TERRITORY QUALITY AND GROUP SIZE IN THE SUPERB
FAIRY-WREN *MALURUS CYANEUS*

In recent decades there has been much interest shown in the evolution of communal or cooperative social systems in birds (e.g. Brown 1978; Koenig & Pitelka 1981; Emlen 1982). A central theme of recent hypotheses has been that each individual raised within the group faces the choice between two options; either to remain within the group and perhaps to act as a non-breeding helper, or to disperse to an unoccupied territory or breeding vacancy (e.g. Emlen 1982). The potential costs and benefits to the individual's fitness associated with these options have been widely considered (e.g. Brown 1978; Koenig 1981; Emlen 1982). There are generally considered to be two conditions that will favour the retention of potential helpers within the natal group; (1) if such retention enhances the subsequent reproductive success of group members and (2) if there exists a shortage of suitable, unoccupied areas available for independent establishment. In order to fully understand the evolution of cooperative breeding it is therefore necessary to determine the proximate factors that influence the presence, or number, of helpers within a group.

It has been found for a number of cooperatively breeding species that group size often varies in relation to habitat (e.g. Gaston & Perrins 1975; Brown & Balda 1977; Gaston 1978; Stacey & Bock 1978; Roberts 1979; Trail 1980). In the present study, I made an examination of the relationship between certain habitat variables and the number of helpers in groups of the Superb Fairy-wren *Malurus cyaneus*. I studied nineteen groups of Wrens, including seven pairs without helpers, at Eastwood State Forest near Armidale NSW (30°15'S, 151°44'E), during the 1982/83 breeding season. Most of the birds in the study area had been previously colour-banded.

In the Superb Fairy-wren breeding pairs are often accompanied by non-breeding helpers, usually the offspring of the pair from several generations (Rowley 1965). These helpers, as in other malurid wrens (e.g. *Malurus splendens*, Rowley 1981), participate in the feeding and care of nestlings and fledglings.

Superb Fairy-wrens are usually associated with dense shrubs, or thickets, upon which they depend for nest-sites and refuge (Rowley 1965). At Eastwood State Forest, however, there was little understorey, probably due to the presence of grazing animals, particularly cattle, within the forest. Wrens were found in areas of the forest that had been disturbed by logging or partial clearing of the vegetation. This disturbance resulted in the presence of woodpiles and fallen trees, areas of dense sapling growth, and invasion by the exotic

blackberry bramble *Rubus vulgaris*. Wrens were found in association with these thickets, but brambles in particular were favoured as nest-sites and refuges.

Within each territory a number of habitat variables were measured and tested for correlation with group-size. Group-size (GSIZE) was defined as the maximum number of adult birds (i.e. those at least one year old) occupying a territory during the breeding season. About thirty observations of each group were mapped and used to calculate territory size (TAREA). The boundaries of territories were further defined from observations of territorial disputes between neighbouring groups. Groups ranged in size from simple pairs to a group of seven birds with a mean group size of 3.3 birds (S.D. = 1.4, N = 19 social units). Territory size ranged from 0.83 to 2.55 ha (mean = 1.46 ha, S.D. = 0.48, N = 19 territories).

The number of trees and shrubs in twenty 20 m^2 quadrats within each territory was recorded in four separate categories: NTREE 01 = the number of trees (other than *Acacia* spp) 0 to 5 m in height; NTREE 02 = the number of trees (other than *Acacia* spp) over 5 m in height; NACACIA = the number of acacia trees and; NSHRUB = the number of woody shrubs. The presence of acacias (89% of which were recorded as being less than 5 m in height) was recorded separately since they seemed to be preferred as foraging sites over eucalypts (H.A. Ford pers. comm.).

A line-intercept method (Lucas & Seber 1977) was used to estimate the total area covered by woodpiles, fallen trees and dead branches within each territory (AWOOD) and the proportion of the territory covered (PWOOD). The total area of blackberry brambles (BAREA) and their volume (BVOL) was measured for each territory, and the proportion of the territory covered by brambles (PBAREA) was calculated. A percentage canopy cover (CCOVER) was estimated visually from forty sample points within each territory.

All of the habitat variables were tested for correlation with GSIZE by determining the relevant Pearson correlation coefficient. The variable NSHRUB was omitted from the analysis because very few shrubs were recorded in the sample.

RESULTS AND DISCUSSION

Three of the habitat variables measured were significantly and positively correlated with GSIZE (Table I). All three (BAREA, BVOL, PBAREA) were related to the

TABLE I

Values for Pearson correlation coefficients obtained for correlations between variables mentioned in text. N = 19 social units.

	GSIZE	TAREA	BVOL	BAREA	PBAREA	NACACIA	NTREE01	NTREE02	AWOOD	CCOVER	PWOOD
GSIZE	1.00										
TAREA	−0.47*	1.00									
BVOL	0.66**	−0.48*	1.00								
BAREA	0.67**	−0.48*	0.98***	1.00							
PBAREA	0.73***	−0.57*	0.95***	0.96***	1.00						
NACACIA	−0.34	0.56*	−0.59**	−0.59**	−0.55*	1.00					
NTREE01	−0.26	0.17	−0.44	−0.47*	−0.47*	0.42	1.00				
NTREE02	−0.04	0.31	0.04	0.09	−0.06	0.12	0.40	1.00			
AWOOD	−0.43	0.62**	−0.57*	−0.56*	−0.53*	0.67**	0.29	0.17	1.00		
CCOVER	−0.21	0.52*	−0.42	−0.40	−0.39	0.51*	0.18	0.46*	0.52*	1.00	
PWOOD	−0.37	0.43	−0.54	−0.53*	−0.49*	0.58**	0.32	0.17	0.97***	0.45	1.00

  * $p < 0.05$
 ** $p < 0.01$
*** $p < 0.001$

amount of brambles present on a territory. Of the nineteen Wren territories found at Eastwood State Forest, only three contained no brambles at all. These 'poorer quality' territories were occupied by pairs without helpers (Fig. 1). Apart from these few poor quality territories, Wrens were not found to occupy areas of the forest devoid of dense bramble growth.

