefitted from additional numbers of helpers-at-the-nest, because this would have allowed more chicks to be produced at a reduced cost to each group member. Earlier data from this population may have shown this positive effect of group size on group productivity (see Zahavi 1974, Brown 1975), and the overall effect of group size was clearly positive in more recent data collected at Hatzeva (Zahavi 1990). However, the positive linear increase in group productivity presented by Zahavi (1990) was only apparent in one year for group sizes up to seven birds, with the relationship varying between two different breeding seasons and the ranges of group sizes available. The present study includes a

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**Table 1.** Results from multiple regressions, where group size is forced into the equation and then group size squared was added only if the partial r^2 was significant (as indicated by *). Results are given for (A) provisioning data, and (B) chick data. Estimated slopes of partial regressions ‘b’ and P-values are given for both effects. Sample sizes are 27 groups throughout, except for prey type variables where it is reduced to 23 groups, and chick mass variables where it is 25 groups.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Group size</th>
<th>Group size²</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>b</td>
<td>P</td>
<td>b</td>
</tr>
<tr>
<td>(A) Total visits</td>
<td>1.33</td>
<td>0.002</td>
<td>-0.77</td>
</tr>
<tr>
<td>Visits per bird</td>
<td>-0.17</td>
<td>0.039</td>
<td>-0.50</td>
</tr>
<tr>
<td>Prey size</td>
<td>-0.04</td>
<td>0.015</td>
<td>-0.66</td>
</tr>
<tr>
<td>No food</td>
<td>0.06</td>
<td>0.999</td>
<td>-0.35</td>
</tr>
<tr>
<td>Larval prey</td>
<td>-0.03</td>
<td>0.206</td>
<td>-2.27</td>
</tr>
<tr>
<td>Invertebrate</td>
<td>0.03</td>
<td>0.194</td>
<td>2.02</td>
</tr>
<tr>
<td>Vertebrate</td>
<td>0.00</td>
<td>0.095</td>
<td>2.30</td>
</tr>
<tr>
<td>Vegetable*</td>
<td>-0.15</td>
<td>0.024</td>
<td>0.01</td>
</tr>
<tr>
<td>Faecal sacs</td>
<td>-0.01</td>
<td>0.059</td>
<td>-0.09</td>
</tr>
<tr>
<td>(B) Brood size</td>
<td>0.17</td>
<td>0.018</td>
<td>-0.28</td>
</tr>
<tr>
<td>Fledglings</td>
<td>0.24</td>
<td>0.012</td>
<td>-0.30</td>
</tr>
<tr>
<td>Chick mass</td>
<td>0.16</td>
<td>0.764</td>
<td>-2.17</td>
</tr>
</tbody>
</table>

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Fig. 2. The effect of group size on the mean size of prey delivered per visit. Best fit line is shown (y = 1.91 - 0.04x).
Table 2. Results from multiple regressions of the effect of group size and brood size. Results are given for (A) provisioning data, and (B) chick data. Estimated slopes of partial regressions 'b' and P-values are given for both effects. Sample sizes are 27 groups throughout, except for prey type variables where it is reduced to 23 groups, and chick mass variables where they are 25 groups.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Group size</th>
<th>Brood size</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>b</td>
<td>P</td>
<td>b</td>
</tr>
<tr>
<td>(A) Total visits</td>
<td>1.21</td>
<td>0.008</td>
<td>0.68</td>
</tr>
<tr>
<td>Visits per bird</td>
<td>-0.20</td>
<td>0.038</td>
<td>0.24</td>
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<tr>
<td>Prey size</td>
<td>-0.04</td>
<td>0.021</td>
<td>0.20</td>
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<tr>
<td>No food</td>
<td>-0.01</td>
<td>0.517</td>
<td>0.02</td>
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<tr>
<td>Larval prey</td>
<td>-0.05</td>
<td>0.083</td>
<td>0.11</td>
</tr>
<tr>
<td>Invertebrate</td>
<td>0.06</td>
<td>0.051</td>
<td>-0.13</td>
</tr>
<tr>
<td>Vertebrate</td>
<td>-0.01</td>
<td>0.031</td>
<td>0.01</td>
</tr>
<tr>
<td>Vegetable</td>
<td>0.01</td>
<td>0.550</td>
<td>-0.01</td>
</tr>
<tr>
<td>Faecal sacs</td>
<td>-0.01</td>
<td>0.354</td>
<td>-0.04</td>
</tr>
<tr>
<td>(B) Chick mass</td>
<td>0.39</td>
<td>0.490</td>
<td>-2.27</td>
</tr>
</tbody>
</table>

