

THE RELATIONSHIP OF HABITAT QUALITY TO GROUP SIZE IN HALL'S BABBLER (*POMATOSTOMUS HALLI*)

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A central problem in evolutionary biology concerns the ecological role of operational altruists (Brown 1975a), or helpers (Skutch 1961), as they are known in certain avian communal or cooperative social systems. Critical to the understanding of their role is determination of the factors controlling their numbers in a group. The present study approaches this question by examining some of the proximate factors that influence flock size in a species of bird with a communal social system (*sensu* Lack 1968, Brown 1975a). We believe that knowledge of proximate factors will help us to understand the ultimate factors that are responsible for the adaptive aspects of operational altruism in such social systems. The adaptive value of helpers has been discussed elsewhere (e.g., Brown 1974).

Hall's Babbler (*Pomatostomus halli*) was favorable for this study because its flocks are distinct and the members of a flock readily counted. The species occurs in relatively open habitat so the flocks are easy to find and follow at a distance with minimal disturbance to the birds. Babblers of the genus *Pomatostomus* occur throughout Australia in suitable habitat. The behavioral ecology of *P. temporalis* has recently been studied by Counsilman (1974) and King (1974). Babblers in the genus *Turdoides* have been studied by Zahavi (1974), Gaston and Perrins (1974) and Gaston (1976). In *P. temporalis*, fertilized eggs are produced by a single pair that is aided in various other aspects of the care of the young by helpers (King 1974). The flock consists of the pair plus the helpers. Limited evidence suggests that this is also true in *P. halli* (Balda and Brown 1977).

Using behavior of the babbler flocks to indicate their order of preference for various types of habitat, we found three vegetational indices of home range quality. We used these to test for correlations between home range quality and flock size.

METHODS

Parallel transects were established 30.5 m apart throughout each home range, with no fewer than four transects per home range. Each 15.2 m interval along the transect was assigned to one of six habitat

types. The amount of cover per habitat type was estimated using the line intercept method (Canfield 1941). A 15.2 m steel tape was placed on the ground, and the distances covered by the overstory (trees and shrubs separately) were recorded. The distances of all herbaceous plants (grasses and forbs combined) intercepting the line or 1 cm to the right of the line also were recorded. Percent cover for a stratum was determined by summing the total distance the line was intercepted by the stratum and dividing this sum by the total length of the transect lines. We sampled 198 m in habitat type I; 213 m in II, 167 in III; 91 in IV; 258 in V; and 46 in VI. The number of 15.2 m sampling lines varied from 37 to 45 per home range depending on size and shape (Table 2).

Each flock was followed for one 4-h period commencing no later than 0930. During this period, we made numerous counts to accurately determine the number of individuals in the flock. The maximum count was our estimate of the size of the flock. As the flock moved, we marked its location with plastic flagging so that transects could be established later within the area utilized.

The amount of time spent on different foraging substrates was determined for individual birds (Table 7). Observations commenced only when a bird moved from one substrate to another and ended when the bird again changed substrates. The substrate categories were ground, tree trunks, tree branches, and shrubs. The data may be slightly biased toward the latter three categories because when disturbed (possibly by us), the birds flew into the trees, where they became more conspicuous.

Our observations were made 20–27 August 1974. It was early spring, and most adult female Hall's Babblers had not begun to incubate eggs. We found one clutch of Hall's Babbler eggs (26 August), which indicates the stage of the breeding season.

Statistical methods were taken from Sokal and Rohlf (1969) and Siegel (1956).

STUDY AREA

Hall's Babbler, first described as a species in 1964, is known only from a small region mainly in south-central Queensland (Macdonald 1973). Our main study area was 31.0 km W of the bridge over the Warrego River in Cunnamulla on the road to Eulo. Our second study area was the home range of flock number 6, 21.0 km W of this bridge. Both areas are almost perfectly flat and are covered by patches of grassland and low, open woodland.

We found Hall's Babbler only in Mulga woodland (*Acacia aneura*). Although Mulga constituted the dominant tree (roughly 70% of all trees) in these areas, trees and shrubs of many other species also were present. The area was used for grazing cattle and in one area, horses. Although other babblers, *P. temporalis* and *P. ruficeps*, occurred within a few



FIGURE 1. Habitat of Hall's Babblers. Type I.



