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Short sketches from the long history of cooperative breeding in Australian birds

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Abstract. We review the early literature and correspondence on two cooperatively breeding Australian passerines, the Superb Fairy-wren, *Malurus cyaneus*, and the White-winged Chough, *Corcorax melanorhamphos*. We show that recognition of cooperative breeding in these species was widespread in the nineteenth century, prompting experiments and formulation of adaptive hypotheses. These early studies precede by decades the work of Alexander Skutch, who is generally credited with the 'discovery' of helping behaviour in Central American birds. We discuss why this early literature has been ignored.

Introduction

In the introduction to the first edition of *The Emu* in 1901, it was noted that, in regards to Australian ornithology, 'there are technicalities to be settled, doubtful points to be cleared up, and mysteries of nesting, &c., to solve' (Anon. 1901: 3). In this review, we attempt to settle a technicality that has sold Australian ornithology short for over 65 years. In brief, cooperative breeding among birds was not first demonstrated in 1935 by the North American, Alexander Skutch, as is frequently stated. Instead, we show that reports of the phenomenon were commonplace in the early literature on Australian ornithology. As reported by Craig (1990) for the New Zealand avifauna, early Australian naturalists repeatedly described helping behaviour. We review the early literature and correspondence on the two cooperative species that have since attracted most attention, the Superb Fairy-wren, *Malurus cyaneus*, and the White-winged Chough, *Corcorax melanorhamphos*, to show that recognition of group-living and cooperation was ubiquitous. We uncover what we believe are the earliest experimental investigations of cooperative behaviour (in 1879 and 1907), and point to the original formulation (in 1928) of the skills hypothesis, an adaptive explanation of helping behaviour that is also usually credited to Skutch (1961). We speculate on reasons for the neglect of this earlier literature, and suggest that it would be dangerous to perpetuate geographical biases in future investigations of avian social systems. We have inserted several excerpts from the literature to support our arguments. In some instances we have italicised specific parts of these excerpts in order to add emphasis.

Cooperative breeding

Cooperative breeding among birds refers to the mating system in which more than one pair of individuals exhibit parent-like behaviour toward offspring of a single nest or brood (Brown 1978; Cockburn 1998; Hatchwell and Komdeur 2000). Such systems establish the evolutionary dilemma that some individuals (called 'helpers' or 'auxiliaries') appear to behave altruistically: not only do these individuals delay both dispersal and independent reproduction, but they also endure the physiological costs of helping in order to raise young that are not their own. Charles Darwin (1859: 269) recognised that the evolution of helping behaviour (specifically of sterile worker insects) was therefore 'possibly fatal' to his theory. Cooperative systems have thus generated considerable scientific interest, both empirical (e.g. Woolfenden and Fitzpatrick 1984; Brown 1987; Koenig and Mumme 1987; Stacey and Koenig 1990) and theoretical (e.g. Wilson 1975; Axelrod and Hamilton 1981; Emlen 1982; Brown 1987; White *et al*. 1991; Koenig *et al*. 1992). Indeed, this issue has been labelled *the* central theoretical problem in sociobiology (Wilson 1975).

Given the intense scientific interest in cooperative breeding, it is important that its history be properly documented. Many reviews of avian cooperative breeding and considerable numbers of empirical studies begin with a statement that the first record of helping behaviour can be traced to Skutch (1935). Indeed, this has almost become standard practice (e.g. Rowley 1968; Brown 1978, 1987; Brown and Brown 1990; Stacey and Koenig 1990; Emlen 1991). Even recent authors who rail against the chauvinism of northern temperate workers commit the fallacy. Stutchbury and Morton (2001: 56) exclaim 'The first description of helpers at the nest came from none other than Skutch (1935)!'

Steve Emlen (1991: 302) writes:

> Skutch's first published account in 1935 of cooperative breeding described extra adults provisioning young … Helpers (also called auxiliaries) at the nest were first described by Skutch in

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1935. Skutch's observations raised a number of intriguing questions. Who were these extra adults? Why were they not breeding on their own? And why were they raising another's young?

These are indeed pertinent questions, but they have a history that can be traced for decades prior to 1935.

