

Twinkling lights or turning down the dimmer switch? Are there two patterns of extinction debt in fragmented landscapes?

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The decline and local extinction of many woodland birds across southern Australia is continuing and seems likely to continue for a long time even though broad-scale clearing has ceased in many regions. The small proportion of remaining vegetation and its fragmented and degraded nature will probably mean that a long-term extinction debt will have to be paid. For some species this will be through the process of successive extinctions of sub-populations and lack of recolonization due to poor dispersal ability, leading to ultimate extinction of the metapopulation. However, many bird species in Australia travel locally and regionally to exploit resources that vary in time and space (rich-patch nomads), and appear to be quite capable of dispersing in fragmented landscapes. Many of these too are declining and we need to understand the processes involved in their decline. Making the matrix more hospitable may reverse the declines of the poor dispersers. However, a different approach may be needed to assist the rich-patch nomads, such as re-establishing key resources. This will involve a better understanding of their natural history.

Key words: woodland birds, dispersal, limiting resources, interspecific competition.

INTRODUCTION

IN common with numerous taxa in fragmented and degraded landscapes around the world, many of the birds of eucalypt woodlands across southern Australia are experiencing ongoing declines (Olsen *et al.* 2005; Watson 2011). Several ecological processes contribute to these declines, including an inability or unwillingness to disperse among vegetation remnants, competition from aggressive native species, high predation rates on nests, declining quantity and quality of food, and other critical resources (Ford *et al.* 2001). Broad-scale clearing of native vegetation leads directly to the decline and extinction of many species, but species loss may continue long after vegetation loss has ceased.

MacHunter *et al.* (2006) recorded the loss of an average of nine bird species from eucalypt forest remnants in Victoria over 22 years. Saunders (1989) documented species extinctions at several scales from remnants up to the region in the Western Australian Wheatbelt after a period of extensive habitat loss and fragmentation. Several bird species have gone extinct and others teeter on the brink in the Mount Lofty Ranges of South Australia, where 90% of the forests and woodland had been cleared, mostly long ago (Ford and Howe 1980; Possingham

and Field 2001). I shall discuss this last example in more detail later.

The pattern of delayed species loss in vegetation remnants and fragmented landscapes closely resembles what is called faunal relaxation in land-bridge islands (Diamond 1972). The theory of island biogeography states that the number of species on an island depends on a balance between extinction and colonization (MacArthur and Wilson 1967). Extinction is influenced by the size of the island and the colonization by its isolation. New islands that have originated from rises in sea level have a smaller area than the section of the mainland from which they originated, and are also isolated from the mainland. Hence, they should have a smaller “equilibrium” number of species. Diamond (1972) briefly mentioned that faunal relaxation is also likely to occur when forests on mainlands are cleared and fragmented.

Tilman *et al.* (1994) first used the term extinction debt to describe time-delayed but deterministic extinction and Malanson (2008) has described the origins and development of this concept. (Wikipedia (2011) also gives an excellent overview of the concept.) At its most general, extinction debt is simply the anticipation of species relaxation in remnants. However, Tilman *et al.*

(1994, 1997) incorporated the concept of metapopulations to explore the processes of faunal relaxation in fragmented landscapes and also to predict the types of species that might be most susceptible to extinction. A metapopulation is the population of a species across a landscape, which consists of numerous sub-populations on individual remnants (Hanski 1994). In fragmented landscapes, the extinction debt is paid as sub-populations are lost at a greater rate than new remnants are colonized until the whole metapopulation goes extinct (Tilman *et al.* 1994, 1997). Nee and May (1992) produced a model of the way in which several species could coexist across many patches if they differed in their dispersal ability and competitive dominance. Basically, good competitors can dominate any patches that they occupy. On the other hand, good dispersers can colonize patches from which the good competitors are absent. Of course, any species that is a good disperser and good competitor would likely occupy all patches exclusively. Hence, there could be a trade-off between colonizing or dispersal ability on the one hand and competitive ability on the other. Tilman *et al.* (1994, 1997) designed models of species coexistence in highly fragmented landscapes, which showed that good competitors and poor dispersers were most at

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risk of extinction. Although the argument that poor dispersers are candidates for extinction has been generally well accepted, the idea that good competitors may also be susceptible has been criticized, for instance by McCarthy *et al.* (1997).