Despite the reduction in prey size delivered in larger groups, the total number of visits increased in larger groups, and as part of this there was a reduction in the proportion of larger vertebrate prey items delivered to the nest in larger groups. This result matches additional experimental data showing that when individual babblers increase their visit rate to the nest, they also decrease the size of the prey they deliver as well (own unpubl. obs.). Despite the reduction in prey size delivered in larger groups in the present study, groups with more helpers must still have delivered greater amounts of biomass to the nest. This is because there was a linear increase in the number of fledglings produced by larger groups, with no significant reduction in the mass or quality of young produced.

So, what relevance do the results of the present study have for the adaptive explanations for helping-at-the-nest in Arabian Babblers? Clearly, the linear
increases in provisioning effort and number of fledglings produced by greater numbers of helpers are inconsistent with earlier suggestions that helping-at-the-nest in this system operates as a signal for social prestige (Zahavi 1974, 1990). Although helping effort per bird decreased with group size, this was more consistent with patterns expected from incomplete compensation mechanisms for collaborative investment in the young in the nest, rather the interference between helpers that is predicted by social prestige theory (Zahavi 1974, 1977, 1990, 1995). This conclusion is supported by the fact that decreases in provisioning effort with group size occurred equally in both parent and helpers (Wright 1997), and that there were no observations of any behavioural ‘interference’ as described by Carlisle and Zahavi (1986) and little evidence of chick-feeding acting as a signal between group members (see Wright 1997).

High helper-offspring relatedness and the consistently positive effect of helping behaviour on the number of fledglings produced means that there are obvious kin-selected benefits from helping-at-the-nest in this species (Hamilton 1964, Maynard Smith 1964). In fact, only one individual out of the 139 birds observed feeding chicks in the present study was known (from individual group history observations) to be completely unrelated to the young in the nest. Two thirds of babbler groups were ‘simple’ family groups, with helpers-at-the-nest always consisting of full, or at least, half sibs of the young in the nest. About one third of groups were non-family groups, because they had more than one male that was unrelated to (and competed for matings with) the breeding female. In such ‘male complex’ non-family groups, more than one male could have been the father of the chicks. However, these males were always related to each other, and so even if they did not gain any paternity in the brood, they were at least the uncles or half-brothers of any young that they fed in the nest. Such high within-group relatedness means that chick-feeding may also have provided individuals with indirect fitness benefits by reducing the provisioning effort required of other related group members.

In Arabian Babblers, different group members show similar chick-provisioning effort (Wright 1997), irrespective of relatedness (J. Wright, P. G. Parker, K. Lundy and A. Zahavi unpubl. data). This, and the clear positive effect of group size on group productivity, makes it possible that helping in Arabian Babblers could have been selected for via direct fitness benefits gained sometime following the nesting attempt, resulting from living, reproducing and dispersing from an enlarged group. Such helping as pseudo-reciprocity (Connor 1986), or as mutualism based on the benefits arising from group augmentation (see Brown 1987), has been suggested because helpers themselves obtain specific benefits from adding more younger (and usually subordinate) members to the group (Woolfenden and Fitzpatrick 1978, 1984, Ligon 1981, Brown 1983). This could result from young group members specifically assisting and being of use to the individuals that helped raise them (Ligon 1983), or simply from helpers benefitting as a by-product of young group members acting in their own best interests as a normal part of the group (see Connor 1986, 1995). In the case of Arabian Babblers, subordinate group members take an active and often equal role in all group activities from age one year onwards. Therefore, within just a year, any new fledglings very quickly become valuable group members, probably posing little threat in terms of reproductive competition to any of the older (and therefore much more dominant) helpers.