What Skutch did and did not achieve

Skutch (1935) realised that over-enthusiasm for the recently formulated theory of territoriality (which had established that, in most instances, breeding pairs should actively expel other individuals from around their nest site) may have resulted in a tendency to overlook situations in which breeding pairs receive assistance at the nest by conspecifics. He suggested that helpers could be either juveniles from an earlier brood of the current reproductive season, or unmated birds from previous years. Skutch also included a category of 'mutual helpers', which was a largely incorrect, group-selectionist explanation of coloniality (e.g. 'group-rearing' of young by Emperor Penguins, *Aptendodytes fosteri*). His principal contribution was to describe in detail observations of the cooperative behaviour of three species of Central American birds. He had recognised the presence of a single auxiliary helping at the nests of Banded Cactus-wrens, *Heleodytes zonatus*, as well as multiple auxiliaries at the nests of Brown Jays, *Psilorhinus morio*, and Black-eared Bush-tits, *Psaltriparus melanotis*. He was able to deduce, on the basis of bill colouration, that the helpers at the Brown Jay nests were yearlings, and assumed that they were the offspring from the previous season. Skutch did not himself raise any questions regarding the adaptive significance of this behaviour.

It is surprising that workers steadfastly claim that the concept of a helper at the nest was first recognised by Skutch (1935) given that Skutch himself has from the first (1935), and repeatedly (Skutch 1961, 1987), acknowledged the existence in the scientific literature of accounts of helping behaviour prior to his own celebrated paper. In 1935 Skutch noted that helpers had been observed at the nest in British Moorhens, *Gallinula chloropus* (Grey of Fallodon 1927), Barn Swallows, *Hirundo rustica* (Forbush 1929) and two species of bluebirds (Western Bluebirds, *Sialia mexicana*: Finley 1907; Mountain Bluebirds, *S. currucoides*: Mills 1931).

Skutch (1935) also admitted that other records of alloparental behaviour in birds might also exist although they had escaped his attention. This was indeed the case (Craig 1990; Hemmings 1994). Biologists had already alluded to the presence of helpers at the nests in three New Zealand species: Wekas, *Gallirallus australis* (Guthrie-Smith 1910), Pukekos, *Porphyrio porphyrio* (Guthrie-Smith 1925) and Brown Skuas, *Catharacta skua lonnbergi* (Guthrie-Smith 1914, 1925; Stead 1932).

Furthermore, as we demonstrate herein, numerous detailed and perspicacious descriptions of cooperative breeding existed in the Australian ornithological literature substantially prior to 1935. This is shown by the early studies of two endemic Australian species — Superb Fairy-wrens, *Malurus cyaneus*, and White-winged Choughs, *Corcorax melanorhamphos*. Although both are cooperative breeders, the two species have relatively distinct social systems (see below). As a consequence, scientists came to realise that they are cooperative via quite different routes. As we demonstrate, early ornithologists very quickly realised that Superb Fairy-wrens were cooperative. In contrast, this deduction took considerably longer with respect to Choughs, which is at first surprising given that Choughs are obligatorily cooperative (Heinsohn 1992; Heinsohn and Cockburn 1994).

Cooperative breeding in Superb Fairy-wrens

Superb Fairy-wrens have an extraordinary mating system that combines cooperative breeding with extreme levels of extra-group mating. Each territory is occupied by a dominant pair that may be assisted in feeding nestlings and fledglings by as many as four male helpers, and accompanied by additional young of the year, as well as unrelated females that settle in the territory to overwinter (Rowley 1965; Mulder 1995; Dunn and Cockburn 1996). Although all the adult males on the territory produce sperm and are capable of siring young (Mulder and Cockburn 1993; Dunn and Cockburn 1999), the female typically cuckolds all the males who help raise young, instead initiating matings with males as much as five territories from her own (Mulder *et al.* 1994; Double and Cockburn 2000). Females prefer to mate with sires that spend the winter in blue plumage (Mulder and Magrath 1994; Dunn and Cockburn 1999; Green *et al.* 2000), a trait that is attainable only by high-quality males (Peters 2000; Peters *et al.* 2000, 2001). It seems that all fairy-wren species combine cooperative breeding with rampant infidelity (Brooker *et al.* 1990; Tuttle *et al.* 1996; Rowley and Russell 1997).

