- Collins, B.G. & Briffa, P. 1983. Seasonal and diurnal variations in the energetics and foraging activities of the Brown Honeyeater, *Lichmera indistincta*. Australian Journal of Ecology 8, 103-111.
- Gessaman, J.A. & Nagy, K.A. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. Condor 90, 662-668.
- Hooge, P.N. 1991. The effects of radio weight and harnesses on time budgets and movements of Acorn Woodpeckers. Journal of Field Ornithology 62, 230-238.
- Klaassen, M. 1992. Transmitter loads do not affect the daily energy expenditure of nesting Common Terns. Journal of Field Ornithology 63, 181-185.
- Massey, B.W., Keane, K. & Boardman, C. 1988. Adverse effects of radio transmitters on the behavior of nesting Least Terns. Condor 90, 945-947.

- McMahon, A.R.G. & Franklin, D.C. 1993. The significance of Mountain Swamp Gum for Helmeted Honeyeater populations in the Yarra Valley. Victorian Naturalist 110, 230-237.
- Menkhorst, P. & Middleton, D. 1991. The Helmeted Honeyeater Recovery Plan: 1989–1993. Department of Conservation and Environment, Melbourne.
- Paton, D.C. 1980. The importance of manna, honeydew and lerp in the diets of honeyeaters. Emu 80, 213-226.
- Pearce, J.L., Burgman, M.A. & Franklin, D.C. 1994. Habitat selection by Helmeted Honeyeaters. Wildlife Research 21, 53-63.
- Runciman, D., Franklin, D.C. & Menkhorst, P.W. 1995. Movements of Helmeted Honeyeaters during the non-breeding season. Emu 95, 111-118.
- SAS Institute Inc. 1991. JMP version 2.04: Software for Statistical Visualization. SAS Institute Inc., Cary, USA.

Differences in Social Behaviour Between Populations of the Australian Magpie *Gymnorhina tibicen*

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The phenomenon of cooperative breeding, or in particular helping behaviour, has been recorded in a number of species of Australian birds (Rowley 1975). 'Helping' is the feeding of nestlings and/or fledglings by individuals other than the genetic parents (Jamieson 1989). In most published cases, helping behaviour is characteristic of a species, although helping may not occur in all groups in all years (e.g. Russell & Rowley 1988).

The Australian Magpie Gymnorhina tibicen, although listed amongst communal breeders by Rowley (1975) and Gaston (1978), was not seen to exhibit helping behaviour, even when a study was specifically designed to search for evidence of it in a New Zealand population (Veltman 1989a). Later observations by Brown & Farabaugh (1991) on the same population observed feeding of nestlings by second year birds but only rarely. Helping has not been reported in any main-

land Australian populations of the species, although Thomas (1974) reported auxilliaries at nests of Tasmanian magpies. However, cooperative defence is a characteristic of the species and is seen in all populations in mainland Australia, Tasmania (Hughes & Mather 1991; Farabaugh et al. 1992) and New Zealand (Veltman 1989a).

The Australian Magpie has a distribution covering most of Australia, with a number of distinct colour forms (Slater et al. 1990). In northern Australia, birds are black-backed (sub-species *Gymnorhina tibicen tibicen*), in the south-east birds are white-backed (*G. tibicen hypoleuca*) and in south-western Australia males are white-backed and females are black-backed (*G. tibicen dorsalis*). In all areas, they defend year-round territories (Farabaugh et al. 1992). There is significant variation in sizes of territorial groups among populations

Table 1 Territory area, number of birds per territory and number of birds fledged per territory in the two populations of Australian Magpies in the 1992 and 1993 breeding seasons compared with data for the New Zealand population at Linton from Veltman (1989a). Means and standard errors are presented and correlation co-efficients (Spearman's Rank) between the variables territory area, number of birds per territory (excluding young of that year), and number of birds fledged per territory 'fledglings'. *P < 0.025, **P < 0.001, ***P < 0.001.