In fact, Diamond's (1975) work on real animals (birds) on real islands (around New Guinea) anticipated the disperser-competitor trade-off. One group of species, which he called "super tramps", occupied small offshore islands, but were absent from larger islands. Diamond suggested that these species were good at dispersing and colonizing new islands, but were poor competitors and unable to survive on species-rich islands. In contrast, many species of birds found in the lowlands of New Guinea appeared unable or unwilling to disperse even 60 yards (55 metres) from the mainland to offshore islands. Large islands have a rich avifauna, so that the species restricted to them (called high-S species by Diamond 1975) would be subjected to strong interspecific competition. They would have to be good competitors to survive, in Diamond's words, they "overexploit [resources] and starve out other species". These species were also absent from land-bridge islands, probably due to chance extinction after isolation and failure to recolonize (Diamond 1976).

In this essay, I shall use Australian treecreepers to describe an example that appears close to the specific concept of extinction debt as argued by Tilman *et al.* (1994, 1997), i.e. progressive loss of species with poor dispersal ability that may also be good competitors. I shall then contrast this with the regional pattern of decline that is happening in several species of Australian honeyeaters (Meliphagidae). Here the process appears very different from the Tilman model.

PATTERNS OF DECLINE

Twinkling Lights

The Australian treecreepers (Climacteridae) are close to the

basal root of the passerine birds (Christidis and Boles 2008). They forage by climbing the trunks and branches of trees, then flying downwards to a nearby tree; although some species also forage on the ground (Noske 1985). They rarely sustain flight for long distances, and there are few records of them dispersing beyond 2 km (Higgins *et al.* 2001). The Brown Treecreeper *Climacteris picumnus* is the largest treecreeper, which often forages on the ground, and occurs in woodland and mallee across much of eastern Australia (Barrett *et al.* 2003). These habitats have been extensively cleared and fragmented and Brown Treecreepers are one of the species most affected by this habitat loss (Watson 2011).

My colleagues and I have described the progressive loss of Brown Treecreepers from remnants in a fragmented landscape in northern New South Wales, which gives the appearance of the payment of an extinction debt (Ford *et al.* 2009). Some sub-populations in the 1980s had ten or more breeding groups. These declined to a few groups, then to one or more males, but no females (Cooper *et al.* 2002), before going extinct soon after 2000. Other remnants had a small number of groups or only males in the 1990s (Walters *et al.* 1999) and most of these sub-populations were extinct by 2007. Thirteen sub-populations out of 21 have gone extinct in just under 30 years. I know of no cases of recolonization of sites that have lost the species. Cooper and Walters (2002) moved females to male-only sites, where some stayed and a few bred successfully, supporting the hypothesis that restricted dispersal by females, rather than poor habitat quality, was the main reason for local extinctions.

Brown Treecreepers, therefore, fit the pattern modelled by Tilman *et al.* (1994, 1997) of occurring as a metapopulation, in which poor dispersal leads to colonization of new remnants being much rarer than extinction of sub-populations. They may even be regarded as the best competitors as they dominate

other co-occurring treecreepers and bark-foraging birds (Noske 1979). It is interesting that the competitively inferior White-throated Treecreeper *Cormobates leucophaea* is apparently thriving in fragmented woodland in the region (Ford *et al.* 2009).

The Brown Treecreeper is not the only treecreeper that suffers from problems with dispersal. Radford and Bennett (2004) found that the White-browed Treecreeper, *C. affinis*, tended not to occur in small, isolated patches of suitable habitat (buloke and pine woodland) surrounded by cleared land or unsuitable habitat. The Rufous Treecreeper *C. rufus* has also experienced extinctions in the heavily cleared Western Australian Wheatbelt (Saunders 1989). This is at least partly because populations in fragmented landscapes suffer low breeding success, probably due to low quality of the woodland there, as well as poor dispersal (Luck 2003). It is also interesting that treecreepers are totally lacking from Australia's larger islands (Tasmania, Kangaroo, Melville and Bathurst Islands), despite these containing apparently suitable woodland and forest (Higgins *et al.* 2001).

