FORUM

The role of blackbirds (*Turdus merula*) in weed invasion in New Zealand

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Published on-line: 23 January 2006

Abstract: The naturalised European blackbird (*Turdus merula*) is the most widely distributed avian seed disperser in New Zealand. Together with the native silvereye (*Zosterops lateralis*) they are the major seed dispersers over large areas of New Zealand. I review the international literature on aspects of the ecology and behaviour of blackbirds relevant to their potential for dispersing weeds in New Zealand. Blackbirds eat a wide range of native and exotic fruit including many naturalised species. Their habitat preferences and behaviour result in germinable seeds being deposited in a range of sites, particularly in shrubby habitats, where seedling establishment is likely. Most seeds will be deposited within 50 m but some may be carried a kilometre or more to develop new invasive loci. Blackbirds therefore probably make a major contribution to the development of novel plant communities of naturalised woody weeds. These communities provide fruit more suited to non-endemic native birds and naturalised birds, than to endemic birds. The relative contribution of blackbirds and silvereyes to seed dispersal of native and exotic species requires investigation. The outcome may suggest potential for managing blackbirds as a vector of weed invasions.

Keywords: blackbirds; seed dispersal; weeds; Turdus merula; Zosterops lateralis.

Introduction

New Zealand rural landscapes are changing rapidly as the production base shifts from mainly pastoral farming to more diverse land uses that increasingly include initiatives to restore native vegetation. Managing weeds is important throughout the restoration process and an understanding of their dispersal and establishment is vital. Many woody weeds in New Zealand are fleshyfruited (Timmins and Williams, 1987) and so are eaten by birds. An understanding of bird-mediated seed dispersal is therefore critical to modelling and managing weed invasions (Kean et al., 2003; Overton et al., 2004). Several bird species are involved in seed dispersal in New Zealand (Lee et al., 1991), but the naturalised European blackbird (Turdus merula) is the most widespread (Bull et al., 1985). Native silvereyes (Zosterops lateralis) are almost as widespread, whereas endemic species such as bellbirds (Anthornis melanura) are absent from large areas, particularly in eastern South Island (Bull et al., 1985).

Silvereyes and blackbirds both consume a wide range of fruit, and move frequently between urban sources of weeds (Timmins and Williams, 1991) and semi-natural landscapes (Clout and Hay, 1989; Burrows, 1994; Williams and Karl, 1996, 2002). Studies have described the diet and behaviour of silvereyes in New Zealand (Kikkawa, 1962; Moeed, 1979) and Australia (Stanley, 2001; Stansbury and Vivian-Smith, 2003), the effects on seed germination of gut passage (French, 1996; Panetta and McKee, 1997), and silvereyes' influence on the invasion pattern of climbing asparagus (Asparagus scandens) in Australia (Stansbury, 2001). Blackbirds consume a wide range of native and naturalized fruits in both countries (Bull, 1949; Clelland, 1952; McCann, 1953; French et al., 1992; Allen and Lee, 1992; Burrows, 1994; Williams and Karl, 1996) and have an important role in the dispersal of sweet pittosporum (*Pittosporm undulatum*) beyond its native range in Australia (Gleadow, 1982). Bird post-foraging behaviour is critical to seed dispersal effectiveness (Schupp, 1993) but it has not been studied in blackbirds either country.

To better understand the potential contribution of blackbirds, I reviewed the international literature on these aspects of the ecology and behaviour of blackbirds likely to influence their role in weed invasions in New Zealand.

Habitats of blackbirds

The habitat of blackbirds in their native range is "exceptionally diverse" compared with other European birds, although they prefer to be within c. 100–200 m of cover (Cramp, 1988). They are common in urban areas, orchards, farmland, and woodland throughout Europe (Debussche et al., 1982; Herrera, 1984; Cramp, 1988; Hinsley et al., 1995; Hatchwell, 1996), and in their introduced range in Australia (Berry, 2001) and New Zealand (Bull, 1953; Falla, et al., 1966; Williams, 1969; Dawson et al., 1978; Bull et al., 1985; Moffat and Minot, 1994). In New Zealand blackbirds are found in native and naturalised scrub (Williams and Karl, 2002), isolated lowland native forest fragments (Williams and Karl, 1996) and throughout extensive native forest (Philpott, 1918; Beveridge, 1964; Dawson et al., 1978; Fitzgerald et al., 1989; Spurr et al., 1992; Warburton et al., 1992).

Frugivory by blackbirds

Blackbirds eat mainly insects and earthworms, but also eat fruit when it is available in late summer to winter (Cramp, 1988; Snow, 1988). They swallow a wide range of fruits in Europe, including species that are widely naturalised in North America (White and Styles, 1991) and New Zealand, such as hawthorn (Crataegus monogyna), ivy (Hedera helix), and rowan (Sorbus aucuparia) (Snow and Snow, 1988; Fraga, 1998; Jordano and Schupp, 2000; Paulsen and Hogstedt, 2002). Blackbirds have been observed eating several of these species in New Zealand, as well as many non-European naturalised species (Bull, 1949; McCann, 1953; Allen and Lee, 1992; Burrows, 1994; Williams and Karl, 1996) and most recently, bangalow palm (Archontophoenix cunninghamiana) (Cameron, 2000) and phoenix palm (Phoenix canariensis) in Auckland (J. Sullivan, Lincoln University, Lincoln, NZ, pers. com.).

