CO-OPERATIVE BREEDING IN AUSTRALASIAN BIRDS: A REVIEW OF HYPOTHESES AND EVIDENCE

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Studies of co-operative breeding in Australia and New Zealand have made a considerable contribution to the current understanding of this phenomenon. This review considers the progress that has been made since I. Rowley's pioneering work on the Superb Fairy-wren in the 1950s and 60s in testing hypotheses proposed to explain (a) why individuals refrain from dispersing from their natal territory (i.e. are philopatric) and (b) why philopatric individuals help to raise young that are not their own. I survey all Australian species that have been recorded as breeding co-operatively, and possible explanations for the disproportionately large number of Australian species that breed co-operatively are discussed.

INTRODUCTION

The primary aim of this paper is to review the substantial contribution studies in Australia and New Zealand have made to the current under-standing of co-operative breeding in birds. An additional aim is to review the incidence of co-operative breeding in Australian birds. While it was beyond the scope of this review to collate all records of co-operative breeding in all of Australasia, it would be remiss to ignore the significant contribution to the field made by studies in New Zealand, and so the latter are included in a general review of hypotheses.

For the purposes of this review co-operative breeding is defined as any situation in which more than two individuals provide care in the rearing of a single clutch or brood (except for cases of intraspecific brood parasitism or cuckoldry in which the parasites do not provide any care to their offspring (Brown 1987)). Two broad types

of breeding system fall within this definition of co-operative breeding: (i) situations in which parentage and care of the young in a brood is shared by more than two individuals (variously labelled 'joint nesting', 'mate sharing' or 'communal breeding' (Emlen 1984; Brown 1987); and (ii) situations in which an individual ('helper') performs parent-like behaviour towards young that are not its own offspring (Brown 1987). In the latter category a common pattern is for off-spring raised during a previous breeding attempt to assist in raising their younger siblings at their parents' subsequent nests.

Evolutionary biologists have long been fascinated by co-operative breeding because it poses an intriguing challenge to Darwin's (1854) theory of evolution by natural selection acting upon individuals. When discussing sacrificial aid-giving between individuals of our own species, Darwin (1871; p. 130) acknowledged, 'He who was ready

TABLE 1

Species that have been recorded breeding co-operatively within Australia. Nomenclature follows Christidis and Boles (1994). References for all species are provided in Dow (1980) unless indicated otherwise.

Family	Common name	Scientific name	References
Anseranatidae	Magpie Goose	*Anseranas semipalmata*	
Podicipedidae	Australasian Grebe	*Tachybaptus novaehollandiae*	
Rallidae	Purple Swamphen	*Porphyrio porphyrio*	
	Dusky Moorehen	*Gallinula tenebrosa*	
	Tasmanian Native Hen	*Gallinula mortieri*	
Apodidae	White-rumped Swiftlet	*Collocalia spodiopygius chilligoensis*	Tarburton and Minot 1987
Halcyonidae	Buff-breasted Paradise-Kingfisher	*Tanysiptera sylvia*	
	Laughing Kookaburra	*Dacelo novaeguineae*	
	Blue-winged Kookaburra	*Dacelo leechii*	
	Forest Kingfisher	*Todiramphus macleayii*	
Meropidae	Rainbow Bee-eater	*Merops ornatus*	
Climacteridae	Red-browed Treecreeper	*Climacteris erythrops*	
	Brown Treecreeper	*Climacteris picumnus*	
	Black-tailed Treecreeper	*Climacteris melanura*	
	Rufous Treecreeper	*Climacteris rufa*	
Maluridae	Purple-crowned Fairy-wren	*Malurus coronatus*	Rowley and Russell 1993
	Superb Fairy-wren	*Malurus cyaneus*	
	Splendid Fairy-wren	*Malurus splendens*	
	Variegated Fairy-wren	*Malurus lamberti*	
	Lovely Fairy-wren	*Malurus amabilis*	
	Blue-breasted Fairy-wren	*Malurus pulcherrimus*	
	Red-winged Fairy-wren	*Malurus elegans*	
	White-winged Fairy-wren	*Malurus leucopterus*	
	Red-backed Fairy-wren	*Malurus melanocephalus*	Schodde 1982
	White-throated Grasswren	*Amytornis woodwardi*	Schodde 1982
	Thick-billed Grasswren	*Amytornis textilis*	Brooker 1988
Pardalotidae	Striated Pardalote	*Pardalotus striatus*	
	White-browed Scrubwren	*Sericornis frontalis*	Harris and Newman 1974 cited in Brown 1987
	Large-billed Scrubwren	*Sericornis magnirostris*	
	Speckled Warbler	*Chthonicola sagittatus*	
	Weebill	*Smicrornis brevirostris*	
	Brown Gerygone	*Gerygone mouki*	
	Chestnut-rumped Thornbill	*Acanthiza uropygialis*	
	Buff-rumped Thornbill	*Acanthiza reguloides*	
	Yellow-rumped Thornbill	*Acanthiza chrysorrhoa*	
	Yellow Thornbill	*Acanthiza nana*	
	Striated Thornbill	*Acanthiza lineata*	
	Southern Whiteface	*Aphelocephala leucopsis*	Sandbrink and Robinson 1994
	Banded Whiteface	*Aphelocephala nigricincta*	Blakers *et al.* 1984
Meliphagidae	Red Wattlebird	*Anthochaera carunculata*	Talmage 1993
	Little Wattlebird	*Anthochaera chrysoptera*	
	Striped Honeyeater	*Plectorhyncha lanceolata*	Moffat *et al.* 1983
	Little Friarbird	*Philemon citreogularis*	
	Blue-faced Honeyeater	*Entomyzon cyanotis*	Boles *et al.* 1981
	Bell Miner	*Marorina melanophrys*	
	Noisy Miner	*Manorina melanocephala*	
	Yellow-throated Miner	*Manorina flavigula*	
	Black-eared Miner	*Manorina melanotis*	MacLaughlin 1990
	Yellow-tufted Honeyeater	*Lichenostomus melanops*	
	White-plumed Honeyeater	*Lichenostomus pennicillatus*	
	Black-chinned Honeyeater	*Melithreptus gularis* (*lateroir* race)	
	Brown-headed Honeyeater	*Melithreptus brevirostris*	