A useful metaphor to display the pattern of local then regional extinction by treecreepers is that of a screen with many twinkling lights. The lights represent sub-populations, which are twinkling because their survival is precarious. Progressively more lights go out. Occasionally, a new light may appear, representing a rare colonization of a new remnant. But, over time, fewer and fewer lights are switched on, until finally the whole landscape goes dark.

Turning down the Dimmer Switch

The honeyeaters, Meliphagidae, are the most prolific family of the Australo-Pacific passerine radiation (Christidis and Boles 2008). One or more species of honeyeaters dominate numerically almost all wooded habitats in Australia. Some 20 honeyeater species are found in the eucalypt woodlands of south-eastern Australia, and their fortunes have

varied with habitat loss, fragmentation, and degradation. I shall discuss three species of honeyeater, one endangered, one thriving and the third still common but apparently declining.

The Regent Honeyeater *Anthochaera phrygia* occurs between central Victoria and southern Queensland. Having gone from South Australia and western Victoria, its numbers are now very low in Victoria and Queensland. It occurs regularly in only a few regions in New South Wales (DECC 2004). It is endangered globally but was formerly common, at least periodically, in many parts of its range, up to about the 1950s. It makes sporadic appearances in many locations, which are not readily predictable from our current knowledge (DECC 2004).

It was regarded as a specialized nectar-feeder, highly dependent on the flowering of a small number of eucalypts, especially ironbarks (*E. sideroxylon* and *E. tricarpa*), White Box *E. albens* and Yellow Box *E. melliodora* (Franklin *et al.* 1989). These plants typically occur on the better soils, which have been cleared disproportionately. However, Oliver (1998, 2000) showed that, like most honeyeaters, Regent Honeyeaters visit a wide range of plants, including mistletoes, for nectar, as well as consuming insects and alternative carbohydrates, such as lerp. The periodic occurrences of the species in many parts of its range indicate that it is highly mobile. Regent Honeyeaters have been recaptured up to 176 km from their banding site (Higgins *et al.* 2001) and birds colour-banded in the Capertee Valley in central NSW have been seen elsewhere in NSW and in Victoria (472 km away) and Queensland (534 km away) (DECC 2004). The recent upgrading of the species to Critically Endangered in New South Wales (NSW Threatened Species 2005) suggests that it may be paying part of the Extinction Debt. However, poor colonizing and dispersal ability does not appear to be the primary cause of its decline, it is much more likely that this is

driven by the loss of key resources at critical times, and perhaps by intense competition from other honeyeaters for these resources (Davis and Recher 1993; Ford *et al.* 1993).

Another medium-sized honeyeater, the Noisy Miner *Manorina melanoccephala*, has fared better than the Regent Honeyeater in response to habitat fragmentation and degradation and is now considered a threatening process for other woodland birds (Clarke and Grey 2010). Noisy Miners prefer eucalypt-dominated sites, with a sparse understorey, and in southern Australia tend to favour the edges of remnants or strips of vegetation (Hastings and Beattie 2006; Clarke and Oldland 2007; Maron 2007). Few other small and medium-sized birds occur in Noisy Miner colonies. Removal experiments have shown that it is the Noisy Miner's hyper-aggressiveness that causes this (Grey *et al.* 1998). As a top competitor one might expect the Noisy Miner to be at risk of local extinction, but this is not the case. McCarthy *et al.* (1997) have already pointed out that the Noisy Miner and its congener the Bell Miner (*M. melanophrys*) might be expected, as dominant competitors, to be candidates for paying the extinction debt in fragmented landscapes. The Noisy Miner's success strongly contradicts the models of Tilman *et al.* (1994, 1997).

The Fuscous Honeyeater *Lichenostomus fuscus* is one of the most common birds in the box and ironbark woodlands of south-eastern Australia (Ford and Bell 1982; Ford *et al.* 1985; Mac Nally *et al.* 2009). It was a common bird in Armidale, Northern Tablelands of NSW, in the 1970s, where it is now hard to find. At Imbota Nature Reserve, it was the commonest bird in the late 1970s and early 1980s (Ford and Bell 1982, Ford *et al.* 1985), at a time when the Yellow-faced Honeyeater *L. chrysops* was an uncommon visitor. Repeat censuses at the site in 2008, showed that Fuscous and Yellow-faced Honeyeaters are now about equally common (Ford, unpublished). Fuscous Honeyeaters have

also declined in the northern part of their range in central Queensland (Woinarski and Catterall 2004), elsewhere in NSW (e.g. Selwood *et al.* 2009), and in the southern part of their range in central Victoria (Thomas 2009).