FIGURE 2. Habitat of Hall's Babblers. Type III.

kilometers of our study area, we saw neither in our areas.

RESULTS

The eight flocks of Hall's Babblers we located numbered 5, 6, 7, 8, 11, 13, 14 and 15 birds. Six of these flocks, including a variety of sizes from smallest to largest, were chosen for intensive study. We refer to the area in which we observed a flock as its home range. We observed no instances of overlap in the home ranges although on two occasions neighboring flocks approached within a few meters of each other. Our observations, together with the literature on other species of *Pomatostomus* (e.g., King 1974), fully agree with the assertion that all or most of the home range of each flock of Hall's Babblers is actually an all-purpose territory. However, as we saw few contacts between flocks, we have no information concerning the existence or means of territorial defense, and, thus, we refrain from invoking the concept of territoriality. The concepts of home range and territory are used here in accordance with the definitions and discussion in Brown (1975a).

AVAILABILITY OF HABITAT TYPES

We characterized and divided the vegetation within Hall's Babbler home ranges into six

habitat types based on the general composition of the vegetation. All six types occurred in and adjacent to all Hall's Babbler home ranges and were easily recognized as similar throughout the area of study. The habitat types are numbered in order of their preference by the babblers (see below and Table 6), as nearly as we could determine it. These habitats are characterized as follows:

Type I. A moderate to dense stand of trees 9 to 11 m tall and an open canopy; some tall shrubs scattered throughout, herbaceous layer dense (Fig. 1).

Type II. Moderately closed canopy with trees spaced rather uniformly throughout; shrubs very sparse and herbage lush.

Type III. Typical savannah woodland with trees 7.6 to 9.1 m tall spread well apart; density of shrubs low, those present 1 m or less in height. Small patches of open ground present (Fig. 2).

Type IV. A high density of trees and an almost uniformly closed canopy; canopy height quite uniform and measuring 10 m to the tops of the trees. Understory of scattered shrubs 0.6 to 1.8 m tall and a moderate to thick growth of grasses and forbs.

Type V. Very few shrubs and trees, and

TABLE 1. Habitats of Hall's Babblers. The maximum percent of vegetation cover for a given habitat type is 300, 100% trees, 100% shrubs, 100% herbs.

Habitat Type	Percent Covered by			Relative Abundance
	Trees	Shrubs	Herbs	
I	62	5	78	20
II	82%	1%	74%	22%
III	39	4	42	17
IV	81	21	62	9
V	10	6	11	27
VI	0	0	74	5
				100



FIGURE 3. Habitat of Hall's Babblers. Type V.

TABLE 2. Habitat types available to six flocks of Hall's Babblers.^a

Flock		I		II		III		IV		V		VI		S	P
No.	Size	S	P	S	P	S	P	S	P	S	P	S	P		
1	5	12	5	2	2	18	11	0	0	13	7	0	0	45	25
2	7	5	3	8	3	16	8	0	0	11	5	2	1	42	20
3	8	6	5	4	4	26	10	0	0	9	6	0	0	45	25
4	11	3	2	15	4	4	2	10	3	10	4	0	0	42	15
5	14	15	8	10	5	12	5	0	0	0	0	0	0	37	18
6	15	19	9	15	6	5	5	0	0	0	0	0	0	39	20

^a Vegetation was sampled along linear transects in each home range. Each 15.2 m sample was assigned to one of the six habitat types. The number of vegetation samples of each type, S, is followed by the number of patches (runs), P, of that type.

only scattered clumps of herbs. Many large patches of bare ground present (Fig. 3).

Type VI. Grasslands, having a rather continuous stand of grasses and forbs; trees and shrubs absent.

The study area was a mosaic of these habitats. In some cases the types intergraded, such as between I and II and also III and IV, but in most cases boundaries were abrupt and clearly distinguishable. Types IV and VI were infrequent (Table 1).