Superb Fairy-wrens were one of the first birds observed and described by the early European explorers and settlers. The European *voyageurs* first met with this species in January 1777, at Adventure Bay, Bruny Island, off Tasmania. In the official account of Cook's Voyages (1784: 109), Ellis mentions that the party saw a 'small one, with a pretty long tail, [that] has part of the head and neck of a most brilliant azure colour, from whence we named it *Motacilla cyanea*'.

The early observers quickly developed both a fondness and an understanding of the species. In 1808, Lewin painted and very briefly described only 26 species in his 'Birds of New Holland', one of which was the Superb Fairy-wren. He wrote, 'These birds always go in small companies, having seldom above one male in full plumage' (Lewin 1808: 19). Although he had space to devote only three or four sentences to each species, Lewin was evidently of the opinion that the tendency of Superb Fairy-wrens to occur in small parties, and their sexual dichromatism, were sufficiently important,

if not diagnostic, traits to warrant inclusion in such restricted notes. Evidently, the early observers knew full well that males did not necessarily wear their stunning nuptial plumage at all times. That naturalists were cognisant of this fact from a very early stage would have enabled them to recognise individuals within groups, even in the absence of colour bands.

From 1800 to 1810, George Caley, an explorer and naturalist (who had been sent to New South Wales by Sir Joseph Banks to gather botanical specimens), began collecting birds and writing brief field notes (Currey 1966). These were to become the raw material for the first review of Australian birds (Vigors and Horsfield 1827). Caley's field notes expanded upon Lewin's understanding of the fairy-wrens, and, importantly, imply that biologists were already prepared to entertain the possibility that this species' breeding system may be more complex than first meets the eye:

> They are gregarious, and polygamous to appearance, unless I have been deceived by the young birds possessing the plumage of the female.
>
> Caley, quoted in Vigors and Horsfield (1827: 221)

The familiar and intimate interactions between the adult male and the additional birds were sufficient to suggest to Caley that they were somehow involved in the breeding attempt (thereby suggesting polygamy). Although Caley had indeed been deceived by the appearance of the young birds, he was nevertheless acutely aware that the presence of the 'additional birds' needed an explanation and further investigation.

In combination, these brief, old passages indicate that the early biologists were on the edge of an important conceptual leap, one that had clearly been made by the time the indomitable John Gould published 'The Birds of Australia' in 1841. While Gould's description of Superb Fairy-wrens scarcely mentions their nesting behaviour, the plate that accompanies his text speaks volumes. The scene depicts an adult female and *two* adult males in full nuptial plumage. All three birds are only centimetres from the entrance of the nest. Moreover, *both* males are clearly returning food to the nestling (which in this case happens to be a Shining Bronze Cuckoo, *Chrysococcyx lucidus*). The cooperative relationship of the trio in Gould's painting is unequivocal, and is also described explicitly in the accompanying text (1841: 18): 'the plate represents two males and a female with the nest, the former engaged in feeding a young cuckoo.'

There are few subsequent written accounts of the breeding biology of Superb Fairy-wrens until the 1900s. In 1899 the naturalist Graham wrote a letter to Robert Hall detailing his observations of the breeding biology of Superb Fairy-wrens. Hall (1907: 86) was to publish the letter in his monograph 'The Useful Birds of Southern Australia' a few years later:

> The spring before (1897) I noticed a similar case [of cooperative breeding], so, when in August, 1898, I found a pair of males attending one female in a very isolated patch of cover, which could be easily seen, I determined to watch them right through.
>
> From the first it was evident that one male had the happy possession of the female, and that the other male was tolerated either because it could not, or would not, be driven away. When the female was on the nest the two males were apparently friendly enough, fed, hunted, and camped together.
>
> When the young were hatched out, on the 28th of October, both males fed and attended to them, and right on to the present time (20th June) the partnership continues. This being the third instance of such conduct in three successive seasons leads one to assume it is not an isolated example.

Graham then goes on to describe how both males jointly defended their territory. It is significant that Graham, in the same letter to Hall (1907: 82), stated that these young helpers probably 'pass the first year without breeding'. Australian biologists were apparently aware that young male fairy-wrens were delaying dispersal and helping to raise their younger siblings.