Blackberry brambles provide a favoured and apparently successful nest-site for Wrens at Eastwood State Forest and are also important refuge and roosting

Figure 1. Correlation between the area of blackberry brambles within a territory (BAREA) and group-size (GSIZE). N = 19 social units. (r = 0.67; p < 0.01).

areas. Although little foraging was observed in brambles, Wrens often fed close to brambles where they could retreat if disturbed. Clearly then, at Eastwood State Forest, the amount of brambles contained within a territory provides at least one measure of the quality of that territory. The other habitat variables considered did not seem to be important in determining group size although some of these (e.g. dense sapling growth, acacias and woodpiles) were characteristic of the disturbed areas in which Wrens were found. This observation was borne out by the results of a multiple regression analysis (Nie *et al.* 1975). The backward-stepping multiple regression procedure removes, in turn, the least significant variable from the regression equation until all remaining variables have a significance level less than 0.1. Using this method a regression equation was obtained which explained 53% of the variation in GSIZE (GSIZE = 2.55 + 1.06 PBAREA, $F_{(1, 17)}$ = 19.30, p < 0.001).

Although larger groups defended larger areas of brambles, a negative relationship was found between group size and territory size (r = −0.47; p < 0.05). According to the sufficient-resource hypothesis (e.g. Brown 1964) territory size should be just large enough to provide the resources necessary for survival and reproduction. Thus for a given group size, territory size should decrease with increasing quantity of resources. Negative relationships were found between territory size and the area (r = −0.48; p < 0.05) volume (r = −0.48; p < 0.05) and proportion of a territory (r = −0.57; p < 0.05) covered by brambles. Smaller groups were generally found on territories containing dense stands of acacias, large areas of woodpiles, and dense overstorey vegetation (indicated by high percentage canopy-cover). Positive relationships were found between
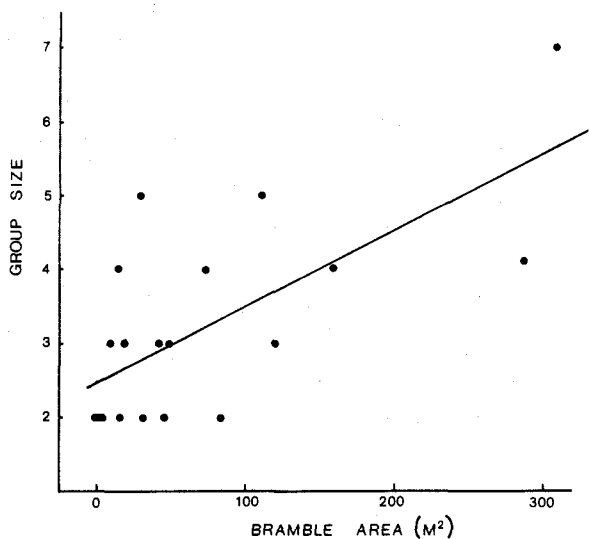
territory size and acacia density ($r = 0.56$; $p < 0.05$), area of woodpiles ($r = 0.62$; $p < 0.01$) and canopy cover ($r = 0.52$, $p < 0.05$).

It is often difficult to find a good measure of territory quality for most species or populations. Some workers have used time-budgets to reveal favoured habitat types (Brown & Balda 1977); vegetation structure (Brown & Brown 1981; Brown *et al.* 1983); or a measure of the available food resources (MacRoberts & MacRoberts 1976; Trail 1980) as potential indicies of territory quality in different species. Ideally however, measures of territory quality should encompass the whole range of physical and biotic factors which influence the survivorship and reproductive success of the resident birds.

At Eastwood State Forest the abundance and distribution of Wrens was found to be largely dependent on the presence of blackberry brambles. The positive relationship between group-size and territory quality found in this population suggests that Wrens occupying better quality territories had either achieved a higher reproductive success than birds on other territories or alternatively, that they had retained a higher proportion of their young as non-breeding helpers.

In summary these results suggest the Wrens are utilising all of the available blackberry brambles and that, within the forest, this type of habitat was saturated. There was therefore a lack of dense understorey vegetation (i.e. better 'quality' areas) that was unoccupied and available for colonization by Wrens. This finding supports the 'habitat saturation' hypothesis put forward by Koenig & Pitelka (1981), which suggests that the retention of offspring within the natal group is favoured when suitable unoccupied habitat is scarce. When opportunities for dispersal are limited by the saturation of suitable habitat, then the optimal strategy for young birds may be to delay dispersal and remain within the natal group. Some of the genetic fitness lost through delayed reproduction may in fact be recouped if non-dispersing individuals are able to enhance the reproductive success of relatives through helping behaviour (Brown 1978). That the presence of helpers may enhance the reproductive success of the breeding pair in the Superb Fairy-wren was demonstrated by Rowley (1965).

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