In certain cooperatively breeding species, the value of subordinate group members is reflected in the fact that they are ‘kidnapped’ (Heinsohn 1991) by neighbouring groups that are in need of helpers (see Connor and Curry 1995). Fledgling Arabian Babblers can also be ‘adopted’ by neighbouring groups of unrelated birds (Zahavi 1990), often resulting in the movement of potential future helpers from large productive groups to much smaller ones that are just starting up and consist of only two or three birds that are in dire need of augmenting their numbers. From the point-of-view of chick-feeding and group productivity in Arabian Babblers, there seem to be obvious benefits to be gained by the breeding pair (and their relatives) from raising, or even stealing, extra group members, irrespective of relatedness. In addition, larger groups have been reported to be better at defending their territory and resisting take-overs from neighbouring groups (Zahavi 1989). Successful dispersal of young birds in single-sex coalitions to take-over breeding positions in neighbouring groups, are also more likely if they are accompanied by greater numbers of subordinate group members (H. Berger unpubl. data). Therefore, in this species there is potential for investment in helping effort by a young bird leading to an improvement in its chances of one day becoming a successful breeder within a large and productive group.

The effect of group size and helping-at-the-nest on the reproductive output of Arabian Babblers cannot be considered without reference to the helpers’ role in the evolution of group-living in this species. Current theory concerning helping-at-the-nest suggests that it is a secondary decision following adaptive delayed dispersal, and ecological constraints to dispersal due to habitat saturation (see Brown 1987, Emlen 1991, Koenig et al. 1992). Hence, every individual in a group of babbiers may help feed the nestlings as a result of kin selection and/or group augmentation, but only because they are living in groups in the first place. Nearly all of the available habitat at Hatzeva appears to be occupied by groups of babbiers. Pairs of birds are rare, usually
occupying marginal territories and failing to breed. However, we still need to show that individual birds only remain as members of a group because they have nowhere else to go, and that pairs of birds could breed successfully if they were given the more favourable territories. Nevertheless, the fact that each successive member of a group of babblers can have such a positive effect on the reproductive output of the breeding pair does have implications for the dynamics and stability of group-living in this species. Recent attempts to combine the ecological constraints model with kin-selection theory have resulted in the powerful framework of Reproductive Skew Theory, which may be particularly relevant to systems such as the Arabian Babbler (see Emlen 1997). Skew theory, as applied to the present dataset, would suggest that dominant babblers will always allow subordinates to stay as members of the group, because of their usefulness as helpers-at-the-nest — thus explaining the consistently large and stable groups seen in this species.

In conclusion, the present study indicates that for the majority of circumstances in which helping-at-the-nest occurs in Arabian Babblers, there is a positive and linear effect of helper number on group productivity. Additional benefits from helpers were also revealed in the reduced provisioning effort required per group member in larger groups. This has implications for any adaptive explanations for helping-at-the-nest, as well as for the evolution of group-living in this species. Although these results show a potential for mutualistic fitness benefits from adding more subordinate members to the group, high within-group relatedness means that kin selection may play an important role in any adaptive explanation for helping-at-the-nest and group-living in Arabian Babblers.

Acknowledgements — I am very grateful to Amotz Zahavi for the opportunity to work on his wonderful birds, as well as for his helpful and stimulating ideas at all stages of this study. Thanks to Sarah Gillingham, Liam Stirling, Jenny Crystal and Amy McKinven for help in data collection, Arnon Lotem for helpful discussions, Walt Koenig for comments on the manuscript, and to Avner Anava and everyone at Hatzeva for help collecting data on babbler group histories and chick mass data, as well as for their hospitality. For precious desk-space in Cambridge and for comments on earlier versions of this work, thanks to Nick Davies. This study was funded by The Blaustein International Center for Desert Studies, Sede Boker Campus, Ben Gurion University, Israel, and a fellowship from NERC, U.K.

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(Received 20 January 1997, revised 8 August 1997, accepted 20 August 1997.)