Table 1 — continued

Family	Common name	Scientific name	References
Meliphagidae	White-throated Honeyeater	*Melithreptus albogularis*	
— continued	White-naped Honeyeater	*Melithreptus lunatus*	
	Black-headed Honeyeater	*Melithreptus affinis*	Blakers *et al.* 1984
	New Holland Honeyeater	*Phylidonyris novaehollandiae*	
	Rufous-throated Honeyeater	*Conopophila rufogularis*	
Petroicidae	Hooded Robin	*Melanodryas cucullata*	
	Eastern Yellow Robin	*Eopsaltria australis*	
	White-breasted Robin	*Eopsaltria georgiana*	
	Western Yellow Robin	*Eopsaltria griseogularis*	
Orthorychidae	Logrunner	*Orthonyx temminckii*	
Pomatostomidae	Grey-crowned Babbler	*Pomatostomus temporalis*	
	White-browed Babbler	*Pomatostomus superciliosus*	
	Hall's Babbler	*Pomatostomus halli*	Brown 1987
Cinclosomatidae	Cinnamon Quail-thrush	*Cinclosoma cinnamoneum*	
Neosittidae	Varied Sittella	*Daphoenositta chrysoptera*	
Pachycephalidae	Crested Shrike-tit	*Falcunculus frontatus*	
Dicruridae	Magpie-lark	*Grallina cyanoleuca*	Aston 1988
Campephagidae	Ground Cuckoo-shrike	*Coracina maxima*	
Oriolidae	Figbird	*Sphecotheres viridis*	Woodall 1981
Artamidae	White-breasted Woodswallow	*Artamus leucorhynchus*	
	Black-faced Woodswallow	*Artamus cinereus*	
	Dusky Woodswallow	*Artamus cyanopterus*	
	Little Woodswallow	*Artamus minor*	
	Grey Butcherbird	*Cracticus torquatus*	
	Pied Butcherbird	*Cracticus nigrogularis*	
	Australian Magpie	*Gymnorhina tibicen*	
Corcoracidae	White-winged Chough	*Corcorax melanorhamphus*	
	Apostlebird	*Struthidea cinerea*	

to sacrifice his life, . . . would often leave no offspring to inherit his noble nature. Therefore it hardly seems probable, that the number of men gifted with such virtues, . . . could be increased through natural selection, that is, by survival of the fittest.'. Williams (1966; p. 194) expressed the dilemma in more modern genetic terminology when he wrote, 'How could natural selection based on the relative role of reproduction of different individuals, favour genes that cause their bearers to expend resources to benefit their genetic competitors?'. Hence, much of the research on co-operative breeding over the last 30 years has attempted to test hypotheses postulated to explain why helpers contribute food, time and energy raising young that are not their own.

Co-operative breeding is of particular interest to Australasian ornithologists since a disproportionate number of species in this region breed co-operatively. For example, currently 80 of the 667 species (12%) that are found on the Australian mainland, Tasmania or surrounding waters that are breeding residents or regular migrants (Christidis and Boles 1994) have been recorded breeding co-operatively (Table 1). By contrast, in a global review of the incidence of co-operative breeding Brown (1987) reported approximately 222 (2.5%) of the 9 016 species of bird in the world bred co-operatively. The number of Australian species recorded breeding cooperatively has risen steadily since Dow's (1980a) review reported 62 such species, and no doubt the figure will continue to increase as more species are studied in detail. Russell (1989), and later Edwards and Naeem (1993), highlighted the fact that, among Australian species with a Gondwanan origin (the 'old endemics'), the incidence of co-operative breeding was extremely high (at least 22%), suggesting that co-operative breeding may have had a long history in Australia. Consequently there are profound theoretical and practical reasons why it is important to understand the evolutionary forces that have led to such a large proportion of the Australian avifauna breeding co-operatively.

Australasian ornithologists also have an historical claim to having helped focus the ornithological world's attention on co-operative breeding. Rowley's (1965) pioneering study of the Superb Fairy-wren was one of the first detailed studies of an individually colour-banded population of co-operatively breeding birds in the world. Furthermore, his was one of the first attempts to quantify the impact of helpers upon the reproductive output of breeding pairs. By demonstrating the abundance of co-operatively breeding species in Australia, Rowley (1968) ruled out any possibility of dismissing reports of helping as a rare, inconsequential or aberrant behaviour pattern — despite its rarity in the northern hemisphere. Hence, the stage was set for studies of Australasian species to make a significant contribution to understanding co-operative breeding in birds.

Given the paucity of basic knowledge of the breeding biology of most Australasian species of birds, most studies have been necessarily descriptive (e.g. Rowley 1965; Parry 1973; Dow 1978a; Craig 1980; Clarke 1988; Poiani 1993a). Some have investigated anatomical or physiological aspects of co-operatively breeding species (Ambrose and Bradshaw 1988; Schmidt *et al.* 1991; Mulder and Cockburn 1993; Poiani and Fletcher 1994). Others have been carefully targeted towards groups of congeneric species exhibiting a range of social systems (e.g. Bell and Ford 1986; Tidemann 1986; Noske 1991) or have studied the biology of a single species in a range of habitats (Ambrose and Davies 1989). Most have struggled to obtain both the essential basic background information on each species' breeding biology and to also make powerful comparative analyses of the traits they observe in different species or at various localities. Nevertheless, these descriptive studies have led to a substantial improvement in our understanding of the general ecology of co-operative breeding in birds, and placed the field on a sound footing to address the key questions posed by co-operative breeding.

Two fundamental and interrelated questions need to be answered if we are to understand co-operative breeding (Brown 1987). The first is why, among co-operative breeders, do some individuals fail to disperse and breed independently, and instead remain on their natal territory (i.e. are philopatric), often as a member of a family group. The second is, given an individual is philopatric, why should it help raise another individual's offspring.

WHY BE PHILOPATRIC?

Detailed studies of the ecology, and in particular demography of co-operatively breeding species, have led to a general hypothesis that some individuals are forced to be philopatric either by (a) ecological constraints making dispersal a more costly tactic than philopatry (Brown 1969b, 1978; Koenig and Pitelka 1981), or (b) the benefits to an individual's fitness of remaining in the natal group outweigh the benefits that could be gained by dispersing and breeding independently as a lone pair (Stacey and Ligon 1987) (Table 2). In effect (a) and (b) are just the two sides of the same cost-benefit equation (Emlen 1991). Three ecological constraints have been postulated to explain why some birds fail to disperse (Table 2). All of these constraints may operate at different times upon a population of a single species.

TABLE 2

Hypotheses proposed to explain why individuals remain philopatric, rather than dispersing to breed independently outside the natal group.

Hypotheses	Proposed mechanism
Ecological constraints hypothesis	(i) Shortage of suitable (or good quality) breeding habitat. (ii) Shortage of mates. (iii) Shortage of skills needed for breeding.
Benefits of philopatry hypothesis	(i) More than a pair of individuals required to breed successfully. (ii) More than a pair of individuals required to successfully defend a territory or resource from conspecifics and heterospecifics. (iii) Reduced predation. (iv) Co-operative hunting.

Considerable descriptive evidence has been collected during long-term studies of colour-marked populations that all available habitat appears to be occupied at times for several co-operatively breeding species (e.g. Splendid Fairy-wren, Russell and Rowley 1993). This is often reflected in the stability of the number of territories available at a site throughout a study

and the speed with which any vacancies are filled (e.g. in the Bell Miner, Clarke 1988; Clarke and Heathcote 1990). As in studies overseas, particular key resources for a species that could potentially be in short supply have been postulated. For example, Noske (1991) suggested the Red-browed Treecreeper may be limited by a scarcity of roost and nesting holes in trees. Attempts to experimentally manipulate the abundance or availability of such resources have been rare (but note Ligon *et al*. 1991).