A run of one or more consecutive samples of the same habitat type along a transect was termed a patch. The observed variation in length of patches can be judged from the data in Table 2. When the sequence of patches along a transect was entered in a matrix of transitional probabilities (Table 3), it was found that the patches were not randomly arranged ($G = 23.87$, $df = 4$, $P = .0001$). Types I and II were adjacent more frequently than expected, and types III and IV-V-VI (combined) were contiguous more often than expected. Conversely, types I and II tended to border types III and IV-V-VI less often than expected. Types I and II were

richer in trees and herbaceous cover than types III, V, and VI (Table 1).

HABITAT USE

The percentages of time that each flock was observed in each habitat during a 4-h morning watch are shown in Table 4. A G test for independence among flocks in the apportionment of time among habitats was highly significant ($P < 0.0001$; $G = 232$; $df = 5$; $n = 240$ min for each flock; type I was pooled with II and types III, IV, V, and VI with each other). Flocks moved from one habitat to another in a 4-h period from 4 to 27 times, for a mean of 13.33 total changes per hour and a mean stay per all habitats of 18 min ($SD = 25.44$; $R = 1-141$). The number of changes between habitats by a flock showed no significant correlation with the patchiness of the flock's home range in the vegetation samples (Table 2, last column) nor with flock size.

HABITAT PREFERENCE

Given the vegetation in its home range, does the flock divide its time randomly among the

TABLE 3. Contiguity of habitat types in home ranges of six flocks of Hall's Babbler, as determined by the number of borders between types proceeding in one direction along a transect.

Preceding Habitat Type ^a		I	II	III	IV + V + VI	
I	O	—	14.00	12.00	2.00	28
	E		8.65	11.94	7.41	28
II	O	11.00	—	3.00	5.00	19
	E	6.93		7.45	4.62	19
III	O	15.00	5.00	—	11.00	31
	E	12.68	9.86		8.45	31
IV-VI	O	1.00	2.00	14.00	—	17
	E	5.96	4.64	6.40		17

^a Preceding Habitat Type: O = observed; E = expected.

available habitat types? To test the null hypothesis that temporal proportions (Table 4) equal spatial proportions (from Table 2) each flock was considered separately, habitats were pooled to eliminate zeros among spatial proportions, and sample sizes were standardized to 100. The choice of sample size was arbitrary but conservative; an n of 100 corresponds to one observation every 2.4 min. The difference between temporal and spatial proportions was highly significant ($P < 0.0001$) for each flock. Therefore, we reject the null hypothesis and suggest that Hall's Babblers favor some habitats and disfavor others.

To reveal the extent and consistency with which a habitat was favored, we plotted (Fig. 4) the percent of time that a habitat was occupied by each flock (from Table 4) against the percent occurrence of that type in the vegetation samples in the flock's home range (from Table 2). If the birds chose a habitat randomly, the ratio of use of that type to its availability for a flock would tend to be 1.0 and the point for that flock on the graph for that habitat would tend to lie on the diagonal. Points above the diagonal show that a habitat was "favored," i.e., the flock spent more time there than expected from its spatial availability to the flock. Points below the diagonal show that a habitat was "disfavored." Figure 4 reveals that habitat types I and II were rather consistently favored and that the other types were relatively disfavored.

Because the availability of habitats differed among the home ranges of flocks, the use/availability ratio for a habitat type is not expected to be the same in all flocks. Variation in use/availability ratios is shown in Table 5. Only the order of preference is expected to be the same. The order of preference was estimated by comparing use/availability ratios dichotomously within flocks only and accumulating the "wins" and "losses" in Table 6, where the resulting order of preference is