Fuscous Honeyeaters are foraging generalists, feeding on nectar, insects and alternative carbohydrates, at a range of heights (Ford *et al.* 1986; Mac Nally *et al.* 2000; Timewell and Mac Nally 2004). However, Mac Nally and Bennett (1997) regarded the species as a habitat specialist, but with high mobility, leading to them predicting a low proneness to extinction in fragmented habitat. Evaluating their predictions, they (Mac Nally *et al.* 2000) found that the Fuscous Honeyeater was more likely to decline in remnants of all sizes than they expected.

Many honeyeaters perform movements in search of flowering trees and shrubs, as I described above for the Regent Honeyeater. Keast (1968) called them "blossom nomads", but I prefer the term "rich-patch nomads" as this can be extended to birds that seek food other than nectar. Keast (1968) recorded Fuscous Honeyeaters moving from woodland into heathland near Sydney. McGoldrick and Mac Nally (1998) described the influx of numerous honeyeaters, including Fuscous Honeyeaters, into ironbark woodlands in Victoria that coincided with the autumn-winter flowering of *E. tricarpa*. The intensity of flowering at localities differs between years, with separate populations of ironbarks flowering asynchronously. Traill (1996 cited by Higgins *et al.* 2001) noted that Fuscous Honeyeaters disappeared from some locations in the non-breeding season of some years, when no eucalypts were flowering. Mac Nally *et al.* (2009) found that Fuscous Honeyeaters declined dramatically in woodlands in central Victoria between the mid-1990s and 2008, coinciding with an ongoing, extreme drought and virtual lack of flowering by eucalypts. This decline was equally as severe in extensive areas of woodland as in fragmented

landscapes. There have been few recoveries of banded individuals, the furthest being 24 km, with others being less than 10 km (Higgins *et al.* 2001). However, the time when lowest numbers were found in central Victoria in 2008, coincided with records of the species in western Victoria (Mac Nally *et al.* 2009) and southern South Australia (Haywood 2010), outside the species' normal range.

The overall pattern then for the Fuscous Honeyeater is one of fluctuating numbers in any locality and region, but probably an ongoing regional decline. It is still common in suitable habitat in much of its range and it seems unthinkable that it should be regarded as threatened. However, the pattern of decline of Fuscous Honeyeaters suggests that the species may be following a similar trajectory to the Regent Honeyeater but some 50 years behind. The ecologically similar Yellow-plumed Honeyeater *L. ornatus* in Western Australia also moves in response to local patterns of nectar availability and may desert localities during drought (Recher *et al.* 2010). Although it may be common in extensive areas of woodland and mallee, it has declined dramatically in many areas because these habitats have been disproportionately cleared and fragmented (Saunders 1989). So, it may behave and respond to habitat loss in a very similar way to the Fuscous Honeyeater.

Given the mobility of the Regent and Fuscous Honeyeaters, it does not appear that their decline is due to their inability to disperse among remnants and rescue sub-populations or colonize new ones. I suggest that in contrast to the vision of twinkling lights a suitable metaphor is that of a regional light, which may flare and fade, but which gradually becomes dimmer everywhere over time.

The Mount Lofty Ranges

It is clear that there are at least two patterns by which bird species of eucalypt woodlands may decline

in fragmented landscapes. The first is through isolation of sub-populations, which may go extinct, and where the species' weak powers of dispersal mean that there is little likelihood of sub-populations being rescued from the brink of extinction or of vacated remnants being recolonized. These resemble many of the species from Diamond's land-bridge islands and are predicted by Tilman's models. These species may also be superior competitors, but this may not contribute to their extinction.