Demographic data from long-term studies have also shown that in Tasmanian Native Hens, Bell Miners and Splendid Fairy-wrens there can be a shortage of females within the population with which to breed (Maynard Smith and Ridpath 1972; Clarke and Heathcote 1990; Russell and Rowley 1993).

A most convincing test of the habitat saturation hypothesis and the shortage of mates hypothesis was conducted in a study of Superb Fairy-wrens by Pruett-Jones and Lewis (1990). Vacancies were created by removing breeding males from their territories. Thirty-one of a possible 33 non-territory-holding male helpers dispersed and filled the vacancies, on average within 5.3 h of the vacancy being created. If, however, the breeding females from the territory had also been removed, male helpers did not disperse to fill these totally vacant territories until the female had been returned. Although this study did not identify what attribute(s) of the habitat made it suitable or unsuitable as a breeding territory, it did demonstrate that philopatric helpers were constrained from breeding independently by a shortage of available mates and habitat suitable for breeding.

While the 'skills hypothesis' has been postulated as an explanation for philopatric behaviour, very few attempts have been made in studies of co-operative breeders to document the ontogeny of the parenting skills necessary for successful repro-duction (e.g. Poiani 1993a). These might include skills in nest construction, care of young, territorial and agonistic interactions, predator detection and avoidance (Brown 1987). Following the observa-tion by Rowley (1978) that White-winged Choughs acquire their foraging skills very slowly, Heinsohn *et al*. (1988) went on to demonstrate that individuals commonly took four years to achieve foraging efficiency and competency in delivering food to young. They suggested that in White-winged Choughs 'young dispersers would have difficulty in successfully raising young in pairs' (Heinsohn *et al*. 1988, p. 184). By contrast, Bell Miner helpers were found to be quite proficient provisioners well before they reached dispersal or breeding age (Poiani 1993a). Until a study can demonstrate that a skilled pair of birds has significantly higher reproductive success than a corresponding pair of the same age that has been prevented from gaining skills, support for this hypothesis remains equivocal.

The first of the potential benefits of philopatry suggests that some species may be incapable of breeding in simple pairs (Table 2). Dow (1980) labelled such species 'obligate communal breeders'. He included within this group the small number of species that appear to always breed co-operatively, but acknowledged that there may be no species that is truly obligate. Heinsohn (1991) presents data that suggest that White-winged Chough pairs at his study site cannot breed unaided, and may indeed fit the description of an obligate co-operative breeder. He postulates '. . . high costs of parental care may be a direct cause of delayed breeding. Young individuals may be constrained from dispersing because of the impossibility of raising young without help . . .' (Heinsohn 1991, p. 876). It remains to be seen whether simple pairs are incapable of breeding successfully throughout the species' range. Since the vast majority of co-operative breeders are known to be capable of breeding successfully as a simple pair, it seems likely that the 'more than a pair needed for breeding' hypothesis would, at best, have limited scope as a general explanation of philopatry.

Similarly, there is circumstantial evidence in only a small number of species that more than two individuals appear essential for the defence of a breeding territory. Craig (1984) argued that in the Pukeko situations could arise where simple pairs were incapable of defending their territory from surrounding groups of conspecifics. Honey-eaters in the genus *Manorina* appear to gain almost exclusive use of a piece of habitat through extreme levels of interspecific aggression by colony members (Dow 1977; Loyn *et al*. 1983). Access to the resources defended by a colony of miners may often be unattainable for a simple pair.

In their review of ecological correlates of co-operative breeding in Australian birds, Ford *et al.* (1988) highlighted the fact that many Australian co-operative breeders were ground foragers and gleaners. They argued that such species were potentially more vulnerable to predation than animals using other foraging techniques. They concluded that species facing high predation pressure could gain greater benefits from group living. However, this could also favour forming flocks of non-breeding floaters (e.g. Australian Magpie, Carrick 1963), as well as philopatry. Furthermore, there is no evidence currently available to suggest that co-operatively breeding species are subjected to higher levels of predation pressure than non-co-operative species. Clearly other factors, in addition to predation pressure, need to be invoked to explain the high incidence of philopatry.

There is little evidence to suggest that many co-operatively breeding species in Australia gain benefits from co-operative hunting in groups, as opposed to hunting alone or in pairs. Balda and Brown (1977, p. 114), however, reported what they regarded as co-operative foraging in Hall's Babbler where birds engaged in 'mutual flushing of tiny insects from the understorey' and 'sharing large parcels of food'. Similarly, there is little evidence to suggest that only philopatric individuals are able to attain the potential benefits of improved thermoregulation achieved by communal roosting, as opposed to non-philopatric individuals that join flocks that roost together. Hence, the benefits of superior thermoregulation are unlikely to be an adequate explanation of the high incidence of philopatry among co-operative breeders.

Overall, most detailed long-term studies of co-operative breeders in Australia have documented evidence that there is a surplus of potential breeders in the population, relative to the number of opportunities for them to breed. The non-dispersal by these surplus individuals may be due to the high costs of dispersal or the benefits of philopatry. Heinsohn *et al.* (1990) argue that many species of bird (including non-co-operative breeders) may be ecologically constrained (e.g. face a shortage of breeding territories), but not all become philopatric. Given the scarcity of long-term studies of non-co-operatively breeding species in Australasia, it is difficult to determine

how frequently analogous non-co-operatively breeding species produce a surplus of potential breeders and whether they are ecologically constrained. More long-term studies of the population dynamics and demography of closely-related non-co-operatively breeding species are needed. Furthermore, because of the logistic difficulties of studying highly mobile co-operatively breeding species (e.g. *Melithreptus* honeyeaters) current studies are biased towards sedentary species. Hence, our current view of co-operative breeders commonly being forced into philopatry by ecological constraints may not hold when a broader range of species is studied, or individual species are studied in different parts of their range under different ecological conditions (e.g. Ambrose and Davies 1989).

WHY DO HELPERS HELP?

Unfortunately the emphasis on identifying the ecological constraints or benefits of philopatry relevant to particular co-operatively breeding species led to the mistaken belief that an explanation of philopatry equated with an explanation of co-operative breeding. In 1982, it was suggested that the habitat saturation hypothesis had 'become the *modus operandi* for ecological thinking concerning the evolution of helping behaviour . . .' (Emlen 1982, p. 32). However, as Brown (1987) has stressed, explaining why an individual may stay at home with its parents or why it might delay breeding, does not necessarily explain why it should act as a helper. Indeed, there are cases where individuals are philopatric but refrain from helping (e.g. Australian Magpie, Veltman (1989); Note, Poiani (1994) has recently suggested an hypothesis to explain why this might be the case).

