

## Spacing and Distribution of Bowers in Macgregor's Bowerbird (*Amblyornis macgregoriae*)

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**Summary.** Bowerbirds (Ptilonorhynchidae) have been described as exhibiting exploded lek mating patterns. Quantitative documentation and analysis of spatial dispersion, however, is lacking for most species despite its importance to a fundamental understanding of social organization. We studied Macgregor's Bowerbird (*Amblyornis macgregoriae*) in eastern New Guinea in 1980 and 1981 to quantify spatial distribution and selection of bower sites in relation to ecological and social factors. Forty-two bower sites were located in approximately 750 ha of mid-montane forest. They were linearly and regularly spaced along ridges with a mean inter-bower distance of  $169 \pm 64$  m SD (range 75–348 m). Statistical analysis showed males to be regularly spaced within available habitat. Discriminant analysis of seven habitat variables measured along utilized ridge lines showed that bower sites differed significantly from potentially available sites with respect to slope and width of ridge, closure of canopy, and density of saplings. Placement of bowers with respect to these factors was not correlated with inter-bower distance. Most males maintained only one bower; four (10%) maintained two bowers simultaneously. Males spent an average of 54% of daylight hours within an activity center of 15–20 m radius surrounding the bower and aggressively defended this area against conspecific males. Marauding pressure on bowers was high, and 39% of all observed mating attempts ( $n=18$ ) were disrupted by neighboring males. Macgregor's Bowerbird exhibits a social system that appears to be intermediate between lek behavior and territoriality, combining the social dynamics and opportunism of the former and the uniform field of display sites and nests of the

latter. We hypothesize that dispersion in this species is partly due to males buffering their display space against intruder pressure. We suggest that strict adherence to the dispersion criterion in classifying promiscuous mating systems may be inappropriate.

### Introduction

Spatial and temporal distributions of animals are thought to reflect direct responses of individuals to their environment and to the presence or absence of conspecifics (Brown and Orians 1970). In the evolution of mating systems it has been suggested that natural selection operates first on social dispersion (i.e., group size and spacing) and secondarily on specific mating patterns within the options allowed by that dispersion (Crook 1964, 1965; Alexander 1974; Jarman 1974; Bradbury and Vehrencamp 1977). Any understanding of the interplay of ecological and social factors underlying spatial patterning is thus an essential step in explaining the evolution of the diversity of mating systems observed in nature.

Selection pressures that affect spatial and social organization in birds have been examined for several groups, including blackbirds (Orians 1961), weaverbirds (Crook 1964), grouse (Wiley 1974), shorebirds (Pitelka et al. 1974), and manakins (Snow 1976), and include resource availability, habitat structure, and predation. Preliminary information on behavior and ecology of bowerbirds (Ptilonorhynchidae) (Marshall 1954; Gilliard 1969; Cooper and Forshaw 1977) suggests a diversity of mating patterns within this group, but detailed data are lacking for most species. Early work by Gilliard (1963, 1969) suggested that 15 of the

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18 species are polygynous with males displaying in exploded lek aggregations. For the Satin Bowerbird (*Ptilonorhynchus violaceus*), Donaghey (1981) has shown that males are, in fact, not clumped but widely and usually regularly spaced in available habitat with females nesting between male territories (but see Vellenga 1980 for a different interpretation of the same pattern). Data in Peckover (1970, 1972) suggest a similar dispersion in the Fawn-breasted Bowerbird (*Chlamydera cerviniventris*). We view the distinction between a clumped and uniform pattern of bower placement to be a critical issue given the presumed importance of bowers in male-female interactions, and the susceptibility of bower structure to destruction by intruders.

The present paper addresses this question of dispersion of bower sites in Macgregor's Bowerbird (*Amblyornis macgregoriae*) in eastern New Guinea in relation to ecological and social factors. Given the recent findings (cited above) that historical interpretations of dispersion in bowerbirds may be in error, it is important to examine the issue in this species as it played a central role in previous discussions of evolution of this group (Gilliard 1956, 1963, 1969; Schodde and McKean 1973).