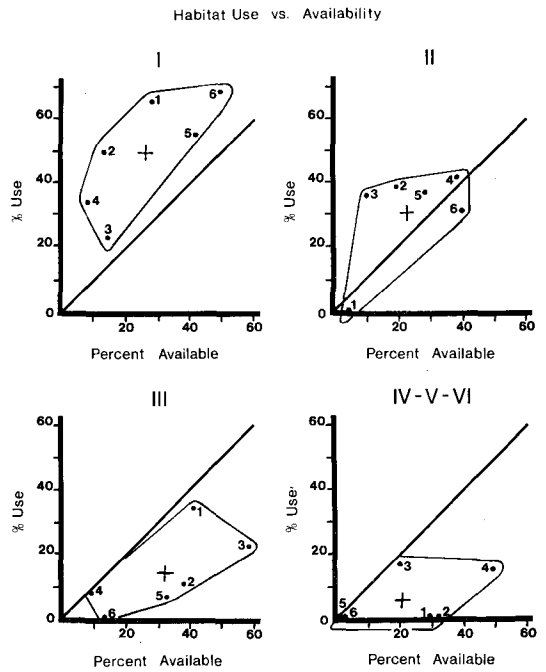


FIGURE 4. Each of the four graphs shows the relationship between temporal use and spatial availability for the six flocks in respect to the indicated habitat types. Each point represents a flock indicated by a number. The crosses show the means. The diagonal ($x = y$) indicates where the points should lie if the proportion of time spent in a habitat by a flock equals the proportion of that habitat in the home range. Habitats with means above the diagonal are referred to as favored; those below as disfavored.

shown. In descending order the six types were favored as follows: I, II, III, IV, V, VI. The significance of the ordering of any two types varies with sample size; some types were infrequent, and preference ranking for these was, therefore, unreliable. The ordering of I, II, and III in Table 6 is consistent with the data in Figure 4. In Figure 4 the more favored types have their bivariate means farther above the diagonal perpendicularly and the less favored types farther below.

Using the values for tree, shrub and herbaceous cover from Table 1, a loose relation-

TABLE 4. Habitat use by six flocks of Hall's Babbler. The figures show the percent of a 4-h observation period spent by each flock in each habitat and the number of moves from one type to another.

Flock	Habitats						Moves
	I	II	III	IV	V	VI	
1	65.83	0	34.17	0	0	0	4
2	50.00	39.58	10.42	0	0	0	7
3	22.50	37.08	22.50	0	17.92	0	19
4	33.75	42.08	8.33	12.92	2.92	0	27
5	55.00	37.50	6.25	0	1.25	0	10
6	68.75	31.25	0	0	0	0	13
Average	49.31	31.25	13.61	2.15	3.68	0	13.33

TABLE 5. Use/availability ratios for six flocks of Hall's Babblers.^a

Flock	Habitats					
	I	II	III	IV	V	VI
1	2.47	0	0.85	— ^b	0	—
2	4.20	2.08	0.27	—	0	0
3	1.69	4.17	0.39	—	0.90	—
4	4.73	1.18	0.88	0.54	0.12	—
5	1.36	1.39	0.19	—	—	—
6	1.41	0.81	0	—	—	—
Average ^c	1.99	1.40	0.43	0.54	0.22	0

^a To obtain ratio in a particular cell, divide the use percent in the corresponding cell of Table 4 by the appropriate availability percent from Table 2.

^b Dash indicates habitat not present in the transects of the home range of a particular flock.

^c Σ use/ Σ availability.

ship between preference for a habitat and the vegetation in that habitat is discernible. The favored types, I and II, have high values for both tree and herbaceous cover. The disfavored types III–VI are low in herbs and/or trees (III, V, VI), with the exception of IV, which is unusually high in shrubs. To understand the habitat preferences of the babblers, it is necessary to consider their foraging behavior. Babblers forage as a close-knit flock, each member constantly potentially reactive to movements and alarms of the others. The proportions of time spent foraging on each of four substrates in five habitat types are shown in Table 7. Babblers forage mostly on the ground, where they gather various small invertebrates and other items somewhat in the manner of a small thrasher or large wren. They are primarily surface-gleaners but also probe depressions and cavities. When alarmed, babblers fly to the trees and shrubs. After an alarm, they work their way back to the ground, foraging on tree trunks and branches as they go. In our study area low grass cover meant many patches of exposed soil and probably less food. Sparse tree cover provided less safety from predators. Therefore, from Table 7 we might expect babblers to prefer habitats that provide in abundance