The emphasis in the last decade upon identifying ecological and demographic correlates with co-operative breeding appears to have been at the expense of detailed testing of hypotheses postulated to explain *why philopatric individuals help* — the primary question that sparked the interest of biologists in co-operative breeding in the first place.

At least 11 distinct hypotheses have been postulated to explain how helpers and the recipients of their aid may increase their fitness through helping (Table 3). The different benefits

of helping postulated by the various hypotheses may be acting additively and are not necessarily mutually exclusive (Emlen and Wrege 1989). This fact has made determining the relevance of each hypothesis in accounting for helping particularly challenging.

TABLE 3

Hypotheses proposed to explain helping behaviour. The Effect on Recipients column refers to whether the hypothesis requires that the effect of the helper's activities has a negative, neutral, or positive effect upon the recipients' fitness.

Hypotheses	Effect on Recipients
Group Selection hypothesis	negative or neutral
Unselected hypothesis	neutral
Experience hypothesis	neutral or positive
Payment hypothesis	positive
Budding-off hypothesis	positive
Predator Avoidance hypothesis	
(a) *sensu* Caraco and Brown (1986)	negative, neutral or positive
(b) *sensu* Brown (1987)	positive
Social Bonding hypothesis	neutral or positive
Mate Acquisition hypothesis	neutral or positive
Reciprocation hypothesis	positive
Indirect Fitness Benefits hypothesis	positive
Parentage hypothesis	positive

Group Selection hypothesis

An early study of co-operative breeding in the Laughing Kookaburra concluded that the system of helpers at the nest 'appears to be a long-term adaptation for reducing fertility . . .' (Parry 1973, p. 81). Such an explanation is really only potentially feasible for reproductive restraint by philopatric individuals. It provides no reason why we should expect philopatric individuals to help. Nevertheless, even if one argues that helping *per se* may lead to reduced fertility in a population, Morton and Parry (1974) pointed out that such a 'group selectionist' argument had serious theoretical limitations (see Maynard Smith 1964; Williams 1966). Because of the very restrictive conditions required for group selection to operate, the hypothesis has not often been considered. Furthermore, there is observational and experimental evidence against the hypothesis; pairs assisted by helpers fledge greater numbers of young than they would have if the helpers had refrained from

helping (e.g. Rowley 1965; Brown *et al.* 1982; Marchant 1985). This is contrary to any hypothesis based upon 'reproductive restraint'.

Unselected hypothesis

Williams (1966) concluded that helping behaviour was simply reproductively frustrated individuals exhibiting misplaced parental care. The hypothesis that helping behaviour has no adaptive explanation has been advocated by several authors (e.g. Jamieson and Craig 1987; White *et al.* 1991). It has been explored and championed most forcefully by Ian Jamieson and John Craig (Jamieson 1986; Jamieson and Craig 1987; Jamieson 1989a; Jamieson 1989b; Jamieson 1991) who argue that 'the feeding of nestlings in communal breeders is maintained by the same stimulus-response mechanism that results in parents feeding their own young or host species feeding parasitic young, a situation where there is no reasonable adaptive explanation' (Jamieson and Craig 1987, p. 80). Because of the effects of helping upon the recipient's and the helper's fitness predicted by this hypothesis are neutral (Table 3), it is debatable how much evidence exists supporting this hypothesis. Should studies that fail to detect any positive effect of help upon the helper or the recipient's fitness (e.g. Nias 1986) be treated as evidence against any kind of selected hypothesis and supportive of the unselected hypothesis (Jamieson 1989a), or as cases where 'not all relevant fitness components were measured' (Emlen *et al.* 1991)? When one considers the numerous mechanisms by which a helper's aid might lead to an increase in the fitness of the recipient breeding pair (Fig. 1.), it is clearly challenging to conclusively demonstrate that effects of helping in a species are neutral.

One prediction of the unselected hypothesis that has proved simpler to test is that helpers 'should, in general, provision any nestlings they come in contact with . . .' (Jamieson 1989a, p. 402). Cases of helpers discriminating among potential recipients in their distribution of aid in the Bell Miner (Clarke 1989; Clarke 1990) have been acknowledged by Jamieson (1991) as being inconsistent with the predictions of the Unselected hypothesis. However, Jamieson (1991) argues results such as those for the Bell Miner (which has more than one breeding pair breeding in a communally defended territory) are

atypical because they do not reflect what occurs in the more typical co-operative breeders (that have a single territorial pair with several non-breeding helpers). Carefully designed experiments are needed to test Jamieson's (1989a) prediction that, 'if selection is acting directly upon helpers, their helping behaviour should be fine-tuned so that non-breeders show a greater predisposition to provision nestlings, or provision with greater intensity, relative to non-breeders of closely-related but non-communal species' (Jamieson 1991, p. 277).

Experience hypothesis

One of the most frequently cited benefits of helping behaviour to the fitness of the helper is that, through helping, an immature or non-breeding bird gains valuable experience and skills that will enhance its reproductive success when later in life it gains an opportunity to breed (e.g. Lack 1968; Rowley 1981; Marchant 1985). Despite the ready acceptance of this hypothesis by many authors, there is little conclusive evidence supporting it. Rowley (1965) reported that experienced unassisted pairs of Superb Fairy-wrens failed to produce any more fledglings than inexperienced unassisted pairs. However, Russell and Rowley (1988) found female Splendid Fairy-wrens that had acted as a helper for one year produced more fledglings than females which had not helped (but only if helpers were present). It should also be noted that the former were also one year older. Heinsohn *et al.* (1988) reported that White-winged Choughs showed a marked improvement in delivering food to young when acting as helpers. They argue that young inexperienced and unskilled dispersers would have difficulty in successfully raising young in pairs. The fact that none of these studies has been able to compare the survivorship and repro-ductive success of philopatric individuals of the same age that have helped, with those that have not (whilst also controlling for confounding factors such as variation in territory quality and the number of helpers the focal individual has assisting it when it breeds), illustrates what an extremely difficult hypothesis this is to test.

Payment hypothesis

Gaston (1978) suggested that philopatric young may impose costs upon the breeders whose territories they share, e.g. increased competition for food and mates, or increased attraction of predators and parasites to the territory. He argued that, 'A portion of the assistance rendered to the breeders can be regarded as 'payment' for the right to remain' (Gaston 1978, p. 1095). This hypothesis predicts that helpers should direct their aid towards breeders whose territories they share, and unhelpful individuals should be evicted by breeders. Contrary to this prediction, Clarke and Fitz-Gerald (1994) found helpers regularly gave aid to breeders whose home ranges they did not overlap. Furthermore, little evidence has accumulated of breeders evicting non-helping individuals, despite very detailed studies of some species (e.g. Russell and Rowley 1988).