Macgregor's Bowerbird is common throughout its geographical range, the central cordillera of New Guinea. It is confined to continuous rainforest, generally between 1,200 and 2,800 m altitude (Schodde and McKean 1973). The species is sexually dimorphic and probably promiscuous. Males construct a maypole bower (twigs piled up around a sapling), solely along ridges, where courtship display and mating occurs. Males maintain bowers for about nine months of the year, but abandon them during the period of molt, from February to April (Pruett-Jones and Pruett-Jones, unpubl.). Breeding is concentrated during, but not restricted to, the months of September through January. The reproductive phenology of this species has yet to be accurately determined. Some aspects of their geographical distribution, taxonomy, and, to a lesser degree, ecology have been reported elsewhere (Frith 1970; LeCroy 1971; Bell 1972; Schodde and McKean 1973).

## Materials and Methods

*Study Area.* The study area (7°16'S, 146°47'E) comprised approximately 750 ha of primary, mixed mid-montane forest on the southwestern slope of Mt. Missim, Kuper Range, Morobe Province, Papua New Guinea. It consisted of a series of four connecting ridges and the expanses between, ranging in altitude from 1,450 to 2,230 m (Fig. 1).

The forest canopy in this area is irregular but complete, standing about 20 to 35 m high with emergents reaching to 45 m. The understory is generally dense. Lower elevations are dominated by Elaeocarpaceae, Euphorbiaceae, Lauraceae (the largest family, with 20 species), and Meliaceae, while ridge lines and upper regions are dominated by *Nothofagus* (Fagaceae) (Whitmore 1975; Pajmans 1976; Pratt, in prep.). The upper edge of the study area merges with the lower reaches of the moss forest. Tree limbs and trunks are heavily covered with epiphytes and some lianes.

Annual precipitation averages 2,000 mm (Pratt, in prep.). Rainfall is irregularly concentrated between November and April, the wet season, but shows considerable annual variation. A moderate dry season occurs between July and October. Daily temperature ranges from 10° to 25° C, with less variability at lower altitude.

*Methods.* Our study was conducted from August through December, 1980 and September to November, 1981. An extensive search for bowers was made over the entire study area. Bower sites were marked, distances between them measured and altitude readings taken at each site. Locations of bowers were plotted on a map produced from an enlargement of a 1:100,000 PNG topographical map.

Ridge lines are prominent features of the landscape and for purposes of our analyses are defined as crests of land from which the ground slopes away on either side at an angle of at least 20° to a point no less than 50 m from the top of the crest. We refer to major ridges as the prominent backbones of mountain sides leading to the summit, and minor ridges as smaller lines, either isolated or running perpendicular to the major ridge into drainages.

At each bower site, and at 20 m intervals between sites along the mid-line of all utilized ridges, the following habitat and vegetation parameters were measured: (1) slope of ridge, measured with a clinometer along the center line, (2) width of ridge, defined as the perpendicular distance across a ridge to the point where the ground drops more than 1 m from the highest point of ground on the crest and estimated visually, (3) height of canopy, from ground to top of canopy, estimated visually, (4) closure of canopy, estimated visually as a percentage while looking upwards through a 10 × 10 cm open square, and (5) absolute density of trees within a 5 m radius of the sample point, in three size classes: (I) 7–20 cm dbh (saplings), (II) 21–40 cm dbh (pole timber), and (III) >41 cm dbh (mature trees). Twenty-meter intervals between sampling points were chosen to provide an adequate number of samples between bowers. Samples were found to be independent with respect to the seven habitat variables measured ( $R \times C$  test of independence,  $P < 0.05$ ).

Bowerbirds were captured with mist nets and individually marked with colored leg bands. Adult males were distinguished by the presence of an orange crest, but females and immature males could not be separated morphologically. During behavioral observations, immature males and females were distinguished by behavioral criteria: if the resident male repelled a female-plumaged bird, it was assumed to be a young male; if the resident initiated courtship display, it was considered a female. Blinds were constructed at seven adjacent bowers along ridge 1 (Fig. 1). Continuous sampling methodology (Crockett Wilson 1977), coupled with instantaneous scan samples at 1-min intervals (Altmann 1974), were employed to quantify behavioral activity, use of space, bower defense, and intrusion pressure by males. All observations were conducted between 06.00 and 18.30 h in 3-h sample periods for a total observation time of 155 h; analysis of time budgets was based on 120 h for five males (see Results). Observation time was not equal

for all males (mean 24 h; range 18–34 h). Samples were, for the most part, randomized with respect to time of day.