both grass as a feeding substrate and trees for security. This expectation agrees with the direct correlation found between use/availability ratios and tree and grass cover. The relationship of flock size to the habitat composition of its home range can be seen from the data in Table 2. Flock size was positively correlated with the relative frequency of patches of favored habitat types (I and II combined) per home range (Spearman rank coefficient = $r_s = 1.0$; $P < 0.01$, $n = 6$). Flock size was also positively correlated with the percent of the total transect distance within a flock's home range that was assigned to the favored types (I and II); however, although $r_s = 0.81$, the correlation lacks statistical significance ($P > 0.05$, $n = 6$). Behavioral and ecological variables (preference, flock size) are both positively correlated with the same features of the habitat, namely, the relative occurrence of types I and II. This observation tends to strengthen the biological meaningfulness of the statistical findings.

In order to determine what features of the six habitats might be responsible for the above correlations, we used the data in Tables 1 and 2 to estimate the proportions of tree, shrub, and herbaceous cover in the home range of each flock. An estimate of the percent of

TABLE 6. Dichotomous comparisons of habitat use/availability ratios within six flocks of Hall's Babblers. Values in the table represent the number of times the habitat type on the left had a higher ratio than the habitat type at the top of the column. The four ties are omitted from this table and from the statistical tests but are shown in the totals.

Habitat with Higher u/a	Habitat with Lower u/a						Totals ^a			Probability ^b
	I	II	III	IV	V	VI	>	=	<	
I	x	4	6	1	4	1	16	0	2	0.001
II	2	x	5	1	3	1	12	1	5	0.072
III	0	1	x	1	3	1	6	0	12	0.119
IV	0	0	0	x	1	0	1	0	3	—
V	0	0	1	0	x	0	1	2	11	0.003
VI	0	0	0	0	0	x	0	1	3	—

^a > : no. of times habitat type in left column had a higher ratio than habitats listed at top; = : no. of times ratio was tied; < : no. of times habitats at top of column had a higher ratio than habitats in left column.

^b The probability of such a distribution is based on a one-tailed binomial test of a 1:1 ratio, which is expected in the absence of habitat preference.

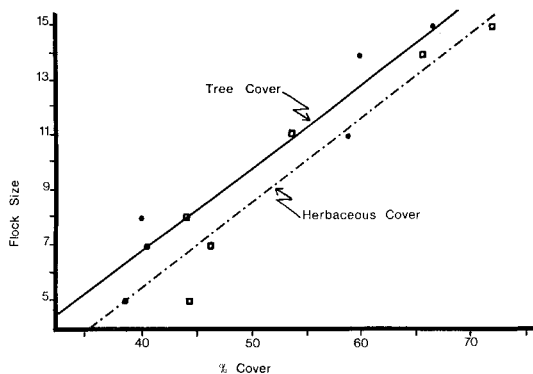


FIGURE 5. Regression of flock size on tree and herbaceous cover. Flock size is positively correlated with the percent of the home range covered by trees (dots) and the percent covered by grass and forbs (squares). For trees $y = -5.59 + 0.31x$; Pearson product-moment correlation coefficient = $r_p = 0.95$; Spearman rank correlation coefficient = $r_s = 0.94$; $P = 0.01$. For herbaceous cover, $y = -7.37 + 0.32x$; $r_p = 0.95$; $r_s = 0.83$, $P = 0.05$.

a home range that was covered by trees was obtained by summing the percent of tree cover in all of the habitat types represented, weighted according to the relative abundance of the types in that home range. This was done for each home range by summing for all habitats the products of the proportion of trees in a habitat times the proportion of that habitat in the home range. The sums for each flock home range are plotted against flock size in Figure 5. The proportion of herbaceous cover in each home range was treated similarly, but the data for shrubs show only a slight and insignificant negative correlation and are not included.

Correlations exist between flock size and percent of tree cover ($r_s = 0.94$, $P = 0.01$) and also between flock size and percent of herbaceous cover ($r_s = 0.82$, $P = 0.05$) as shown in Figure 5. Tree and herbaceous cover also are correlated with each other ($r_s = 0.94$, $P = 0.01$), the principal exception being type VI. As none of the flocks studied had a home range that was rich in trees and poor in grass or vice versa, the effect of varying these factors independently is not shown

in the present data. Such habitats, although nearby, were not occupied by babblers.