Mulder and Langmore (1993) attempted to test this hypothesis in a study of the Superb Fairy-wren by experimentally removing male helpers from territories for 24 h, at different stages in the reproductive cycle of the dominant pair. They reported that upon release, the males were harassed by the dominant male for 'failing to help'. It is debateable whether the aggression shown by the dominant male towards the 'returned' male was purely punishment for failure to help. The male helper's absence may have been perceived by the dominant male as an indication of some threat of cuckoldry by the male helper of the dominant male's social partner, or of neighbouring females with whom the dominant male might also mate (Mulder *et al.* 1994). If the Payment hypothesis was correct, one might have also expected the female breeder to behave aggressively towards the wayward helper. The observation that dominant males were aggressive towards the returned male helpers even during the fertilization and incubation periods (when there were no young present for the helper to feed) suggests that punishment was being metered out for demeanours other than the failure to help. Experiments like Mulder and Langmore's (1993), have tremendous potential to test this commonly cited, but rarely tested, hypothesis.

Budding-off hypothesis

Rowley (1981, p. 247) reported that in the Splendid Fairy-wren '11 out of 19 males attaining breeding status did so by inheritance, and all inherited the widow as well as the real estate'. After making similar observations in a study of

the Superb Fairy-wren, Nias and Ford (1992, p. 242) concluded that the most plausible explanation of co-operative breeding in this species at their study site was that 'individuals hatched on higher quality territories are more likely to delay dispersal if they are eventually able to inherit (or disperse to) a breeding position within a good territory, than risk dispersal and low reproductive success on a poor quality territory.'. In both of these examples territorial inheritance can be viewed as a benefit of philopatry, but not necessarily of helping *per se* — the same benefit could, theoretically, be available to any non-helping philopatric individual (Brown 1987). The distinction needs to be made between a Territorial Inheritance hypothesis (that might well account for philopatric behaviour) and the Budding-off hypothesis advocated by Woolfenden and Fitzpatrick (1978) as a possible explanation of helping. The latter suggests that if the aid given by a helper increases the group's size, it might enable the group to control a larger territory, within which the helper can establish (bud-off) his own breeding territory. Rowley (1981) found no evidence that larger groups occupied larger territories in his study of the Splendid Fairy-wren. Furthermore, as Brown (1987) highlights, this hypothesis predicts that we should see more examples of territorial budding in larger groups and breeder replacement in smaller groups. Such data have yet to be collected for an Australasian species.

Predator Avoidance hypothesis

Another potential benefit to the helper of helping that has been postulated is that by feeding young a helper might reduce the persistent begging of the young that might otherwise attract predators to within the helper's home range. Hence, helping could be viewed as an attempt by the helper to increase its own survivorship (Caraco and Brown 1986). A similar hypothesis is that if additional young are produced as a consequence of the helper's aid, and group size increases, this may also benefit the helper's survivorship by improving the level of vigilance and anti-predator behaviour in the vicinity of the helper's home range due to having more individuals on the look out and avail-able to repel predators. This hypothesis predicts that individuals should have higher survivorship in larger rather than smaller groups (Emlen and Wrege 1989). To test this prediction one would

again need to control for variation in territory quality between groups of differing size. To my knowledge, no such study of the survivorship of helpers living in groups of various sizes has been made.

Social Bonding hypothesis

Helpers may not only improve their own survivorship by helping to produce more young, they might also improve their chance of securing a breeding position — especially if acquisition of a breeding territory requires a co-operative effort by a coalition of individuals (e.g. male coalitions in lions, Packer *et al.* 1988). Helpers may form social bonds with the young they are provisioning. When the helper eventually disperses it may be joined by several of the young it has helped to raise, and as a coalition such a group might have a better chance of acquiring a territory than would a lone disperser. According to this hypothesis the young disperse with the helper because it benefits their fitness to do so, not because they are repaying the helper for its aid.

Cases of dispersal by coalitions of helpers and recipients have been reported in several species (e.g. Tasmanian Native Hen, Ridpath 1972). Heinsohn (1991b) reported that the need for collaborators in White-winged Choughs is so great that individuals from one group will kidnap young from another in order to increase the group's size, and thus enable a new subgroup to form that will disperse to eventually establish a new group. This hypothesis predicts (a) that large coalitions will be more successful in obtaining and defending a territory than smaller ones, and (b) that the act of helping is critical to the formation of such coalitions (Emlen 1991). There are some observations of the Pukeko that are consistent with prediction (a) of this hypothesis (Craig 1984). However, given the difficulty of tracing dispersal events, this hypothesis has proven difficult to test.

Mate Acquisition hypothesis

A shortage of mates of one sex has been reported in many co-operative breeders (see above). Such a shortage could lead to competition among members of the limited sex (generally males) for access to the limiting sex (generally females). Sexual selection theory has often been

invoked to explain the evolution of many extra-ordinary male traits such as elaborate displays and adornments used in courtship, and anatomical features used in combat with other males (Bateson 1983). However, females may also base their choice of mate upon their potential partner's parental-care ability. Reyer (1980) proposed that a non-breeding individual could enhance its probability of pairing with a female by helping to raise her current young. Despite widespread reports of male-biased sex ratios, helpers being predominantly males (see Brown 1987) and numerous accounts of male helpers subsequently pairing with a female breeder they had previously aided (e.g. in the Splendid Fairy-wren, Rowley 1981), this hypothesis has received little attention. Preliminary supportive evidence was found in the Bell Miner where each of five widowed females preferentially paired with the unmated, unrelated, male helper that had contributed the most aid at her previous nesting attempt (Clarke 1989). An experimental test of this hypothesis has yet to be conducted.

Reciprocation hypothesis

The hypothesis of reciprocal altruism suggested by Trivers (1971) has found little support in studies of co-operatively breeding birds. It postulates that helping could be favoured by natural selection if the cost to the helper's fitness of giving aid was less than the benefit obtained when the original recipient of the aid later reciprocated in some manner. This might be through assisting the helper to gain a breeding position or through helping to raise the helper's young.

Heinsohn (1991b, p. 1099) has suggested that in the case of White-winged Choughs 'kidnapping' young, 'reciprocity may in itself be sufficient to cause helping behaviour'. However, Waltz (1981) pointed out that before such a conclusion is justified one needs to demonstrate that any supposed 'reciprocation' of aid given by the initial recipient is a form of repayment to the helper, and not an example of a byproduct mutualism (sensu Brown 1987). The reciprocator may be acting in its own self-interest and might choose to disperse with the kidnappers irrespective of whether the kidnappers had helped raise it or not.

Although the demographic preconditions of overlapping generations caused by delayed dispersal and high longevity are common in co-operative breeders, no data are available that demonstrate that recruitment of the next genera-tion of helpers is dependent upon prior helping associations (Emlen 1991). Emlen (1991) pointed out that species in which more than one breeding pair simultaneously have nests in close proximity could provide helpers with a choice of recipients, allowing an observer to determine if grown young preferentially give aid to individuals that had previously helped to rear them. Such species are known to occur in Australasia (e.g. Manorina spp. Dow 1978b; Clarke 1988) and offer great potential for examining this hypothesis.