		Variables r	neasured	Correlations (r _s)			
	Territory area (ha)	Birds per territory (not fledglings)	Fledglings per territory	Fledglings per magpie	Area <i>vs</i> adults	Area <i>vs</i> fledglings	Adults <i>vs</i> fledglings
Seymour				* .			
1992, <i>n</i> = 26	_	7.81 ± 0.64	1.89 ± 0.27	0.25	_	· —	0.42*
1993, <i>n</i> = 36	4.21 ± 0.21	6.65 ± 0.42	2.89 ± 0.45	0.43	0.64***	0.55***	0.47**
Moggill							
1992, n = 14	7.95 ± 0.43	2.14 ± 0.10	1.43 ± 0.27	0.75	0.41	-0.09	0.11
1993, <i>n</i> = 15	8.24 ± 0.74	2.53 ± 0.19	1.67 ± 0.97	0.66	0.27	0.23	0.13
Linton							
1989, <i>n</i> = 12	5.00	3.7	1.20	0.5	0.23		

from different parts of Australia but there is no strong relationship between back colour and group size, although black-backs tend to live in pairs whereas white-backed and western forms live in larger groups (Hughes & Mather 1991; Robinson 1956). Here we present data on group sizes from an additional population in northern Victoria. We also present evidence of widespread helping in that population and contrast it with two other populations that have been studied in detail where helping behaviour is either limited or has not been observed.

Methods and study sites

Data are reported from two study sites, one in south-eastern Queensland, at Moggill Farm, Kenmore (27°30′S, 152°E) and the other in northern Victoria, near Seymour (37°2′S, 145°9′E). At Moggill Farm, all birds are black-backed. Seymour lies in the zone of intermediates and thus consists of pure white-backed birds, pure black-backed birds and all intermediate forms.

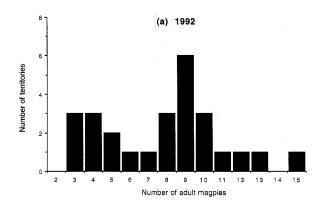
At Moggill Farm, Australian Magpie groups have been studied since 1987. All adult birds are colour banded and the number of territories has varied between 14 and 15 during that time. In Seymour, 26 territories were studied in 1992 and 36 in 1993. Most birds in these territories are individually colour-banded and the variation in back colour patterns in this population means that even unbanded birds within a group can be identified

individually. In 1992, on each of six occasions, territories were observed for 45 minutes and all birds seen either feeding young at the nest or feeding fledglings were recorded. Only those that were colour banded have been included here; on many occasions bands were not seen when birds were fed on the ground, because the grass was very long during that year. In 1993, territories were also watched on six occasions but because a higher proportion of birds were banded, even from the start of the season much more useful data was obtained. Also in 1993, we were better able to gauge the number of females nesting per territory.

Territory boundaries were identified from observations of territorial disputes between banded birds. Territories were mapped in 1992 and 1993 at Moggill Farm and in 1993 at Seymour. Territory areas were calculated by marking boundaries on to 1:20 000 maps. A digitiser was used to measure the size of territories.

Results

Territory sizes were significantly larger in the Moggill population than the Seymour population in 1993 (Mann-Whitney Z = 5.05, P < 0.001), yet the number of birds per territory was significantly smaller (Z = 4.93, P < 0.001, Table 1). In the Moggill population, 12 of the 14 territories consisted of single pairs in 1992; two trios consisted of a pair and a juvenile that had remained from the previous breeding season. Groups were much larger in the Seymour population ranging from 3-15



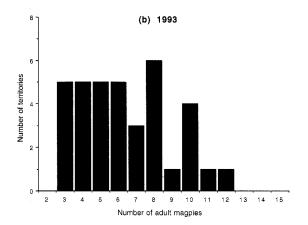


Figure 1 Number of non-juvenile Australian Magpies per territory in the Seymour population in (a) 1992 and (b) 1993.

birds in 1992 and from 3-12 birds in 1993 (Fig. 1). The number of young fledged per group did not differ significantly between the populations in either year (P > 0.05, Table 1).