Not only had Graham accurately described cooperative breeding, he had even conducted experimental studies of Superb Fairy-wren nesting behaviour with the specific objective of demonstrating cooperation:

> *More than one adult male will attend a single brood of nestlings*. Three nests of young were brought from the forest and placed in three cages, somewhat apart. Each nest had its female, which, in one case, was attended by three males, in the second two, and in the third one, *all helping in the task of feeding the young*. In the first-mentioned case this was observed before the nest was removed, and was continued for fourteen days after the removal to new quarters, where the feeding was done through the wires.
>
> Graham, quoted in Hall (1907: 82)

Graham's description is doubly remarkable because this is surely the first removal experiment on a cooperatively breeding bird and because his use of the words 'helping in the task of feeding the young' is, so far as we are aware, the first use of the word 'help'. Furthermore, the first sentence quoted above bears uncanny resemblance to the definition of cooperative breeding used 100 years later in Cockburn's (1998: 141) recent review:

> Cooperative breeding in birds describes social systems wherein more than two individuals combine to rear a single brood of young.

Graham's observations, published in Hall (1907), outline the quintessence of cooperative breeding theory, and evince a level of understanding of the phenomenon that would not be surpassed by any other description of the behaviour for another 60 years, Skutch (1935) notwithstanding.

Biologists continued to discover and record details of this popular species' unusual mating system and became increasingly interested in determining the identity of the group members.

> All the members of the *families* keep together in a company during the year, and from the excess of hen-birds the associa-

> tion suggests polygamy, but the blue male who 'proudly struts his dames before' is but the mate of one and the father of the others … [Although the female offspring] are dismissed to take upon them domestic duties of their own … unmated males will assist a mated pair in feeding and tending the nestlings.
>
> Lucas and Le Souëf (1911: 324)

As Caley had intimated 100 years earlier, the presence of the multiple, dull-plumed birds suggests that a single male occupies a harem of females. However, 100 years of observation of such familiar and sedentary birds is a long time: and the identity of the additional birds in a fairy-wren group was no longer questioned. Lucas and Le Souëf (1911) plainly understood that the juvenile females dispersed to establish a new territory, whereas the young males remained philopatric to help at the nest of the parents. It had become quite apparent that the helpers are social-family members.

For the next 50 years ornithologists provided increasingly detailed accounts of this species' cooperative behaviour (e.g. Ashby 1912; Ford 1918; Mathews 1922 and references therein; Huemann 1927; Bryant 1928; Rowley 1957). Early workers even began to ponder its adaptive significance. For example:

> The Superb Blue Wren (*Malurus cyaneus*) is called, in some districts, the Mormon wren, on account of his *apparent* harem of little brown ladies. These are most likely the young of the year's first brood; and sometimes 'big brother' even assists in tending his new little sisters and brothers. At Wandin I saw two fully-plumaged males engaged in supplying a nest full of hungry youngsters with 'small game.' Evidently 'uncle' was gaining experience preparatory to taking on himself the responsibility of rearing children of his own.
>
> Bryant (1928: 64)

Bryant's suggestion that auxiliary males may receive direct fitness benefits by delaying dispersal and gaining breeding experience has since been resurrected as the skills hypothesis, one of the adaptive hypotheses used to explain the evolution of helping behaviour in birds (Brown 1987; Cockburn 1998). Remarkably, it was Skutch (1961) who resurrected this idea, and it was also mentioned by Selander (1964), who formulated what is now known as the ecological constraints model of cooperative breeding. The skills hypothesis has only recently attracted sophisticated empirical investigation (Komdeur 1996; Khan and Walters 1997).

However, three decades elapsed before the simultaneous and influential use of colour-banding of Superb Fairy-wrens by Bradley and Bradley (1958) and Rowley (1957, 1961, 1965) resuscitated studies of cooperative breeding in the Australian avifauna. These studies were timed perfectly to attract interest, as theoretical debate over the importance of group selection was about to erupt (see below). Rowley's (1965) data were used as the standard textbook model of application of Hamilton's rule to predict kin-selected altruism (Brown 1975; Grafen 1984). However, the parameters used by these authors have since been shown to be incorrect, as helpers are often unrelated to the young they provision, and there is no strong evidence that they enhance group productivity (Dunn *et al.* 1995; Green *et al.* 1995; Cockburn 1998). Instead, helpers benefit older birds by reducing the constraints on female choice (Mulder *et al.* 1994) and allowing dominant males more time to court females from other groups (Green *et al.* 1995). Helpers may help because they are forced to do so (Mulder and Langmore 1993).