DISCUSSION

Our study was necessarily brief and limited in scope. Our objective was not to prove or disprove an hypothesis but to gather data that would enable an intelligent decision about whether further work on home range quality was justified. As explained below we believe it is.

An important question in the study of communal breeding can be stated as follows, using the terminology of Hamilton (1964): is helping behavior selfish, altruistic, cooperative, or spiteful? Because helpers in some species contribute a large fraction of the food given to the young (e.g. Brown 1970, 1972), the altruism hypothesis seemed worthwhile to examine further. As the food given by the helper can be interpreted as a loss to the helper and a gain to the recipient, helping can be classed as operational altruism. However, Hamilton's four categories were defined in terms of individual fitness, and food is not an adequate estimate of fitness. A closer approximation to a measurement of fitness has been obtained in several field studies by observing the production of young. In all cases with adequate samples, groups with more helpers produced more young than groups with fewer or no helpers (Rowley 1965, Maynard-Smith and Ridpath 1972, Parry 1973, Woolfenden 1975). Only Fry (1972) and Zahavi (1974, as re-interpreted by Brown 1975b) failed to find significant correlations.

The possible reasons for this positive correlation must now be examined. A positive correlation seems at first glance to favor the hypotheses of Hamiltonian altruism or cooperation as opposed to those of spite or selfishness. But only a correlation has been shown. Its cause is still not established. One possible cause for the positive correlation, other than the behavior of the helpers, is that the number of young produced by a flock may be a function of the quality of the home range it inhabits. Production of babbler young

TABLE 7. Foraging substrates of Hall's Babblers in five habitat types.^a

Foraging Substrate	Percent of Time/Habitat					Average
	I	II	III	IV	V	
Ground	84.4	84.1	98.9	84.8	79.0	86.2
Tree trunks	12.7	9.3	0.0	2.2	17.5	8.3
Tree branches	2.9	6.2	1.1	13.0	3.5	5.3
Shrubs	0.0	0.4	0.0	0.0	0.0	0.1

^a Data based on 12 h of observation of foraging behavior of individuals in flocks 2, 4, and 5.

may be expected to be higher in areas having a richer food supply and more trees for safe refuge from predators. Similarly, flock size and the number of helpers may also be higher in rich home ranges for the same reason. In this view, which is not necessarily ours, both production of young and flock size are effects of single causes, namely, home range quality. Positive correlations between flock size and production of young could, therefore, be spurious.

It is notoriously difficult to estimate home range quality, an abstract measure based on fitness. We have employed the birds' time budgets to reveal their habitat preferences and then used these preferences to rank the quality of habitat types. The order of preference is from I to VI, as explained in the results. We then reasoned that home ranges that were rich in the favored habitat types would be of higher quality than home ranges that were poor in the favored types. As flock size was correlated with the frequency of patches of favored habitat types (I and II), we interpret this as a correlation between flock size and one index of home range quality.

We also wanted to know what features of the favored habitat types were important to the babblers. We then converted our data on the proportions of habitat types in each home range to yield cover values for trees, herbs, and shrubs. Again we found correlations with flock size (Fig. 5), and again we interpret them as correlations between flock size and indices of home range quality. We now have three related indices of home range quality. Of course, to the birds, other aspects of their environment that we did not measure (e.g., food) are also important. It would be interesting to explore the reasons why tree and herb cover correlate with behavioral preference and flock size. The main point, however, is that three indices of home range quality derived from observations on habitat preference correlate with flock size.

We emphasize that our indices of home range quality were derived completely independently of flock size. The indices are based on habitat preference, not on reproductive success and survival. In other words, the reasoning is not circular.

The ultimate test of an index of home range quality is its ability to predict realized fitness. Our method appears to predict important components of fitness successfully; flock sizes were larger in home ranges that scored high on our three indices. A larger flock presumably was more successful at reproduction and

survival than a smaller one over the preceding year or two. In theory, a large flock might also arise by attracting immigrants. However, dispersal of babblers from one flock to another is low, at least in *P. temporalis*, because the young tend to stay in their natal flock until maturity and even later (King 1974, Counsilman and King, pers. comm.). It seems more likely that dispersal in communally breeding species would have the opposite effect; more emigrants would come from large flocks than small ones, and small flocks would receive more immigrants than large ones (as seems to be true in *Aphelocoma ultramarina*, Brown, unpubl. observ.). Dispersal would then tend to reduce the correlation between flock size and home range quality.