No correlation was found between territory area and number of adults at Moggill in either 1992 or 1993 but at Seymour, in 1993, there was a significant positive correlation between territory area and both the number of adults and the number of fledglings. Also, the number of adults was significantly correlated with the number of young fledged in both years at Seymour whereas no such relationship was observed in the Moggill population. This was not merely a reflection of the smaller sample size at Moggill, as the correlation coefficients were very close to zero (Table 1).

During nesting and breeding in Seymour, we observed that in any territory, only a single female was

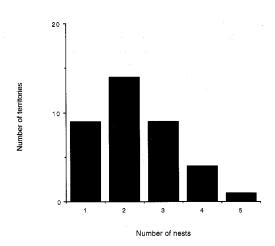


Figure 2 Histogram showing the number of active nests per Australian Magpie territory in the Seymour population in 1993.

ever seen building at a nest. Likewise, only a single female incubated the eggs. She was often observed being fed by a male but only one male was ever seen feeding any particular incubating female. Once the eggs hatched, other members of the group were occasionally observed feeding nestlings at the nest (Table 2). Other members of the group were commonly seen feeding the fledglings. This included adult males and females, subadults and juveniles. In total, some form of helping was observed in 17 of 26 territories in 1992 and in 17 of the 36 territories in 1993. In 1993, when more useful feeding data were collected, 33 of 43 fledglings that were seen being fed three or more times showed some evidence of being fed by birds other than their parents, i.e. by more than one male, more than one female, or by a juvenile (Table 2). These figures are likely to be underestimates of the proportion of territories where helping occurred and more long-term observations are required to obtain an accurate estimate of the % of territories with helpers.

By part way through the breeding season most groups had more than one nest (Fig. 2). These were usually built sequentially by different females, so that young in them were at different stages of development. Our observations at particular nests were limited, but suggested that in most but not all cases the second and third females were not helped by a male. In 1992, we observed a female that had incubated eggs in one nest and had been feeding nestlings there fly to another nest, in which the eggs had been incubated by a second female, and feed those nestlings. In two other territo-

Table 2 Helping behaviour observed in the Seymour population of Australian Magpies from observations on 26 territories in 1992 and 36 in 1993. Data on the feeding of fledglings is more detailed for 1993 than for 1992 because a greater percentage of birds was banded.

	Ne	Fledglings*		
Helping behaviour	1992	1993	1992	1993
Feeding by more than one male	5	1	4	9
Feeding by more than one female	4	4	14	17
Feeding by a juvenile	0	0	6	22
Number of nests where evidence of helping	9	7		
Number of nests where feeding was observed	33	49		
Number of fledglings observed being fed				68
Number of fledglings observed being fed ≥ 3 times (and with potential helpers in group)				43
Number of fledglings fed by a helper				33
A female fed at more than one nest	3	1		
A male fed at more than one nest		3		

^{*} Number of nests/young where behaviour was observed.

ries, females were observed flying to nests other than their own with food in their bills but they were not actually observed feeding the nestlings there. In 1993, a female whose nest failed began feeding nestlings in a neighbouring nest. In another territory, containing four young from two separate nests, a single female was seen feeding all four of them as fledglings. In the same territory in 1993, each of two females fed each of three fledglings on a number of occasions.

At Moggill, no bird other than the two presumed parents has ever been observed either visiting the nest or feeding the fledglings.

Table 3 A summary of differences observed between Australian Magpie populations at Moggill, Linton and Seymour in size of territories and breeding behaviour.

	Moggill, Qld	Linton, NZ (Veltman 1989a)	Seymour, Vic.	
Group size	2-3	2-6	3-15	
Territory size	Medium	Large	Small	
Flock present	Not really	Yes	Yes	
Helping by non-parents	No	No or rare	Yes	
Nests/territory	1	1-2	1-5	
Defence	All birds	All birds	Most birds, some sentinels	

Table 3 summarises the differences observed between the Moggill and Seymour populations, as well as those recorded by Veltman (1989) and Brown & Farabaugh (1991) for magpies in New Zealand. While group sizes are smallest at Moggill and largest in Seymour, territory sizes appear to be smallest in Seymour and largest in New Zealand.