Cooperative breeding in White-winged Choughs

White-winged Choughs are large (350–380 g), sexually monomorphic, Australian passerines. Active nests can be found from July through to February in open sclerophyll forests throughout much of Eastern Australia. Their mud nests are massive (30 cm diameter), highly visible structures, typically mounted on eucalypt branches 5–20 m from the ground (Rowley 1978).

Cooperative breeding in Choughs is enforced by a difficult foraging niche. A breeding pair is unable to gather sufficient food to prevent complete brood loss through starvation (Heinsohn 1991*a*; Boland *et al*. 1997). As a result, parents must have at least two additional helpers to successfully fledge even one young (Rowley 1978; Heinsohn 1991*a*, 1992). Thus, Choughs are *obliged* to breed cooperatively in cohesive groups of 2–20 birds (Heinsohn 1992). Almost all (97%) Chough nests are attended by groups containing at least three members (n = 336 of 348 nesting attempts: combined data from Rowley 1978; Heinsohn 1992; Boland 1998). Groups are composed equally of both sexes, and group members of all ages contribute to every aspect of reproduction, including nest building, nest defence, and incubation and provisioning of nestlings and fledglings (Rowley 1978). Combined, these facts ensure that observing the cooperative nesting behaviour of Choughs tends to be a relatively simple affair.

White-winged Choughs were first formally described on 15 March 1817 by Vieillot. The intense sociality of Choughs was recognised from the outset. Despite their brevity (only five sentences), the first field notes published on Choughs had to remark on one of their most distinguishing features: 'it is gregarious' (Vigors and Horsfield 1827: 265). It was not until 1846, however, that John Gould was to provide a fuller description of their behaviour. Gould almost immediately discusses their sociality: 'it usually occurs in small troops of from six to ten in number' (Gould 1846: 16). Soon after, he becomes the first to ponder the question of their breeding behaviour:

> The nest is a conspicuous fabric, composed of mud and straw, resembling a bason [sic] and usually placed on the horizontal branch of a tree … it has often struck me that more than one female deposited her eggs in the same nest, as four or five females may be frequently seen either in the same or neighbouring trees, while only one nest is to be found.

Thus, by 1846 the wheels were in motion: it is unmistakably apparent that all of the individuals in a breeding group

of Choughs are occupied with only one nest. This provided Gould with two possible alternative explanations: either the clutch (typically four or five) was laid by one female, or four or five females laid one egg each. Gould had no evidence at his disposal for or against either hypothesis. Choughs are sexually monomorphic, so sex ratios could not be inferred. Gould, an Englishman, of course, cut his teeth on the idea of a standard breeding pair defending a territory. Perhaps, as a result, he could not shake off the presupposition that *any* individual at a nest must be a breeder and thus opted for the first explanation. Even though many groups contain only four or five birds yet still incubated four or five eggs, Gould was reluctant to presume that some individuals were attending a nest that did not contain their own offspring. Instead he assumed that a single male must have possession of a harem of breeding females. Gould, however, could not reach this conclusion with the Superb Fairy-wrens given that the bright blue plumage of the helpers clearly reveals that they are all male.

Gould's assumptions regarding the Choughs were treated as essentially aphoristic and accordingly recapitulated by various workers for the next 50 years (e.g. Broinowski 1890; Campbell 1900). Broinowski (1890: 35), for example, virtually paraphrased Gould (1846):

> It is generally found in groups of from six to ten … another strange thing about this bird is that apparently several females deposit their eggs in the same nest, since on trees where there is only one nest, four or five birds are seen.

