

Co-operative Breeding — a Gondwanan Perspective

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In his recent survey of the occurrence of co-operative breeding, Brown (1987) concluded that 'surveys of the taxonomic distribution of avian communal breeding systems have revealed numerous independent origins but little scope for interpretation along phylogenetic lines except within genera or sub-families' (Brown 1987, p. 43). Brown followed the taxonomy of Peters as interpreted by Morony *et al.* (1975). As a result, some interesting taxonomic correlations of co-operative breeding in Australian birds remained obscured. This note attempts to reveal these correlations.

In older systems of classification such as that used by Brown, 'convergent morphological characters have resulted in the clustering of Australo-Papuan species with groups based upon European, Asian and African types' (Sibley & Ahlquist 1985, p. 1). Thus, the Australian Babblers (*Pomatostomus*) were included in the sub-family Timaliinae with the Asian Babblers (*Turdoides*), the Australian 'robins' in the sub-family Muscicapinae, and endemic Australasian groups such as *Orthonychinae*, *Malurinae* and *Pachycephalinae* were placed as sub-families of the Family Muscicapidae. Passerines in Australia were assumed to have derived from a northern source and to have reached Australia in a series of invasions (Keast 1981).

Recent systems of classification based upon phylogeny indicated by DNA hybridisation (Sibley & Ahlquist 1985) and electrophoretic and chromosome studies (Christidis & Schodde in press) recognise the existence of a major passerine radiation in Australia during the period when Australia was isolated from other continents and still drifting northwards towards Asia. Sibley & Ahlquist (1985) recognise two major groups of the sub-order Passeres, which DNA hybridisation studies indicate diverged c. 58-60 million years (m.y.) ago: the parvorder Corvi and the parvorder Muscicapae, each with three super-families. The Muscicapae, with super-families Turdoidea, Sylvoidea and Fringilloidea, includes all passerines that are not members of the Corvi. Most families of the living Corvi are still confined to Australasia and Sibley & Ahlquist (1985) suggest that the group probably originated in Australia because the oldest lineages are still confined to Australia and New Guinea. The three super-families of the Corvi, in Sibley & Ahlquist's classification, include most Australian passerines (258 species, Schodde 1975; families marked with an asterisk include co-operative breeding species). In the super-family Menuroidea are the Menuridae, Ptilonorchinidae and Climacteridae*; the super-family Melipha-

goidea includes the Maluridae*, Meliphagidae* and Acanthizidae* and the super-family Corvoidea includes the Eopsaltridae*, Orthonychinae*, Pomastomatidae* and the Corvidae* with sub-families Cinclostomatinae, Corcoracinae*, Pachycephalinae*, Monarchinae and Corvinae. All the Muscicapae in Australia (64 species; Schodde 1975) are relatively recent arrivals, migrants, vagrants or introductions: finches, reed-warblers, pipits, larks etc.

The phylogeny and classification of Christidis & Schodde (in press) differs slightly from that of Sibley & Ahlquist, but not in the essential point, that one or two lines gave rise to the majority of Australian passerines in a major radiation.

Sixty-eight species of co-operative breeders occur in Australia, of which 57 are passerines (from Brown's Table 3:1, plus *Malurus coronatus* — Rowley 1987). All of these latter belong to old endemic families of the early Australian radiation and none to the more recent arrivals. Thus, of 258 species of these old Australian endemics, at least 22% (57/258) are co-operative breeders, compared with the overall incidence for passerines world-wide of 3% calculated by Brown (1987). These figures are conservative because there are inadequate data on many Australian Neotropical and African species.

The high level of co-operative breeding in Australian passerines has long been recognised (Rowley 1969, 1976; Dow 1980), but phylogenetic correlations were masked as so many Australian species were misclassified in Afro-Eurasian families. According to Sibley & Ahlquist's phylogeny, many of the Australian families with a high incidence of co-operative breeding have been distinct for 35-40 m.y., and are some of the oldest established passerine families, for example, the Climacteridae, Maluridae, Acanthizidae, Eopsaltridae, Orthonychidae and Pomastomatidae. The 'recent arrivals', the (Muscicapae), none of which have become co-operative breeders, must have arrived since the time when Australia approached close enough to Asia for invasion to have occurred (15-20 m.y. ago; Powell *et al.* 1981). This suggests that co-operative breeding evolved in the environment of Australia before this happened. At that time, the Corvi dispersed from Australia to Asia and beyond, and some of these, such as the North American Jays *Aphelocoma* spp. became co-operative breeders elsewhere, again suggesting an early origin for co-operative breeding.

This suggests that in trying to relate the high level of cooperative breeding in Australia and the tropics to ecological factors, we should consider not only present environments, but past history as well. The large numbers of cooperative breeding species in Australia does seem to be correlated with the number of non-migrant species and high survival, together with a climate and diet that allows parents and offspring to live together all year round in the same area (Brown 1987; Ford *et al.* 1988).

Early in the Australian passerine radiation, the warm humid aseasonal climate of the early Tertiary favoured the development of dense forests across much of Australia. Marked climatic fluctuations have continued from the mid-Miocene (15 m.y. ago) to the present and increasingly frequent periods of aridity have led to the restriction of Closed Forests to eastern coastal areas and the development of extensive areas of xeric vegetation. Nevertheless, apart from small glaciated areas, temperatures remained moderate, and the extremes of cold and seasonal drought experienced elsewhere have not occurred (Specht 1981). The numerous large scale migrations of Europe and North America do not occur generally in Australian passerines. Only a few of the 'old endemics' are migratory, many (especially honeyeaters) are nomadic, and there is a large array of resident omnivores and insectivores. Dow (1980) found no clear-cut result from his analysis of the possible effects of environmental influences on the occurrence of co-operative breeding in Australia; clearly the range of present-day Australian climates is favourable to it, except perhaps the most seasonal ones. This would suggest that in Australia the old endemic passerines for much of their long evolutionary history have been in an environment that has predisposed them to co-operative breeding. However, other factors must be involved, because most species are not co-operative, and even members of the same genus may differ. Some of these factors are discussed by Ford *et al.* (1988).

Yom-Tov (1987) recently demonstrated that the old endemic Australian passerines have significantly smaller clutch sizes than old world passerines, and there is some evidence of their greater longevity (Fry 1980; Woinarski 1985). It would seem that co-operative breeding is yet another aspect of life history that developed early and has persisted during the evolutionary history of the passerines in Australia.

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