Because we sampled habitat preference at the inception of the breeding season, we probably obtained estimates that were relevant to reproduction. In theory, habitat preference in winter may be different. However, these babblers are non-migratory, and in *P. temporalis*, most flocks remain on their territories all year. Conceivably habitat preference also may differ during the period when the nestlings or fledglings are being fed. But, as the disfavored habitat types had less tree and herbaceous cover and more bare earth, it is difficult to envision how this might be. On the contrary, we might expect them to be even more disfavored as the weather becomes hotter and dryer, and as moist microclimates become more restricted to shade.

Our correlations center on home range quality, not quantity. Conceivably a large, poor home range may be as good as a small, rich one for babblers. If this relationship existed in our area, we would not expect it to alter the behavioral preferences. It would, however, be expected to result in a lack of correlation between flock size and vegetation cover if larger area fully compensated for inferior quality. Our findings of positive correlations between flock size and home range cover estimates show that the area of a home range in Hall's Babblers is secondary in importance to its quality. Also, our crude measurements of home range area did not show an inverse correlation with flock size.

We may now return to the correlations found by other authors between number of helpers and number of young produced. We were unable to study the feeding of young in Hall's Babbler because we had to leave before the eggs hatched. However, as the social system of *P. halli* resembles that of *P. temporalis*, it is reasonable to expect most or all of the extra birds in flocks of *halli* to be-

come helpers and to feed the young. Because the number of helpers in a flock tends to equal the flock size minus the two breeders, our correlations between flock size and habitat quality indices also can be interpreted as correlations between number of helpers and habitat. The fact that helpers are of variable quality in all studies of helpers complicates but does not invalidate such correlations.

Detailed evidence for a correlation between flock size and habitat quality in a communal species has not been published previously, although abstracts claiming such a correlation in *Turdoides* species have appeared (Gaston and Perrins 1974, Gaston 1976). The existence of such correlations does not prove that habitat variations are solely responsible for variations in flock size and number of helpers. By the same token, the existence of correlations between flock size and breeding success does not prove that more helpers cause more reproductive success. Conceivably both habitat quality and the number of helpers influence reproduction and survival. The point we would like to stress is that the information in the present literature is inadequate to assess the relative roles of helpers and habitat. There can be no proof that either helpers or habitat are ecologically significant until investigators measure and, preferably, control both variables simultaneously.

The only study showing a positive correlation between number of helpers and number of offspring in which habitat quality was partially controlled seems to be that of Woolfenden (1975). Florida Scrub Jay (*Aphelocoma c. coerulescens*) pairs on the same territories produced more young in years when they had more helpers. If these territories can be shown to be similar in quality from one year to the next, then the effect of the helpers could be distinguished from the effect of territory quality.

Because habitat characteristics have not been rigorously assessed and/or controlled in past studies, we must question the prevailing ideas that avian helpers significantly raise the fitness of those whom they help. As an effect of helpers on the fitness of recipients is necessary to invoke kin selection, it follows that the role of kin selection in the evolution of avian communal breeding systems also must be questioned.

SUMMARY

In Hall's Babbler, a communally breeding species, flock size at the inception of the

breeding season was positively correlated with vegetational indices of home range quality. Babblers foraged mostly in the grass and flew up to trees for refuge when disturbed. The size of the flock was positively correlated both with the amount of herbaceous cover (indicating foraging potential) and the amount of tree cover (indicating potential refuge from predators). These observations are among the first to provide systematic evidence for any communally breeding bird that flock productivity is correlated with habitat quality. This relationship suggests that previous positive correlations between flock productivity and flock size in other species may be entirely or partly due to differences in habitat quality among the flocks. The contribution of helpers to breeding success is, therefore, questioned.

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