To statistically test whether dispersion of bower sites along the occupied ridge habitat was random, regular, or clumped, intersecting ridges were viewed as one continuous line with bowers as points along that line. The distribution of inter-bower distances was then compared with random distributions based on the broken-stick model (MacArthur 1957), a random numbers table, and the Poisson distribution. The broken-stick model assumes a one-dimensional space that is randomly partitioned (May 1977; Pielou 1977); it is equivalent to the null hypothesis that all sets of segment lengths (i.e., distance measurements) are equiprobable (Pielou 1981). Random distances were generated with the equation,

$$N_m = \frac{1}{S} \sum_{I=1}^m \frac{1}{S-I+1}$$

where  $N_m$  is the proportional length of the  $m$ -th segment of a line divided into  $S$  random lengths. We also created a simple random distribution of points along a line with a random numbers table and the resulting inter-point distances were calculated. This distribution did not differ significantly from that generated by the broken-stick model ( $\chi^2 = 4.46$ ,  $df = 3$ ,  $P > 0.05$ ).

The Poisson analysis was performed by projecting a linear arrangement of cells of varying lengths onto the linear distribution of bower sites. The numbers of points (bowers) per cell was then compared to the expected Poisson distributions. Four cell lengths (75, 100, 150, and 200 m) were used. Coefficients of dispersion (C.D.; variance to mean ratio) were calculated for each distribution as a quantitative description of dispersion. Variance to mean values of one imply a random distribution; a value  $> 1$  implies a clumped distribution; a value  $< 1$  implies a regular or spatially uniform distribution (Sokal and Rohlf 1969).

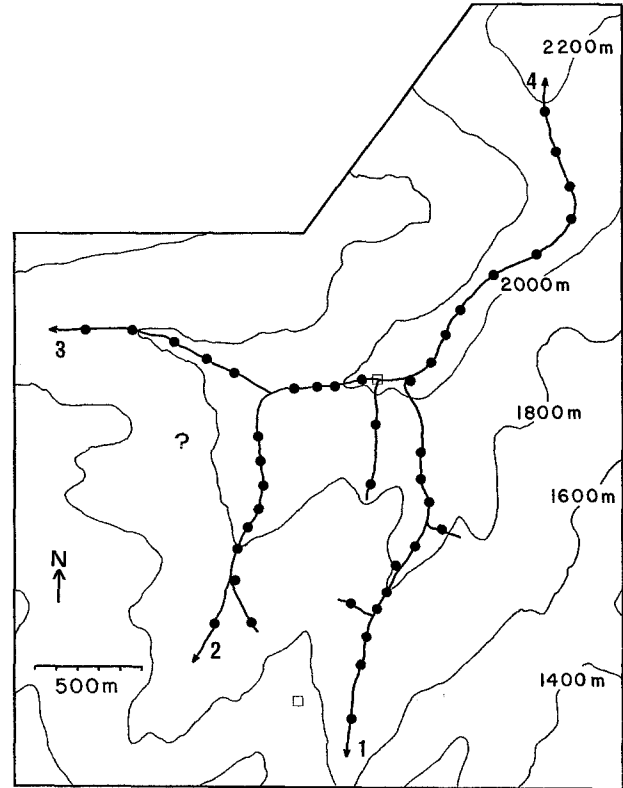
Habitat variables measured at bower and non-bower sites were subjected to discriminant function analysis to examine selection of habitat. The standardized discriminant function coefficients were used to test for significant separation of these two classes of sites (Nie et al. 1975).

## Results

### *Dispersion of Bowlers*

Forty-six active bowers were located during 1980 along 6,788 m of major and minor ridge lines traversing the study area (Fig. 1). All major and some minor ridges were occupied by bowerbirds. Bowlers were located between 1,680 and 2,195 m altitude. Others were found above the study area along ridge 4, towards the summit. None was found below the study area along ridges 1, 2, and 3 although birds were occasionally seen in these areas (Beehler, pers. commun.). Bowlers were only located on ridges and most (40, 87%) were found directly on the ridge crest. Six (13%) were found 3–30 m off the crest on relatively level areas of the slope.