The second pattern is where species appear well able to disperse, but nevertheless progressively decline within a region. They are not such obvious candidates to repay the extinction debt, and are or were common species in more continuous habitat. These species probably rely on a succession of resources spread through time and space and move among them either locally or sometimes over some distance. Interestingly, Diamond (1975, 1976) identified species that fed on patchy and seasonal food resources, such as nectar, as requiring a large area to provide the full range of food over time. About one quarter of species missing from all land-bridge islands fall into this category (Diamond 1975). From the mobility of honeyeaters, I would argue that a continuous area of native vegetation may not be required, as long as all key resources are available somewhere.

I have suggested metaphors for these two groups. First, the poor dispersers show a picture of twinkling lights that progressively switch off altogether. The second group shows a more general picture of dimming regionally until they finally fade out.

To be of value in planning conservation and management, these patterns need to be identified in other species. Payment of the extinction debt appears to be more advanced in the eucalypt forests and woodlands of the Mount Lofty Ranges, which are isolated from the eastern forests and have been

extensively cleared. This presents the opportunity to identify bird species lost or threatened by the two processes that I have described. Garnett and Crowley (2000) listed eight species that have gone extinct, and Possingham and Field (2001) named eight additional species that are now rare and for whom extinction seems likely. The latter listed a further 16 species (the living dead), for which there is a real chance of extinction in the next 200 years. Surveys since 1999 have now shown that even many quite common species are declining in the region (Szabo *et al.* 2011). I have tentatively allocated 24 out of these 32 species into either the group of poor dispersers or into the group of rich-patch nomads (Table 1). We require better knowledge of their dispersal ability and resource requirements to be confident that they are placed in the correct category. I suggest that at least half of the species may belong to the latter group, and hence would require management that goes beyond providing better connexions in the landscape.

The poor-disperser group actually contains many species characteristic of heathland or grassland rather than woodland. This is another uncanny echo of the New Guinea land-bridge islands, where Diamond (1975) found that one third of species missing from all islands live in habitats other than forest, such as grassland or swamp. The mobile resource specialists include nectar-feeders, but also a seed-eater, two insectivores and two cuckoos, which need to find suitable hosts. The scale of movement of the mobile resource specialists can be highly variable. For instance, insectivores, such as the Restless Flycatcher (*Myiagra inquieta*), may simply have large home ranges (Paton *et al.* 2010 found they moved over 100 ha in 10 days), whereas Regent Honeyeaters could travel through most of their range over a lifetime. The pattern of use of nectar sources is best known in the Mount Lofty Ranges, probably because so little native vegetation remains. Honey-

eaters may travel up to 100 km, probably over cleared country, among sites where plants flower in different seasons. However, it is the summer-flowering plants, such as *Banksia marginata* and *Eucalyptus leucoxylon*, which have declined most, because they occur on the richest soils, where the vegetation has been cleared most (Paton *et al.* 2010). Lambeck and Saunders (1993) found that honeyeaters converged on one small patch of *Banksia prionotes* that flowered in late summer in the Kellerberrin district of the Western Australian Wheatbelt. Limitation by the loss of this link in the chain of resources places the populations of many species under stress.

DISCUSSION

Implications for Management

The extinction debt does not have to be paid only by species going extinct, it can be paid by improving landscape structure (Hanski and Ovaskainen 2002) and by habitat reconstruction (Possingham and Field 2001). If there are two different processes leading to decline, then the two groups of species will require different types of

management. The poor dispersers are perhaps easier to conserve, with the focus on landscape structure. First, the matrix between their sub-populations will need to be made more hospitable, through the provision of corridors and protection and replacement of scattered trees. They will probably require some effort to maintain or improve the quality of their habitat, for instance by providing suitable food and nesting sites, as well as some protection from predators. There has been substantial investment in wildlife corridors to link remnants of woodland. However, species such as Brown Treecreepers (Doerr *et al.* 2011) and Superb Parrots *Polytelis swainsonii* (Manning *et al.* 2006) may disperse through scattered mature trees in farmland in preference to newly planted corridors. Scattered trees are being lost through death, dieback, wild weather or intentional clearing (Manning and Lindenmayer 2009). Replacement trees need to be planted now and gaps filled with clumps of trees.

Whereas many of the approaches that are adopted for poor-dispersers may also be valuable for rich-patch nomads, others are required. Here the focus will be on habitat quality.