While some workers were prepared to accept Gould's assertion (that the entire group attend only one nest) on face value, others appeared to need definite proof. In September 1879, Hermann Lau attempted to 'prove beyond doubt' (Campbell 1900: 66) the existence of this apparent anomaly – that the entire group attend only one nest. Lau did not believe in indirect methods of obtaining data: he was able to ascertain clutch size by 'sending my black climber up a tree to fetch me a nest with the complement of eggs' (in Campbell 1900: 66). Moreover, Lau had a surefire method for confirming cooperation:

> The Black Magpie (*Corcorax*) is gregarious, living in small troops of from five to fifteen, and is dispersed all over the [Darling] Downs. Together they commence building one nest, its material being simply mud mixed with dry grass … on which five or six eggs rest. The whole company attend to one nest, as I have proved, shooting two birds from the nest, and seeing a third sitting next day.
>
> Lau, quoted in Campbell (1900: 66)

This heavy-handed 'experimental' protocol revealed what simple observation had already confirmed: that more than two birds were sitting on the nest. Given that as many as 15 birds were sharing at most six eggs, it is mathematically obvious that not every group member can be a breeder. Since all Choughs were known to attend the one nest, clearly some group members must be auxiliaries.

Despite quoting the entire passage (above) from Hermann Lau, this elementary mathematical reasoning seemed to have also eluded Campbell (1900). He professed that the question 'do the females lay each one or more eggs?' was still 'an important point to be settled' (Campbell 1900: 66).

This question was, in fact, in the process of being answered. By 1889 North had realised not only that 'it is well known that often more than one pair of birds assists in the construction of one nest', but also that 'the usual number of eggs for a sitting is four, but as many as eight have been taken from a single nest' (North 1889: 189). It was becoming obvious to North that four eggs was the modal clutch of a single female, not the product of four different females. He would confirm this in 1901 in his magnum opus 'The Nests and Eggs of Birds Found Breeding in Australia and Tasmania':

> Moving about in small flocks of from five to ten in number … Several birds assist in the construction of each nest, and frequently three or more may be observed busily engaged at the same time on one nest … [A] flock of six birds … all assisted in the construction of a nest … in a large number of sets [ie complete clutches] now before me, the greater portion of the eggs belonging to the sets of four, or five, from each nest are, as a rule, alike in shape, size, colour, and disposition of markings … [Some sets, however,] contain two or more distinct types of eggs.
>
> North (1901: 21–22)

By 1901 North had demonstrated that the typical clutch of a female Chough is four or five eggs. In fact, he was so certain of this that smaller clutches required special explanation:

> In several instances, however, I have found nests with only two or three incubated eggs, or young ones … It is possible that they may have had a portion of their contents abstracted by a Raven or Crow.
>
> North (1901: 22)

It had become unequivocal that in the majority of Chough nests only one female will lay, indicating that the supernumerary birds were not themselves breeders. Since these birds were nonetheless participating in the rearing of the offspring, they must be helpers at the nest.

These facts were to be reiterated by several workers in the early 20th century (e.g. Hall 1907; Austin 1908; White 1912). By 1908, Austin (in Mathews 1926) had been following several Chough groups for more than 20 years and had compiled an impressive data set:

> During 1908 I made a special study of their eggs and examined twenty-seven complete clutches, which ranged from three to eight, but I found in every case where there were more than five eggs in a nest, they were of two distinct types, but when there were five or less I am quite satisfied they were laid by the same female. A whole flock assists in the building of the nest, *but* I am of the opinion that a very small percentage of the females lay each year.
>
> Austin (1908), quoted in Mathews (1926: 417)

Likewise White (1912: 208) stated:

> They move about in large communities, giving their weird and mournful whistle; when one flies off they all follow … If a bird

> should be wounded, the whole party come fussing round with wings drooping and tail spread out, uttering loud calls of alarm … Many birds seem to assist in building the wonderful mud nest, *but* I am of the opinion that *only* one bird lays in it; the clutch varies much, for three to seven eggs will be found in the nest.

Clearly, both Austin's and White's use of the words 'but' (rather than the equally applicable 'and') indicates that they realised that cooperative breeding was an unusual concept. Regardless, these workers were now prepared to take this stance given the mounting weight of evidence collected not only from observations of Choughs but also from several other Australian species including the fairy-wrens.