Each bower was maintained by a single resident male. Four males (10%) maintained two bowers 3–24 m apart (considered together as the site of the resident). The study population thus consisted



**Fig. 1.** Map of the study area. Dark circles indicate bower sites active during 1980. Bold lines represent the major and minor ridge lines where bowers were built and thin contour lines show relative topography of the area. Open squares indicate locations of the two field camps utilized during the study. The question mark indicates an area of rugged terrain where minor ridges were not thoroughly searched. The four major ridges are numbered for reference in the text

of 42 males and their bowers. Mean of 40 inter-bower site distances was  $169 \pm 64$  m SD (range 75–348). Comparison of the frequency distribution of inter-bower distances with random distributions generated from the broken-stick model and random numbers table (Fig. 2) shows that no small distances ( $< 75$  m) and relatively few large distances were observed. Differences between observed and random distributions are significant (G-test,  $P < 0.001$ ) and the null (random) hypothesis is rejected.

The observed distribution also differs significantly from the Poisson distribution at each interval length (G-test,  $P < 0.001$ ). Coefficient of dispersion values ranged from 0.21 to 0.55, indicating a spatially uniform distribution of bower sites along the ridges.

Seventeen rudimentary bowers were found at mid-points between established sites at various times during the display season. These are incomplete, ephemeral structures, built and used by one

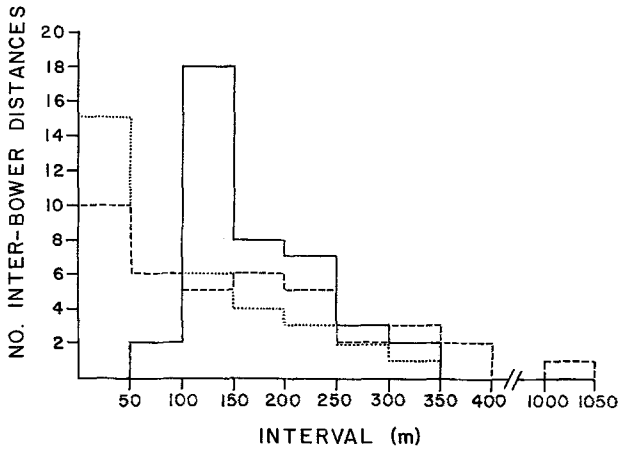


Fig. 2. Comparison of frequency distribution of observed inter-bower distances (solid line) with random distributions generated from the broken-stick model (dotted line) and a random numbers table (dashed line)

or more (up to five) sub-adult males for varying lengths of time before being abandoned. Rudimentary bowers generally consisted of a simple clearing around the base of a sapling, with or without a short pile of sticks, but always lacking a proper maypole. Most (15, 88%) were built along ridge lines.

#### Habitat Characteristics of Bower Sites

In the discriminant function analysis 329 habitat samples, representing variables measured at 44 bower and 285 non-bower sites, were included. There was significant separation between sites and non-sites (Table 1) and the classification routine correctly identified 75% (247 of 329) of the cases as sites or non-sites.

The standardized coefficients indicate relative contribution of the seven variables to the discriminant function. In order of importance, the four variables that contributed significantly are (1) closure of canopy, (2) slope of ridge, (3) width of ridge, and (4) density of saplings (size class I) (Table 1). Comparisons of group means indicate that bowerbirds select areas of greater closure of canopy and density of saplings along wider and more level ridges. Discriminant analysis assumes independence of variables measured (Green 1979). The above four variables were not significantly correlated with each other and, therefore, each apparently has an independent effect on choice of habitat by the birds. The uniformity of bower dispersion together with the importance of selection of habitat implies specific rules by which males settle along ridge lines. These are discussed later.