Indirect Fitness Benefits hypothesis

Following the publication of Hamilton's (1964) theory of inclusive fitness, there has been consider-able debate among students of co-operative breeding as to the relative importance of indirect fitness benefits (sensu Brown 1980) gained from helping (see Brown 1987 for a review). This hypothesis postulates that helpers can increase their own inclusive fitness, if, through helping, they increase the production of non-descendent kin. Two predictions flow from this hypothesis. The first is that helpers should generally be close relatives of the recipients of their aid. The second is that the aid given by the helpers should increase the recipients' (breeders or nestlings) fitness, and thereby the indirect component of the helper's inclusive fitness.

Early consideration of this hypothesis focused on the simple question of whether recipients were close relatives of the helpers. While many studies reported that helpers were offspring from the breeders' previous broods (e.g. Rowley 1965; Parry 1973; Noske 1980), some studies reported such large numbers of helpers (e.g. > 22 male helpers in the Noisy Miner, Dow 1979) that it was felt improbable that all helpers were close relatives. Nevertheless, species like the Miners (Manorina spp.), in which an individual helper may provide aid to several different breeding pairs within a single breeding season, provide an opportunity to see if helpers preferentially distribute their aid to close relatives as opposed to non-relatives. Such preferential distribution of aid to close relatives by helpers has been documented in the Bell Miner (Clarke 1989). In the vast majority of co-operative breeders so far described, helpers appear to be close kin of the recipients of their aid (Brown 1987). While such

observations are consistent with the indirect fitness benefits hypothesis, they fall far short of demonstrating that helpers substantially increase their inclusive fitness through the production of non-descendent kin. This requires data on the lifetime reproductive success of generations of helpers and breeders of known genetic relationship to one another. Using data collected during their intensive long-term study of the Splendid Fairy-wren, Russell and Rowley (1988) calculated the effect of helping upon the helper's inclusive fitness. They concluded that 'If 1 or 2 years' helping is followed by several years breeding, then the indirect contribution to fitness from one to two years helping is relatively insignificant. But for the significant number of birds which help but never get the chance to breed, inclusive fitness is entirely indirect. Those birds which disperse and do not achieve a breeding vacancy do not have even that.' (Russell and Rowley 1988, p. 139). However, subsequent genetic analyses of the parentage of the young produced by a group (Brooker *et al.* 1990) revealed that at least 65 per cent of young were not fathered by any of the males in the group (contrary to the assumptions made by Russell and Rowley 1988). Brooker *et al.* (1990) acknowledged that this unexpected mating pattern affects the earlier inclusive fitness calculations (Russell and Rowley 1988). Future attempts to calculate the relative importance of the direct and indirect fitness components of inclusive fitness will need to combine detailed lifetime reproductive success data with molecular analyses of relationships between the individuals involved — currently a very costly exercise.

Parentage hypothesis

Early in the study of co-operative breeding in Australasia researchers believed that some of the young being cared for by helpers were the helper's own offspring; either as a consequence of co-operative polyandry or polygyny (Frith and Davies 1961; Rowley 1965; Maynard Smith and Ridpath 1972), or cuckoldry perpetrated by a helper (Dow 1978a). Having observed female Noisy Miners mating with more than one male during the reproductive cycle, Dow (1978a, p. 82) suggested that it could be advantageous for the female to copulate promiscuously, '. . . if the bond or association with a mating partner increase his propensity to care for her young later.'. Dow and Whitmore (1990) suggested that

promiscuity could have been the first step towards co-operative breeding in Noisy Miner. By contrast, only monogamous matings have been observed in the congeneric Bell Miner (Clarke 1988; Poiani and Fletcher 1994). However, the observation of male helpers feeding brooding females (Poiani 1992) and subsequent analysis of gonadal development of helpers in this species have led Poiani and Fletcher (1994) to suggest older male helpers may be siring offspring without openly challenging the male breeder.

The recent application of molecular techniques to determine parentage of young has revealed that some of the young being provisioned by helpers are indeed the helper's own offspring (Brooker *et al.* 1990; Mulder *et al.* 1994). However, in both studies the mating pattern revealed by the genetic analyses differed substantially from that deduced from behavioural observations. Rather than the Superb Fairy-wren being co-operatively polyandrous, as suggested by Rowley (1965), Mulder *et al.* (1994) reported that 76 per cent of young were sired by males from outside the social group. Similarly, instead of the high levels of inbreeding thought to be occurring in the Splendid Fairy-wren (Rowley *et al.* 1986), Brooker *et al.* (1990) found that the paternity of only 27 per cent and 8 per cent of young were consistent with the senior male or a male helper in the group (respectively). Analysis of paternity in the Noisy Miner (T. Poldmaa, pers. comm.) has failed to detect the promiscuity reported in earlier studies (cf. Dow 1978a). All of these studies suggest reproductive strategies more under the control of the female breeders than has often been acknowledged in the past.

Based on these recent genetic analyses, it is clearly inadequate to assume that social parentage and partnerships (i.e. who is observed caring for whom; who is paired with whom) can routinely be equated with genetic parentage or partnership. Nevertheless, even with high levels of extra-pair paternity and maternity, it is clear that a large proportion of helpers must still be caring for young that are not their own offspring. Dow and Whitmore (1990, p. 570) suggest this is not an insurmountable problem for the Parentage hypothesis — 'If males that copulate with a female behave as though they have fathered her offspring, then a female could actively recruit auxiliary males through multiple copulations.'.

However, helpers in many species are sexually immature and incapable of being the parents of the young they raise (e.g. Bell Miner, Clarke 1984). For such individuals, hypotheses other than the Parentage hypothesis must be considered.

DOES HELPING HELP?