Discussion

Obviously there are some very striking differences in behaviour between Moggill and Seymour magpies. Possibly the most important finding here is that in Seymour, helping appears to be a normal behaviour among members of the territorial group. Such behaviour has not previously been documented in any other population of magpies in mainland Australia and only rarely in New Zealand (Veltman 1989a; Farabaugh et al. 1992). That helping has not been observed in the Moggill population is not surprising as most territories held only pairs. However, in New Zealand, where larger groups are common, a concerted effort to observe helping behaviour reported none (Veltman 1989a). Only when food was added to territories was a magpie observed provisioning nests other than her own (Veltman 1989b). Therefore, it is not merely because Seymour groups are larger that helping occurs there.

Such differences in behaviour within species could

be due to differences in the environmental conditions in which they occur. For example, Veltman (1989a) suggested that the absence of helping behaviour in magpies in New Zealand could be related to the presence of a non-territorial flock, where young birds would go rather than remaining in their natal territories. In Seymour, however, there is both a flock (consisting of over 100 birds, during November 1992, and over 150 birds in 1993) and the presence of helping behaviour. So this explanation is not feasible. Ford et al. (1988) suggested that delayed dispersal and cooperative breeding may be more likely where food resources are predictable and where young birds are particularly vulnerable to predation. Such differences may exist between Moggill and Seymour but would require a lot of further work to measure them. Relatedness among group members is being examined currently using DNA fingerprinting and this will allow us to determine whether helping occurs more often in groups of closely related individuals and whether individuals are more likely to help close relatives as was shown for Pied Kingfishers (Rever 1984), White-fronted Bee-eaters (Emlen & Wrege 1988) and Bell Miners (Clarke 1988).

The tendency for females already feeding their own young to feed the young of other females has also been recorded in Bell Miners (Clark 1984, 1985). It tends to support the suggestion of Jamieson (1989) that helping has arisen as a by-product of selection for philopatry, resulting in birds living communally. He suggested that birds may feed all begging young because this behaviour would have been strongly favoured by selection, so strongly that the feeding of individuals other than their own offspring may not have been strongly selected against. Evidence that close relatives are more likely to be helped than non-relatives may provide evidence against this theory.

The other interesting difference observed between the Seymour and Moggill populations is the much larger groups in smaller territories at Seymour. Such differences cannot be explained solely on the basis of greater food availability in Seymour because if this was the only difference between the two populations, then smaller territories with the same group sizes would be as likely.

The significance of the difference in territory sizes between the two study sites should probably be interpreted with some caution. In general the habitats in the two study sites are similar, both consisting of farmland, with paddocks containing stock (and thus short grass) and scattered trees. In both Victoria and Queensland,

territory sizes are likely to vary significantly with habitat. In south-east Queensland, when territory sizes were examined over a wide range of habitat types, from suburban parks to bushland, territory sizes varied between 2-26 hectares and were strongly negatively correlated with the area of grass per hectare (Hughes et al. 1983). Thus, the differences in territory sizes observed in this study cannot be generalised to geographic regions as a whole.

On the other hand, differences in group sizes appear to show a more consistent trend. Group sizes in Queensland are seldom greater than three (Hughes & Mather 1991), while further south they are larger, with an average of 3.75 in Canberra (Carrick 1972), 4.84 around Adelaide (Shurcliffe & Shurcliffe 1974) and 3.50 around Melbourne (Hughes & Mather 1991). The Seymour population has still larger groups (7.1 in 1992 and 6.4 in 1993) than any of those previously recorded on the eastern Australian mainland (but note, Tasmanian and Western Australian groups are in the same range: Hughes & Mather 1991; Robinson 1956).