Table 1. Summary of discriminant function analysis of seven habitat variables measured along utilized ridge lines listed in order of their importance. Coefficients greater than  $\pm 0.4$  are italicized

Variables	Group means $\pm$ SD		P	Standardized discriminant function coefficients
	Sites	Non-sites		
Canopy cover	90.7 $\pm$ 6.3	81.7 $\pm$ 15.8	<0.001	<i>0.543</i>
Ridge slope	9.2 $\pm$ 8.0	12.6 $\pm$ 8.6	0.015	-0.477
Ridge width	7.6 $\pm$ 5.2	5.5 $\pm$ 3.6	0.001	<i>0.463</i>
Tree I density	15.5 $\pm$ 3.4	13.2 $\pm$ 3.9	<0.001	<i>0.411</i>
Canopy height	27.7 $\pm$ 3.8	26.4 $\pm$ 3.8	0.027	0.277
Tree III density	1.7 $\pm$ 1.1	2.0 $\pm$ 1.1	0.202	-0.207
Tree II density	2.4 $\pm$ 1.4	2.6 $\pm$ 1.4	0.358	-0.103

#### Behavioral Activity at Bowers, Use of Space, and Nesting

Fifty-seven bowerbirds (36 males, 19 uncrested birds, and two nestlings) were individually color-banded during the study. All marked males were identified as residents of bowers within the study area. Of the 42 males with bowers, only one was uncrested. Of the seven adjacent bowers where behavioral sampling was conducted, five were maintained throughout the period of study in 1980. Males at the other two disappeared and the sites were not reoccupied before observations ended in late December.

The five persistent males spent an average of 54% (range 20–75%) of daylight hours in attendance or within 20 m of their bower. During attendance, an average of 71% (range 49–91%) of their time was spent quietly perched five to ten meters above the bower, 14% (range 5–34%) vocalizing, 12% (range 3–21%) in maintenance activity of the bower, and 3% (range 1–6%) interacting with visiting or intruding birds. Residents visited their bowers a mean rate of 1.4 times each hour (range 0.6–2.0) and vocalized twice each hour (range 0.6–4.0). Mean length of visits was 4.6 min, and vocalizations 4.7 min. Residents attended their bowers during all hours of the day without a strong diurnal cycle. Comparisons of activity levels among males revealed significant differences in all categories except percentage of time spent interact-

ing with visitors ( $\chi^2$  goodness of fit test;  $P > 0.05$  for percent time in interaction,  $P < 0.05$  for all other categories).

*A. macgregoriae* is an accomplished mimic (Gilliard 1969; Cooper and Forshaw 1977). Both adult and uncrested males exhibited broad and variable vocal repertoires, mimicking other species of birds as well as sounds produced by inanimate objects (Pruett-Jones and Pruett-Jones, in prep.). Most vocalizations were given from traditional song perches within the 20 m activity radius or at the bower itself. Males also sang as far as 60 m down-slope from their bowers. Adjacent males with relatively small inter-bower distances (i.e., 75–125 m) were, at times, in vocal contact and counter-singing was observed. For the population as a whole this was not the case.

Macgregor's Bowerbirds were observed to forage at fruiting trees singly or in small groups, including adult males, and the latter appear to overlap extensively in their use of fruit resources. Males were occasionally observed to forage within the core area around the bower, but were also seen at fruiting trees off the ridge which were used by other males.

Interactions with visitors of either sex occurred on average 0.31 times per hour (range 0.11–0.61). A resident male aggressively defended his bower whenever another male came within the core area, but few aggressive interactions were seen away from this area or at mid-points between bowers. Males marauded bowers (i.e., disassembled the maypole structure) of others when residents were absent. Of 20 intruding males observed, nine partially or completely destroyed the resident's bower. Mean rate of marauding was 0.10 times per hour (range 0.05–0.23). Thus, males suffered some form of bower destruction, on average, once every ten hours. Most intruders were repelled by the resident male upon his return. Repair of a damaged bower by the resident took several minutes up to five or more hours depending on the severity of destruction. Birds of paradise, megapodes, large ground pigeons, and the other ptilonorhynchid (*Ailuroedus melanotis*) on the study area were chased out of the core area as well as conspecific males.

Eighteen courtship sequences and mating attempts were observed. Thirty-nine percent (of 18) were disrupted by neighboring adult or sub-adult males, which often raided in small groups of two or three. Only one successful copulation was seen. In all other cases the female left on her own with the male remaining at the bower. Mean duration of courtship sequences was 3 min 18 s (range

0.5–30.0 min). No significant correlation between inter-bower distance and disruption rate was found, but may be a result of small sample size. The highest rate of disruption was experienced by the male with the nearest neighbor.