These passages also indicate a developing appreciation of the stability of Chough groups. This cohesion combined with the tame disposition of Choughs permit detailed and longitudinal observations, and it was not long before Australian ornithologists (e.g. Campbell 1900; Austin 1908, in Mathews 1926) realised that Chough groups tend to remain faithful to their nest sites, making it a simple task to identify groups:

> They breed here in great numbers, often using the same nest year after year, just adding a little fresh mud to the top rim. If a nest falls down after using it, and before the next breeding-season, they will often build a new nest in the same tree. One flock has lived about my house for over twenty years, and for as long as I can remember they have reared their young in the same tree.
>
> Austin (1908), quoted in Mathews (1926: 416)

This enabled observers to follow the fate of the fledglings and it was thus only a matter of time before biologists appreciated the consanguineous association of a Chough group. This is portrayed frequently throughout the early literature on Chough breeding biology, though it is most succinctly stated by Howe (in Mathews 1926: 419):

> They are local to an extraordinary degree and can always be met with in small *families* in the same spot for years. We have never noticed more than one nest being occupied in any given spot, though a lot of birds were seen in that locality. It is possible that some of them perhaps don't reach maturity for a few years.

Brown (1987: 9) emphasised that the breakthrough of Skutch (1935) was in showing that juveniles did not disperse and hence that 'the resultant *groups existed all year*.' The work by Austin and Howe (in Mathews 1926) indicate that this breakthrough had already long been made.

By the 1920s cooperative breeding behaviour was a well-accepted fact in Australia, with accounts occurring even in the popular press. Chisholm (1929), for instance, mentioned that a Chough group 'combines for the purpose of nest-building'. By 1934 he had coined the term 'community nest-building' (which he distinguished from 'nesting in communities') as a shorthand appellation for the behaviour (Chisholm 1934: 243).

One year later, Skutch published his account of the same phenomenon.

Cooperative breeding in other Australian species

An equally detailed history of the scientific understanding of cooperative breeding could have been assembled for several other Australian species, including (but not confined to) Grey-crowned babblers, *Pomatostomus temporalis*, Sitellas, *Neositta chrysoptera*, Dusky Woodswallows, *Artamus cyanopterus*, and, of course, Apostle birds, *Struthidea cinerea* (e.g. Campbell 1901; North 1901; Hall 1907; White 1914; Mathews 1922, 1923, 1926; Chisholm 1929, 1934: and references therein). Helpers at the nest had even been recorded for species that are very occasionally cooperative (e.g. White-naped Honeyeaters, *Melithreptus lunatus*: Mathews 1922). All of these species were known to cooperate prior to Skutch's findings in 1935. To quote but one example:

> The queer grey jumpers, the 'twelve apostles', of inland Australia, construct their mud nests on the company principle also … I saw a flock of perhaps ten grey jumpers approach a nest and *four* birds take turns at sitting in it, each remaining cuddled down for only half a minute or so. Possibly that nest contained babes and the chattering birds were, like so many human females, taking turns at mothering the progeny!
>
> Chisholm (1929: 63–64)

Why was cooperative breeding discovered so early in Australia?

Cooperative breeding is such a rare phenomenon in North America that in 1933 Skutch had to trek to the foothills of the Sierra de Merendón in what was then disputed territory between Honduras and Guatemala to observe its occurrence (Skutch 1987). He needed to make his observations from inside a hide, in what was evidently a visually occluded habitat. It is little wonder that only two years later Skutch (1935: 257) avowed that proving a brood was being raised by more than the standard breeding pair was difficult 'because their discovery requires a more concentrated attention than is commonly devoted to studies of nesting birds.'

By contrast, Australian birds are not only commonly cooperative (Rowley 1968; Dow 1980; Ford *et al*. 1988; Clarke 1995; Cockburn 1996), but many species are extremely easily observed. For example, Gould (1848) said of the Superb Fairy-wren:

> It is abundantly dispersed over every portion of the colony of New South Wales … The members of this genus are among the most beautiful of the Australian birds … No bird can be more tame and familiar, for it frequents the gardens and shrubberies of the settlers, and hops about their houses as if desirous to court, rather than shun, the presence of man … They will frequently build their little nest and rear their young in the most populous places. Several birds are reared annually in the Botanic Garden in Sydney, and I saw a pair busily employed in constructing a nest in a tree close to the door of the Colonial Secretary's office in that town.
>
> (Gould 1848: 18)

The overt and sometimes obligatory cooperative nature of such a large proportion of our avian species means it is prob-

ably easier to observe helpers at their nest than to not observe them, unless wearing the ideological blinkers imposed by familiarity with birds from other parts of the world. As we have noted, European explorers first recorded Superb Fairy-wrens in 1777 off Tasmania. Bass and Flinders were still 20 years away from discovering that Tasmania was an island. Evidently, Superb Fairy-wrens are easier to locate than Bass Strait.

