The Mistletoebird and Australian Mistletoes: Co-evolution or Coincidence?

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The mutualism involving the Mistletoebird *Dicaeum hirundinaceum* and the Australian mistletoes (Loranthaceae and Viscaceae) dispersed by birds is well-known (Keast 1958). The principal food of the Mistletoebird is mistletoe fruit and the bird is apparently the principal disperser of Australian mistletoes (Liddy 1983). The specificity of the interaction is unrivalled among seed dispersal systems in Australia (Serventy 1973). Calder (1981) and Blakers *et al.* (1984) stated that the Mistletoebird has co-evolved with Australian mistletoes. If this was the case, one would expect the Mistletoebird and Australian mistletoes to have shared a long evolutionary association. In this paper, I argue on the basis of biogeographical evidence that this is not so and suggest that Australian mistletoes co-evolved with old elements of the Australian passerine fauna, such as the honeyeaters, long before the colonisation of Australia by the Mistletoebird.

The Australian mistletoe flora has three elements with different origins (Barlow 1983). The small genus of stem parasites, *Muellerina* (Loranthaceae), is a primitive Gondwanan element. However, most loranthaceous mistletoes belong to an autochthonous element derived from Gondwanan stocks, which radiated after the final separation of the Australian and Antarctic landmasses in the late Oligocene (Barlow 1983). This group is characterised by the largest and most abundant genera of Australian mistletoes, *Amyema* (36 Australian species) and the endemic genus, *Lysiana* (eight species). The third element of Australian mistletoes is the Viscaceae and a small number of Loranthaceae whose progenitors entered Australia via Indo-Malaysia some time after the collision of the Australian plate with the Sunda archipelago in the mid-Miocene (about 15 million years before present).

The Mistletoebird is the only species of *Dicaeum* in Australia. Because it is closely related to (and perhaps conspecific with) allopatric taxa throughout Indo-Malaysia, Mayr & Amadon (1947) and Salomonsen (1961) considered that *D. hirundinaceum* was a relatively recent immigrant to Australia. Mayr (1944a,b) thought that *D. hirundinaceum* colonised Australia in the late Pliocene or Pleistocene, and R. Schodde (pers. comm.) suggests that the species has been in Australia for one or two million years at most.

The absence of the Mistletoebird from New Guinea suggests that the species may not have reached Australia until after the formation of Torres Strait during the Holocene. Australia and New Guinea were connected by a broad landbridge in the region of the Arafura Sea and Torres Strait at the height of the last glaciation (Nix & Kalma 1972). New Guinea has a diverse mistletoe flora (Barlow 1974) and a spectrum of wooded habitats that Mistletoebirds inhabit in Australia, e.g. mangroves, savanna, lowland and montane rainforest (Keast 1958). *D. hirundinaceum* is replaced in New Guinea by *D. pectorale* and *D. geelvinkianum*, which represent a different phylogenetic line within *Dicaeum* and which recently colonised New Guinea.

Because bird-dispersed mistletoes have been present in Australia for much, if not the whole, of the Cenozoic (Barlow 1983), what birds dispersed mistletoes during the Tertiary if the Mistletoebird was not present? Honeyeaters (Meliphagidae) were among the first passerine families to radiate in Australia, judging from their antiquity (Sibley & Ahlquist 1985), the extent of the radiation and their occupation of numerous ecological niches (Keast 1976, 1981). At least nine species have been recorded feeding on the fruits of various mistletoes (Reid 1986), including the frugivorous Painted Honeyeater *Grantiella picta* that spe-

TABLE 1. Records of birds feeding on the fruits of Australian mistletoes. Shown are the number of mistletoe species for which there are records. Data for seed predators (parrots, cockatoos, etc.) are excluded. Information from Reid (1986).

Bird species	Australian mistletoe genera			Other genera
	Muellerina	*Amyema*	*Lysiana*	
Mistletoebird	2	6	2	2
Painted Honeyeater	0	5	0	0
Total, all Australian honeyeaters	0	6	2	0
Other native species	0	2	1	2
Total, all species	2	7	2	3
No. of bird-dispersed mistletoe species	4	36	8	34

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cialises on mistletoe fruit and disperses the seeds (Liddy 1983; Reid 1986). Table 1 shows that honeyeaters feed on a similar range of Australian mistletoes as does the Mistletoebird, although observations of the seed vectors of the majority (83%) of mistletoes are not yet available. The frugivorous bowerbirds (Ptilonorhynchidae) are another old Australasian family (Sibley & Ahlquist 1985) that may have dispersed Australian mistletoes during the Tertiary and early Pleistocene, although there are as yet no records of them feeding on mistletoe fruit.

In conclusion, the Mistletoebird colonised Australia at some stage during the Pleistocene, and perhaps as late as the Holocene, certainly late in the history of the evolution of Australian mistletoes and their co-adaptation with birds as dispersers. I suggest that the evolution of *Dicaeum* with Oriental mistletoes in Indo-Malaysia pre-adapted the Mistletoebird for co-existence with the diverse Australian mistletoe flora. The Mistletoebird would have immediately begun to feed on the fruits of the mistletoes that it encountered in Australia and disperse their seeds, because it was pre-adapted to feeding on mistletoe fruits and the mistletoes were pre-adapted to being dispersed by birds. Thus, the mutualism between the Mistletoebird and Australian mistletoes represents a novel association of ecologically congruent, previously adapted taxa, rather than a finely tuned, co-evolved system.

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