Females visited males at a mean rate of 0.19 times per hour (range 0.06–0.33). They arrived at bowers singly or in small groups of two to four, but only one bird interacted with the resident at any one time. Males displayed to as many females as came to the bower. Females visited and engaged in courtship with up to three adjacent males. Females were never seen perched with a male in the vicinity of a bower, and no interactions between males and females were observed away from bower sites.

Two active nests were located in 1980 and four in 1981. All nests were found on or within 30 m of the crests of the same major and minor ridge lines where bowers were placed. Nests were found about midway between adjacent bowers, and were a mean 116 m (range 69–130 m) from their respective nearest bower. During 1980, 23 h were spent watching one nest during the incubation and brooding stages. The female was the only bird observed to incubate the single egg or feed the nestling. No adult male was ever seen near the nest. The diet of the young consisted of both fruit and insects.

## Discussion

Does Macgregor's Bowerbird form leks? Positive statements to that effect (Gilliard 1963, 1969) were based on qualitative, and usually casual, observations of relatively few bowers. Our study has allowed, for the first time, statistical analysis of dispersion in this species. The findings clearly indicate a spatially uniform distribution of bowers and nest sites along suitable ridge line habitat. Whether this pattern is exhibited across the species' entire geographical range remains to be determined. Schodde (pers. commun.) has indicated, however, that the dispersion we observed is consistent with observations he made in other areas, of bowers being "dispersed at rather regular intervals."

Bradbury (1981) defines lek systems according to four criteria: (1) no male parental care, (2) no significant resources required by females at the display site, (3) female choice possible, and (4) clumped distribution of males. Macgregor's Bowerbird meets the first three criteria, but males are not clumped on an arena. A similar situation was found in the Satin Bowerbird (Donaghey 1981).

It remains to be documented, in fact, whether any bowerbird species meets all four of these criteria.

It is worth examining this issue in greater detail, however, considering the wide variability in dispersion in promiscuous species (Bradbury 1981; Oring 1982) and the increasing need to distinguish between descriptive and functional criteria for classification of mating systems. In this species an important consideration is the extent and exclusiveness of the males' territories along the ridges. We observed males to defend mainly a small area (20 m radius) around their bowers, but agonistic interactions were occasionally recorded along the ridge line between bowers. One interpretation of this is that males defend only the bower site and inter-bower distances are regulated by other factors (e.g., resources, predation, etc.). Alternatively, males may defend large, abutting territories at the onset of bower construction (June–July) but once female visitations begin males shift the focus of their defense to the bower itself. Because our study commenced mid-season we cannot, at present, distinguish between these two interpretations. Seasonally flexible defense of boundaries has been observed in other dispersed polygynous species (Gullion 1967; Bendell and Elliot 1967; Lack 1968; Brown and Orians 1970; Ellison 1971).

Clarification of the restriction of bower placement to ridge habitat is requisite for meaningful interpretation of the observed spatial pattern. This restriction has been well documented (e.g., Mayr and Rand 1937; Mayr and Gilliard 1954; Bell 1972; Diamond 1972; Schodde and McKean 1973). Based on discriminant analysis of habitat variables (Table 1), relatively level, wide areas with good cover characterize selected sites. Whether ridge lines offer such characters more frequently than do side slopes is not presently known. We interpret the importance of these specific features as influencing choice of bower sites along a given ridge, rather than selection of the ridge itself. Alternative hypotheses are that males' vocalizations are more audible from elevated ridges, males encounter more females traveling between drainages by placing their bowers on ridges, or that it is a historical artifact of past competitive interactions with sympatric congeners. We do not subscribe to the notion that because bowers are restricted to ridge lines they are, therefore, clumped. Ridge lines appear to be the only acceptable areas for bower placement and are, subsequently, the only potentially available display space. In our study area all such habitat was filled with a uniform field of males.