One of the biggest challenges is to identify the full range of key resources that are exploited or were important before being lost by clearing. This is difficult as the species may be absent from habitats with such resources for much of the time. We need to understand just why Restless Flycatchers, which feed on large insects and spiders in grass, need such a large home range. We do not know the full range of locations and resources used by Regent Honeyeaters, a species that seems to disappear for months at a time. The other species in the third column of Table 1 may be less elusive but a research priority for them would be an attempt to track individuals year-round. Most are too small for attaching satellite transmitters, though this would be feasible for Square-tailed Kites and Glossy Black-Cockatoos.

Another issue for these mobile resource specialists is whether birds that turn up outside their “normal” ranges, such as the Fuscous Honeyeaters in western Victoria and South Australia, become survivors that return to their usual range or whether they are simply doomed.

Table 1. Species identified by Possingham and Field (2001) as extinct, extremely rare or at risk of extinction in the longer term in the Mount Lofty Ranges, which I have attempted to allocate to the group of poor dispersers or rich-patch nomads, as described in this paper.

Category	Poor Dispersers	Rich-patch nomads
Extinct	Ground Parrot <i>Pezoporus wallicus</i> Azure Kingfisher <i>Ceyx azureus</i> Rufous Fieldwren <i>Calamanthus campestris</i>	Swift Parrot <i>Lathamus discolor</i> Glossy Black-Cockatoo <i>Calyptorhynchus lathami</i> Regent Honeyeater <i>Anthochaera phrygia</i>
Extremely Rare	Spotted Quail-thrush <i>Cinclosoma punctatum</i> Bush Stone-Curlew <i>Burhinus grallarius</i> Little Lorikeet <i>Glossopsitta pusilla</i>	Brown Quail <i>Coturnix ypsilophora</i> Square-tailed Kite <i>Lophoictinia isura</i> Flame Robin <i>Petroica phoenicea</i>
Living Dead	Painted Button-quail <i>Turnix varius</i> Beautiful Firetail <i>Stagonopleura bella</i> Southern Emu-wren <i>Stipiturus malachurus</i> Chestnut-rumped Heathwren <i>Hylacola pyrrhopygia</i> Brown Treecreeper <i>Climacterus picumnis</i> Bassian Thrush <i>Zoothera lunulata</i>	Pallid Cuckoo <i>Cacomantis pallidus</i> Tawny-crowned Honeyeater <i>Glyciphila melanops</i> Black-chinned Honeyeater <i>Melithreptus gularis</i> Shining Bronze-cuckoo <i>Chalcites lucidus</i> Restless Flycatcher <i>Myiagra inquieta</i> Singing Bushlark <i>Mirafra javanica</i>

CONCLUSIONS

I have argued that there are at least two groups of birds that are showing different patterns of decline in fragmented and degraded landscapes. Both may ultimately contribute to the extinction debt, either through progressive loss of sub-populations leading to meta-population loss or to regional decline to disappearance. This is undoubtedly a gross simplification. Both groups are heterogeneous. Threatening processes occur at different scales, due to different processes, in what has been called an extinction filter (Brashares 2010). Generalizations are dangerous and misleading. Each species responds to habitat fragmentation and degradation in an idiosyncratic manner (Simberloff and Abele 1976). There is still a great need for conservationists to understand the basic ecology of individual species (Simberloff and Abele 1976; Bennett and Radford 2010), as we perhaps do for the Brown Tree-creeper. In the end our ability to arrest the decline of woodland birds depends on how well we know the individual species, and understand the ecological processes leading to decline, such as dispersal, inter-specific competition and predation. Surely there are enough ornithologists, ecologists and conservationists in Australia for us to be able to achieve this?

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Biography

HUGH Ford is an Emeritus Professor in Zoology at the University of New England. His research over the last 38 years has focused on the ecology and behaviour of Australian passerine birds. He is a firm believer that successful conservation needs to be based on good science. In turn, good ecology should be founded in a sound knowledge of natural history. Hugh has published widely, he wrote "The Ecology of Birds: an Australian Perspective" the first book of its kind in Australia. He was the editor of "The Emu" from 1981 to 1985. He was awarded the D. L. Serventy Medal for outstanding contributions to publication in the field of ornithology in the Australasian region and has supervised 60 postgraduate students.