Of the 11 hypotheses postulated to account for helping behaviour, six assume that the aid given by the helper has a significant positive effect upon the fitness of the recipient breeding pair (Table 2). This raises the question: Does helping really help? If it does not, then these six hypotheses can be rejected. The two components of a breeder's fitness that the aid given by a helper may affect are: a, its reproductive success and, b, its survivorship. Several mechanisms by which these two
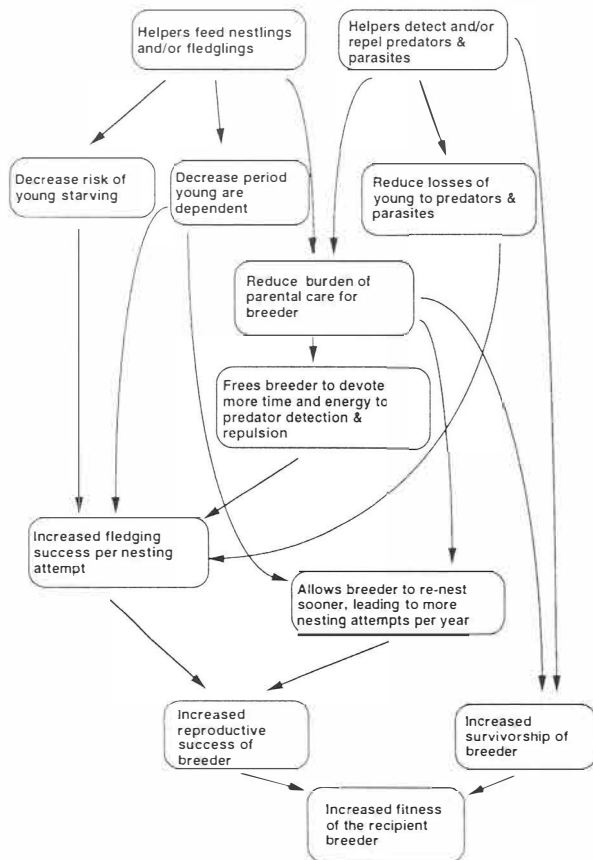

Figure 1. *Mechanisms by which the aid given by helpers might lead to an increase in the fitness of the recipient breeding pair.*

components can be affected have been suggested (Fig. 1). The most obvious is that the aid provided by the helper results in more young being produced per breeding attempt. This might be due to the helpers' activities increasing the young's food supply or reducing the probability the young suffer predation or parasitism.

Rowley's (1965) study of Superb Fairy-wrens was the first to demonstrate that pairs with helpers fledged more young than those without. Similar results were obtained in studies of a number of other species (Maynard Smith and Ridpath 1972; Parry 1973; Marchant 1985; Heinsohn 1991c). However, a similar number of studies have failed to find such an effect (Craig 1979; Rowley 1981; Nias 1986; Hemmings 1989; Sherley 1990). Even if pairs with helpers did fledge more young, such a correlation could also have been due to the pairs with helpers occupying higher quality territories (e.g. Nias 1986) or being more experienced breeders than pairs without helpers (Brown and Balda 1977). In order to control for these confounding variables an elegant experimental study was carried out on Grey-crowned Babblers (Brown *et al.* 1982). Helpers were removed from a random selection of groups, and the fledging success of these experimental groups was compared with that of control groups whose membership had not been diminished. Experimental groups produced only one third as many fledglings as the control groups, indicating that helpers did, indeed, increase the number of young produced per nest in this species.

In the search for mechanisms by which helpers might increase fledging success, studies that have measured the influence of helpers upon the amount or rate at which food is delivered to the nestlings, or the growth rates of nestlings, have generally failed to detect any significant increase due to provisioning by helpers (Parry 1973; Rowley 1978; Brown *et al.* 1978; Dow and Gill 1984; Tidemann 1986; Poiani 1993b, cf. Clarke 1984 and Heinsohn 1991b). A more common observation has been that, as helpers contribute more to the provisioning of young, breeders reduce their contribution (Brown *et al.* 1978; Dow 1978b; Tidemann 1986; Ambrose and Davies 1989; Sherley 1990). A reduction in the provisioning burden of breeders could free the breeders to devote more time and energy to other activities like predator detection and repulsion (Rabenold 1984). It could also reduce the energetic cost to

the breeders of each nesting attempt, enabling the breeder to renest sooner; this allows the breeding pair to complete more attempts in a single breeding season (Fig. 1). Evidence of such an effect has been found in the Grey-crowned Babbler and Splendid Fairy-wren. Larger groups had shorter intervals between clutches and more nesting attempts per year than smaller groups (Brown and Brown 1981; Russell and Rowley 1988). In both cases nests with helpers in attendance did not have greater success on a per egg or per nest basis. However, as Russell and Rowley (1988) have stressed, it is critical to consider the effects of helpers upon the seasonal or lifetime productivity of breeders in multi-brooded species, rather than just single nesting attempts.

A lightening of the provisioning burden of breeders might also lead to increased longevity of breeders due to a reduction in the cost of reproduction (Fig. 1). Breeding female Splendid Fairy-wrens with helpers were more likely to survive to the next breeding season (74.4%) than females without helpers (55.4%). The presence of helpers had no effect on the survival of breeding males (Rowley and Russell 1988). A similar result was obtained in a study of the Rifleman, *Acanthisitta chloris* by Sherley (1990).

Considering the complexity of the pathways depicted in Fig. 1, caution must be taken before one concludes that a helper's efforts *do not* result in an increase in the recipient breeder's fitness; especially if only one or two of the possible pathways have been examined (Emlen *et al.* 1991). Clearly, long-term data on both the reproductive output of pairs and the genetic parentage of all the young produced are needed before conclusions can be drawn regarding the effect of helpers' activities upon the lifetime reproductive success of breeders. Estimates of the lifetime reproductive success of males, without accompanying genetic data on paternity of young, must be treated with great caution, as was acknowledged by Rowley and Russell (1989) in their study of the polygamous Splendid Fairy-wren. The 17 years of data available for the Splendid Fairy-wren are also sobering when one considers how long a 'long-term' study must be to encompass important ecological events in unpredictable environments. Rowley *et al.* (1991) sub-divided their data set into three periods (of five years, seven years and four years respectively) based upon the fire history of the study site. They found

a significant effect of group size upon the reproductive success of pairs in the first two periods but not in the third! Whether a study period includes potentially significant ecological events like bushfires, droughts, floods or cyclones can have major effects upon the generality of the conclusions that can be drawn in unpredictable climatic regions like much of Australia.

WHY ARE THERE SO MANY CO-OPERATIVELY BREEDING SPECIES IN AUSTRALIA?

The disproportionate abundance of co-operatively breeding species among the Australian avifauna has been a puzzle that has intrigued ornithologists since the earliest studies (e.g. Rowley 1965). In his major review of the taxonomic distribution of co-operative breeding, Brown (1987, p. 43) concluded that there was 'little scope for interpretation along phylogenetic lines except within genera or sub-families.'. However, Russell (1989) pointed out that phylogenetic correlations with co-operative breeding were present, but had been masked by so many Australian species being misclassified as members of Afro-Eurasian families. Based upon phylogenies determined by DNA hybridization, electrophoretic and chromosome studies, she argued that co-operative breeding was disproportionately common among the old endemic families of the early Australian radiation that had been distinct for 35–40 m.y. This was not to suggest that these families were 'locked' into breeding co-operatively, irrespective of prevailing environmental conditions, but simply that it was possible that certain families may possess a phylogenetic predisposition that makes co-operative breeding more likely in some families than others. Russell and Rowley (1993b, p. 501) point out, however, that the above observation 'does not explain why it [co-operative breeding] evolved in the first place.'.