Exactly what characters make certain ridges

suitable or unsuitable for bower placement are unknown. All major ridge lines in the study area were utilized, but not below 1,680 m altitude despite the presence of female-plumaged birds in these areas. Relatively few minor ridges were utilized compared to the number present.

Analysis of habitat showed that bower location can be roughly predicted by four variables: closure of canopy, slope of ridge, width of ridge, and density of saplings. This specificity of site choice, coupled with the regular dispersion of bowers, implies set rules by which males settle and space themselves out. One possibility is that ridge lines consist of alternate, evenly spaced patches of suitable and unsuitable habitat. This is improbable. More likely, the ridge habitat is sufficiently fine-grained that, given regular spacing governed by other factors, males can always find suitable sites close to where they settle. This would suggest that not all potentially suitable sites along ridges are being used. Our observation of old, inactive bowers between presently active ones supports this interpretation. These inactive sites were also regularly distributed. Furthermore, no correlation was found between habitat availability and inter-bower distance.

Resource availability does not appear to directly influence male dispersion as males do not forage exclusively on territories. However, it may be indirectly important through its effect on female use of space and resource exploitation. If the spatio-temporal distribution of resources is such that female movements increase relative to those of the male, neither females nor resources would be defensible, and male dispersion could be a function of the geometry and size of female home ranges (Bradbury 1981). Testing this hypothesis is the focus of our current research.

The regular and wide spacing of males might be explained by the vulnerable nature of the bower structure and the pressure on males to protect it. The bower is the site and center of courtship display and mating, and represents a substantial investment of time and energy in construction and maintenance. Because bowers are essential to display, their destruction represents a temporary reduction in the resident's potential reproductive fitness. Due to the susceptibility of bowers to marauding, males should space themselves out to minimize the possibility of bower destruction. We suggest that intrusion pressure from neighbors acts to maintain a minimum distance between males within the constraints of bower placement along ridges and potential influences of female movements. Adult and sub-adult males appeared to in-

teract as "local groups", marauding bowers and disrupting displays of rivals one to four sites away. No significant correlation was found between inter-bower distance and intrusion rate. However, given that males interact with rivals beyond their immediate neighbors, such a correlation would not necessarily be expected.

Female visitation rates were relatively low, and the opportunity for mating should be limited for all males. Each encounter with a female, therefore, is potentially vital to a male's reproductive success. Males should be selected to maximize their time available for display; this would be partly achieved by maintaining large inter-bower distances and thereby minimizing possible disruptions of mating attempts. Also, by spending a large percentage of their time at the bower, males would simultaneously be available to receive females and to guard against intruders. Such a strategy is supported by our observation that males spend greater than half the day near their bowers, with only 12% of this time involved in actual maintenance. Wide spacing of males (mean inter-bower distance of 300 m) is also attributed to mating interference and bower marauding by conspecifics in the Satin Bowerbird (Donaghey 1981).

We conclude that Macgregor's Bowerbird does not exhibit lek behavior. This is based on the observed spatial pattern of regularly dispersed bowers as well as the location of nests, the limit of male-male contact and interactions with neighbors, and the hypothesis that susceptibility of bowers to destruction, and their importance in mating success, would not allow for evolution of classical leks in this group (cf. Pruett-Jones and Pruett-Jones MS). Our data suggest that the mating system of Macgregor's Bowerbird may prove to be classifiable as promiscuity (Wittenberger 1979) or dispersed male-dominance polygyny (Oring 1982). However, if males do defend only a small display space around the bower and feeding occurs outside its boundaries, with males overlapping in use of foraging areas, then functionally this system resembles a lek, except that display territories are non-abutting and interspersed with nests. Other behaviors, such as the grouped-nature of marauding by males and multiple visits to males by females, are also akin to lek behavior.

The implications of our findings raise questions about the relative merits of criteria for lekking which are of interest beyond this species. Strict adherence to dispersion as a criterion in classifying promiscuous mating systems may be inappropriate. If the female home range size model (Bradbury 1981), or a version of it, proves correct, then varia-

tion in dispersion of many promiscuous species might be explained by a common underlying gradient of female movements in response to resource availability. Classifying such systems according to dispersion belies their functional similarities and precludes a potentially greater understanding of evolution of mating systems that could result from more direct comparison of divergent patterns.

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