Comments

Bell Miners and the Farming Hypothesis — a Comment

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A recent paper by Aldo Poiani (1993) presented interesting data about food of Bell Miners *Manorina melanophrys* and concluded that his work failed to produce strong evidence for the 'farming hypothesis'. His definition of the farming hypothesis is much narrower than I had intended when I introduced the farming analogy (Loyn 1987) in an article summarising a series of translocation experiments (Loyn et al. 1983; R. Loyn et al. unpubl. data). Hence, to avoid confusion it should be pointed out that Poiani's conclusion applies only to a subset of the farming analogy as intended. The basic conclusions of the early work still stand, as acknowledged by Poiani, and have been put to practical use in the recovery program for the Helmeted Honeyeater *Lichenostomus melanops cassidix* (Menkhorst & Middleton 1991). Poiani's conclusions also stand, and confusion only arises from use of a common label (my farming analogy and his farming hypothesis).

Translocation experiments

The original translocation experiments showed that when Bell Miners were removed, major psyllid infestations were eliminated in a few weeks by dramatic influxes of other birds including thornbills *Acanthiza* spp., pardalotes *Pardalotus* spp., honeyeaters *Meliphagidae* and rosellas *Platycercus* spp., which collectively consumed psyllids faster than the Bell Miners had done when they were in occupation (Loyn et al. 1983). These birds had formerly been excluded by the aggressive territorial attacks of the Bell Miners. The rosellas were particularly proficient because they held the leaves with their feet and scraped psyllids off with their bills. After a few weeks, psyllid numbers had usually been reduced to undetectable levels and the invading birds departed, leaving a lower density of birds than when Bell Miners were in occupation. Some bark-gleaning birds (White-throated Treecreeper *Cormobates leucophaeus* and Varied Sittella *Daphoenositta chrysoptera*) also invaded and departed, but were mainly taking prey other than psyllids.

The experiments showed that the territorial aggression of Bell Miners was necessary for them to maintain their main food supply, providing a unique experimental demonstration of the hypothesis that territorial defence is both effective and necessary to maintain a food supply for these birds. They showed that the productivity of the system is maintained by the actions of the Bell Miners, which I considered analogous to farming. The results have various implications and may help explain why young Bell Miners rarely succeed in establishing breeding territories away from their natal colonies (Clarke 1988; Clarke & Heathcote 1990). They also showed the power of common forest birds to control insect infestations. All of these conclusions are accepted by Poiani. His hypothesis relates to one of at least three possible mechanisms, and his data suggest that it plays if anything a minor role.

Mechanisms for observed protection of psyllids by Bell Miners

The translocation experiments showed that the Bell Miners' main food supply would be decimated by other birds in the absence of territorial defence. The simplest mechanism involves Bell Miners excluding other birds and occupying enough space so that they do not deplete their own food supply. Poiani accepted the evidence for this which he classed as mechanism (a). It may be a matter of semantics as to whether the farming analogy applies but my intention was that it should; the analogy is with a basic form of farming or game management in which domestic or wild animals are protected against predators in order to maintain high populations and a sustained source of food for the protectors. The common denominator between Bell Miners and human farmers is that their behaviour (defence or husbandry) does more to conserve their food supply than their harvesting does to deplete it.

In our papers we also suggested that two other mechanisms could help maintain high psyllid populations and presented some evidence for them although we recognised that this was not strong. We recognised

(but did not adequately emphasise) that these extra mechanisms were not necessary to explain our main observations. One of these was classed by Poiani as mechanism (b), in which Bell Miners avoid eating the psyllid nymph and just take the nutritious and inanimate covering lerp (or the honeydew exuded), leaving the psyllid to grow another lerp (which we showed could be done in one or two days).

The mechanism is attractive because it required no consideration of bird densities, rates of feeding or spacing mechanisms. It is analogous to a farmer producing milk, wool or eggs, with meat only as a minor product. But a farmer who produces beef, lamb or chicken meat is still a farmer in the usual sense. Ratios of milk to beef distinguish dairy farmers from beef farmers, not farmers from non-farmers. So even if Bell Miners are indiscriminate about whether they take lerps alone or psyllids as well, the farming analogy can still apply.

The final mechanism we suggested (c), was that Bell Miners could meet their requirements by selecting large psyllids or lerps, leaving smaller psyllid nymphs to grow (as in fisheries management with minimum sizes for allowed take). We have not observed Bell Miners taking the smallest classes of psyllid and lerp but need more quantitative data. Their size and energy needs may deter Bell Miners from eating the smallest psyllids that are taken by smaller birds with individual pecks and by larger birds (rosellas) through indiscriminate consumption of all psyllids and lerps on a leaf. Perhaps the diversity of invading birds, as well as their abundance and voracity, allows them to deplete the invertebrate fauna more thoroughly then can be done by a single species of uniform size with a limited repertoire of foraging techniques. Our results provide clear evidence that they do so.

It is interesting that the lerp-farming mechanism (b) is often grasped as the main crux of the Bell Miner/psyllid relationship, because of its simplicity, and Poiani is right that the evidence for that aspect is inconclusive. Further data would be welcome on the selection of lerps and psyllids of different sizes by Bell Miners and other birds, at various levels of infestation. Are some birds more selective when psyllids are scarce, or quicker to switch to other food sources? Even if no additional mechanism operates, the farming analogy in its broad sense seems pertinent and useful. When a species dominates space by aggressively excluding other species, there may be benefits in the medium term (food production is sustained at high levels) but not in the long term (the trees may die). There may be parallels with our own farming ecology.

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