In regard to answering this question as it relates to the disproportionate abundance of co-operatively breeding species among the Australian avifauna, two broad hypotheses can be recognized. The first is that co-operative breeding is an adaptation to an erratic, unpredictable and often harsh environment that undergoes large fluctuations in ecological conditions like food abundance (Rowley 1965; Harrison 1969; Thomas 1974). The hypothesis suggests that helpers enable breeders

to make the most of occasional good conditions. Little support for this hypothesis has accumulated since it arose and it has been rejected by some authors (Dow 1980b; Russell and Rowley 1993b).

The second broad type of explanation of the abundance of co-operative breeders in Australia suggests that the aseasonal climatic conditions found over much of Australia in the past, and currently, have created conditions in which philopatry is likely to evolve. It has been suggested that the absence of a severe winter favours sedentariness rather than migration (Rowley 1968), creating conditions conducive to family members staying close together (Lack 1968). Possible exceptions to the correlation between co-operative breeding and sedentariness (rather than migratory or nomadic lifestyles) should be noted. The migratory Dusky Wood-swallow, Rainbow Bee-eater and Buff-breasted Paradise Kingfisher, and the nomadic Little Woodswallow are all known to breed co-operatively, while many sedentary species (e.g. Brown Thornbill) do not appear to breed co-operatively, despite many of their congeners doing so (Bell and Ford 1986).

The absence of a severe winter might also lead to increased longevity — creating conditions conducive to overlapping generations of birds occupying a site and group living (Rowley and Russell 1990). This assumes that a territory has sufficient resources to simultaneously sustain both parents and their progeny throughout the year (Ford *et al.* 1988). Ford *et al.* (1988) found co-operative breeding was more common in habitat showing the least seasonality of plant growth, i.e. eucalypt and semi-arid woodlands, rather than wetter or drier habitats. Rowley and Russell (1990, p. 25), while accepting Ford *et al.*'s (1988) general correlation between co-operative breed-ing and climates that are equable within a year, stressed the significance of major fluctuations in ecological conditions that might occur once or twice a decade. They suggest that once or twice a decade breeding success may be nil, but con-versely, one or two years may be exceptionally productive, and long-lived birds may reap the benefits. However, a consequence of being a long-lived resident is that 'all the available good real estate tends to be occupied, posing a problem for dispersing progeny.'.

Ford *et al.* (1988) also found that species that occupy foraging niches regarded by the authors as particularly vulnerable to predators (e.g. ground foragers) were more likely to breed co-operatively than species occupying other foraging niches. They suggested that the young of species occupying vulnerable foraging niches are likely to gain significant predator-detection benefits from group living, i.e. from being philopatric. Hence, they suggest since predation pressure may lead animals to live in groups, it may be a condition conducive to the evolution of co-operative breed-ing. However, the same ecological pressure (predation) appears to have led to a wide range of responses by organisms that do not involve co-operative breeding, e.g. flocking, or cryptic plumage or behaviour. As Brown (1987) stressed, while these various preconditions may be permissive or conducive to the evolution of philopatry, additional hypotheses are needed to account for helping behaviour.

LIFE HISTORY TRAITS OF CO-OPERATIVE BREEDERS

Recently attempts have been made to identify life history attributes that might be correlated with co-operative breeding in Australian birds. Longevity has been suggested as a possible correlate (e.g. Rowley and Russell 1990). How-ever, increased longevity appears to be typical of many Australian species (particularly tropical species) and not just co-operative breeders (Russell and Rowley 1993b).

Australian passerines tend to have smaller clutches than their Northern Hemisphere counter-parts (Rowley and Russell 1991). Furthermore, Poiani and Jermiin (1994) found that co-operatively breeding species in Australia lay smaller clutches than non-co-operatively breeding congeners. Co-operative breeders were also more likely to produce more than one clutch in a breeding season. This is despite co-operative breeders having breeding seasons of a similar length to non-co-operative breeders in Australia (Poiani and Jermiin 1994). The observation that small clutch size and multibroodedness appear to be correlated with co-operative breeding in Australia is intriguing, but sheds little light on the causes of co-operative breeding. For example, is it the aid given to the female breeder by helpers that enables her to produce a greater number of small

clutches within a fixed time-period, i.e. be multi-brooded? Or is multibroodedness a risk-spreading response by the female to predation pressure (that happens to result in a condition that is conducive to the evolution of helpers at the nest, i.e. namely, progeny from a previous brood still being present when the next brood is raised)?

Large-scale comparative studies are currently fashionable in behavioural ecology and are being used to tackle these kinds of questions (e.g. Edwards and Naeem 1993). Large-scale comparative analyses can only ever be as good as the data upon which they are based; unfortunately at present the quality of the data available for most species is very limited. Current knowledge of the propensity of each species to breed co-operatively and accompanying knowledge of basic life history traits is very poor for most Australian passerine species. Very little is known about geographic and temporal variation in these traits for any species. Long-term studies have revealed considerable variability in some species in their tendency to breed co-operatively. For example, Rowley (1981) reports the percentage of pairs with helpers each year varied from 0–c. 82 per cent during a five year study of the Superb Fairy-wren. Despite this variability, species tend to be classified as co-operative or non-co-operative breeders on the basis of whether the species has been frequently documented breeding co-operatively (Poiani and Elgar 1994). There are at least three difficulties with this approach. First, in a region where much of the avifauna has not been studied in detail, such classifications have the danger of being more a reflection of how intensively a species has been studied than a reflection of the species' propensity to breed co-operatively. Second, life history data for a species that has been collected from one range of habitats (e.g. Beruldsen 1980) tend to be analysed alongside data on the propensity of the species to breed co-operatively that may have been collected in another completely different range of habitats. Third, treating what is most probably a continuous variable (i.e. a species' propensity to breed co-operatively) as a categorical variable is likely to greatly reduce the power of any comparative analysis (McLennan and Brooks 1993). For example, it is debateable whether a species such as the Eastern Yellow Robin (for which only 25 per cent of pairs were reported to have helpers (Marchant 1985)) should be regarded as a 'regular

and well-documented co-operative breeder' (Poiani and Elgar 1994), in the same class as species like the White-winged Chough that almost always has helpers at the nest (Heinsohn 1991c).

CONCLUSION

As the quality of life history data available for Australasian co-operatively and, in particular, non-co-operatively breeding species improves, comparative analyses will become increasingly valuable for testing old hypotheses and possibly generating new ones that can be tested experimentally. While the long-term descriptive study has been the common approach of the past, it is clear that the greatest progress in testing hypotheses has been achieved when this approach has been combined with a manipulative experimental approach (e.g. Pruett-Jones and Lewis 1990). Still more powerful tests will be achieved when the experimental approach can be combined with more accurate descriptive data on the paternity and maternity of young based on modern molecular techniques (e.g. Mulder *et al.* 1994). Having reviewed the range of hypotheses relating to why birds breed co-operatively, it is striking how many have yet to be rigorously tested.

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