Why does Skutch receive the credit?

The question remains then, why do so many modern authors on cooperative breeding believe 'the concept of a helper was originated by Skutch in 1935' (Brown 1978: 123)? There are likely to be several factors acting in concert. First, many of the early descriptions of cooperative breeding recapitulated in this review are difficult to access, particularly for overseas workers.

Second, the study of cooperative breeding may have been a victim of geography. As Brown (1987) suggested, until recently scientists and cooperative breeding birds rarely co-occurred. This seems an unsatisfactory explanation given that scientists have been describing the behaviour in Australia for more than a century. A more plausible explanation is that scientists in the Northern Hemisphere (where cooperative breeding is a rare occurrence) were theoretically blinkered by the preponderance of pair-breeding species that typically exclude all conspecifics from their territory (Rowley 1968). Consequently, Northern Hemisphere biologists tended to neglect or even disbelieve reports of cooperative breeding from the antipodes. The possibility of such a bias was articulated by Richdale (1965: 84), a New Zealand biologist who lamented the fact that:

> The phenomenon of three adult skuas at a nest, each one apparently equally devoted to the chicks, has usually caused sceptical comment whenever I have mentioned the fact in Northern Hemisphere circles.

As illustrated by Craig (1990), Richdale's studies of conventional, pair-breeding seabirds were readily quoted by eminent Northern Hemisphere biologists (including Lack 1954, 1966). It was not that long ago that Northern Hemisphere biologists refused to believe in scientific descriptions of the Platypus.

There may be a third reason why Skutch (1935) often receives the credit for discovering cooperative breeding — that being coincidence. Interestingly, the paper by Skutch (1935) 'stimulated almost no further work except by Skutch himself' (Brown 1987: 8). In 1961 Skutch reviewed the literature on cooperative breeding, but still Northern Hemisphere scientists continued to show little interest. That is, until it became 'theoretically possible' following the formal development of kin selection theory to explain the evolution of social behaviour (Hamilton 1964*a*, 1964*b*; Maynard Smith 1964). Much of the impetus for the development of this theory came from the need to replace the conceptually impotent 'group-selection' models of the time (e.g. Wynne-Edwards 1962). In the ensuing controversy both kin-selectionists and group-selectionists repeatedly utilised Skutch's (1961) recent review and his original 1935 article as evidence for their own argument (e.g. Hamilton 1964*b*; Williams 1966). The review by Skutch (1961) had thus appeared at an opportune time and would certainly have served to bring to prominence his 1935 article. Several reviews of helping behaviour followed soon after (Rowley 1968; Lack 1968; Brown and Brown 1978), all stating that Skutch (1935) was the discoverer of helping behaviour.

We hope this review will finally provide the bygone Australian ornithologists with the credit they so richly deserved. It is possible that even earlier accounts may languish unnoticed in antiquarian literature on African or South American birds, as explorers would have encountered conspicuous, cooperatively breeding birds such as ostriches, jays and shrikes long before the European colonisation of Australia.

Is the same mistake being made?

In addition to correcting this error of attribution, we hope that it will also be obvious that fully understanding avian social and mating systems will never be achieved by ignoring the lessons to be learned from most of the world's birds, which live in tropical and southern temperate environments. For example, elsewhere we have argued that the optimism that all cooperative breeding can be explained within the framework emanating from the study of northern temperate species such as the Florida Scrub Jay, *Aphelocoma coerulescens*, and the Acorn Woodpecker, *Melanerpes formicivorus*, is misguided (Cockburn 1996). Indeed, the Florida Scrub Jay can be viewed as an old Australian bird carrying its cooperative legacy to a new home rather than a habitat specialist crippled by the inability to find new habitat in which it can breed (Cockburn 1996). We hope that this historical sketch will sound a clarion call to the readers and authors of the *Emu* as the journal enters its second century.

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