In Seymour, the correlation between the number of potential helpers and the number of young fledged per territory suggests either that more helpers means more food for nestlings, or that more females breed in the larger territories. Further observations are required before we can determine which of these explanations is more likely.

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References

Brown, E.D. & Farabaugh, S.M. 1991. Song sharing in a group-living songbird, the Australian Magpie, *Gymnorhina tibicen*. Part III. Sex specificity and individual specificity of vocal parts in communal chorus and duet songs. Behaviour 118, 244-274.

Carrick, R. 1972. Population ecology of the Australian Black-Backed Magpie, the Royal Penguin and Silver Gull. United States Department of Interior Wildlife Research Report 2, 41-99.

- Clarke, M.F. 1984. Cooperative breeding by the Australian Bell Miner Manorina melanophrys Latham: a test of kin-selection theory. Behavioral Ecology and Sociobiology 14, 137-146.
- Clarke, M.F. 1988. The reproductive behaviour of the Bell Miner *Manorina melanophrys*. Emu 88, 88-100.
- Emlen, S.T. & Wrege, P.H. 1988. The role of kinship in helping decisions among White-fronted Bee-eaters. Behavioral Ecology and Sociobiology 23, 305-315.
- Farabaugh, S.M., Brown, E.D. & Hughes, J.M. 1992. Cooperative territorial defence in the Australian Magpie, *Gymnorhina tibicen* (Passeriformes, Cracticidae), a group-living songbird. Ethology 92, 283-292.
- Ford, H.A., Bell, H., Nias, R. & Noske, R. 1988. The relationship between ecology and the incidence of cooperative breeding in Australian Birds. Behavioral Ecology and Sociobiology 22, 239-249.
- Gaston, A.J. 1978. The evolution of group territorial behavior and cooperative breeding. American Naturalist 112, 1091-1100.
- Hughes, J.M. & Mather, P.B. 1991. Variation in the size of territorial groups in the Australian Magpie *Gymnorhina tibicen*. Proceedings of the Royal Society of Queensland 101, 13-19.
- Hughes, J.M., Pearce, B.J. & Vockenson, K. 1983. Territories of the Australian Magpie in south-east Queensland. Emu 83, 108-111.
- Jamieson, I.G. 1989. Behavioral heterochrony and the evolution of birds helping at the nest: an unselected consequence of communal breeding. American Naturalist 133, 394-406.

- Reyer, H-U. 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the Pied Kingfisher (*Ceryle rudis*). Animal Behaviour 32, 1163-1178.
- Robinson, A. 1956. The annual reproductory cycle of the magpie, *Gymnorhina dorsalis* Campbell, in southwestern Australia. Emu 56, 233-336.
- Rowley, I. 1975. Bird Life. Collins, Sydney.
- Russell, E. & Rowley, I. 1988. Helper contributions to reproductive success in the Splendid Fairy-wren *Malurus splendens*. Behavioral Ecology and Sociobiology 22, 131-140.
- Shurcliffe, A. & Shurcliffe, K. 1974. Territory in the Australian Magpie (*Gymnorhina tibicen*), an analysis of its size and change. South Australian Ornithologist 26, 127-132
- Slater, P., Slater, P. & Slater, R. 1994. The Slater Field Guide to Australian Birds. Lansdowne, Sydney.
- Thomas, D.G. 1974. Some problems associated with the avifauna. Pp. 339-365 in Biogeography and Ecology in Tasmania. Ed. W.D. Williams. Junk, The Hague.
- Veltman, C.J. 1989a. Flock, pair and group-living lifestyles without cooperative breeding by Australian Magpies *Gymnorhina tibicen*. Ibis 131, 601-608.
- Veltman, C.J. 1989b. Effects of experimental food addition on post-natal dispersal, polygyny and reproductive success in pair-defended territories of the Australian Magpie Gymnorhina tibicen. Ardea 77, 211-216.
- Woolfenden, G.E. & Fitzpatrick, J.W. 1978. Inheritance of territory in group-breeding birds. Bioscience 28, 104-108.

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