Both sexes and all ages of blackbirds eat fruit extensively whenever it is available (Snow and Snow, 1988). They swallow fruit up to at least 13 mm diameter and a meal size ranges from about 3 to 14 fruits, depending on fruit size (Snow and Snow, 1988; Paulsen and Hogstedt, 2002). They also eat parts of larger fleshy fruits and may swallow the seeds intact, such as those of banana passion vine (*Passiflora tripartite* var. *mollissima*) (Williams and Karl, 1996).

Foraging behaviour of blackbirds

Blackbirds take fruit mostly while perching but can also take fruit from the ends of branches while in flight. In England they often take fruit from the ground (Snow and Snow, 1988), and in New Zealand podocarp forest they feed more often on the ground and beneath understory vegetation than most other flighted birds (O'Donnell and Dilks, 1994).

Most seeds consumed by blackbirds are defecated (Herrera and Jordano, 1981; Snow and Snow, 1988), although they may regurgitate relatively large seeds such as those of wild cherry (Prunus spp.) (Snow and Snow, 1988; Sorensen, 1981, 1984) and bangalow palm (Archontophoenix cunninghamiana) (P.Money, pers com. to J. J. Sullivan). Swallowed fruits take approximately 30 minutes to be defecated (Sorensen, 1984; Barnea et al., 1991). Germination may be enhanced relative to hand-cleaned seeds (Holthuijzen and Sharik, 1984; Barnea et al., 1991), and this may result in faster seedling growth in rowan (Paulsen and Hogstedt, 2002). Although the response of seeds to passage through blackbirds is highly species-specific (Izhaki and Safriel, 1990; Traveset et al., 2001), several weed species in New Zealand are likely to benefit.

Blackbirds deposit a great deal of seed beneath the bushes in which they are foraging (McCann, 1953; Calvino-Cancela, 2002). This may limit their longdistance dispersal effectiveness compared with more mobile canopy-feeding birds (Hoppes, 1987) such as starlings (Sturnus vulgaris) (Snow and Snow, 1988) that feed in large flocks on heavy fruiting species such as barberry and elderberry (Sambucus nigra) in New Zealand (Williams, 1983). In southern Europe, seed dispersal by migratory blackbirds may be limited when groups stay in individual trees for several days (Hampe, 2003). This would not apply in New Zealand, where blackbirds do not form large migratory flocks, although individuals may move over an altitudinal gradient throughout the year (Dawson et al., 1978; Wilson et al., 1988). During the breeding season they are very mobile and move frequently between a range of forage areas and habitat types (Greenwood and Harvey, 1978; Théry, 1989).

Given the choice of a range of landscape types, post-foraging blackbirds in Spain avoided tall trees and open ground, preferring to alight on mid-height (<1 m) shrubs, even when their next flight was likely to be towards another fruiting mahaleb cherry (*Prunus mahaleb*) tree 2–10 m tall (Jordano and Schupp, 2000). Blackbirds foraging in open landscapes alight on a wide range of substrates, including rocks, stones, bare soil, and vegetative cover (Fuentes *et al.*, 2001), and on wire and wooden fences in grassland (pers. obs.).

Seed dispersal distance

Blackbirds, in common with most passerines, are likely to move most seed less than 100 m (Debussche *et al.*, 1982; Théry, 1989). The few studies of seed dispersal patterns into regenerating New Zealand scrub (Bray *et al.*, 1999) and mixed landscapes (Meurk and Hall, 2000) support this. Most blackbirds feeding on mahaleb cherry in Spain flew less than 30 m before perching, but 4.3% flew further than 30 m (Jordano and Schupp, 2000). Individual seed dispersal distances

by birds may be much greater, occasionally reaching 300 m (Debussche and Isenmann, 1994) or even 800 m (Théry, 1989). Théry (loc. cit.) radio-tracked several blackbirds from autumn to spring across a range of habitat types in rural France, including large areas of open fields. In autumn, the period of maximum fruit availability, one individual flew an average of 46 m in the 15 minutes following ingestion of fruit – approximately half the time required to pass most fruit as mentioned above. Individual birds flew up to 3 km in a day between feeding zones, covering up to 16 ha. Young blackbirds are particularly mobile at this time as they disperse from the breeding habitats (Hatchwell et al., 1996) and have been recorded travelling several kilometres in New Zealand (Bull, 1958). In spring and early summer, the distances flown and the area covered were much lower, only 65 m across in France (Théry, 1989) (for comparison, all areas quoted have been converted from hectares to meters based on an equal sided square). In England, three adjacent blackbird "territories", defined as the total areas within which they spent approximately 90% of their total time, were 55 m across (Greenwood and Harvey, 1978). Within these territories, there were wooded margins and an adjacent field. Only 5% of their foraging in the field was greater than 50-70 m beyond the trees, and this reflected high prey density (Greenwood and Harvey, 1978). These shorter distances are similar to those of breeding blackbirds in New Zealand, where the territory size was in the order of 80 m across in Dunedin (Gurr, 1954), and 65 m across in Lower Hutt, where most adult blackbirds birds moved less than 200 m throughout the whole summer (Bull, 1958). This was in an urban area with houses and more patchy foraging areas, and presumably more discontinuous availability of prey, than the woodland surrounded by fields of Théry's (1989) or Greenwood and Harvey's (1978) studies. Neither in the breeding season, nor in the winter when they feed to a greater extent on fruit, does the territory guarantee the owners an adequate food supply (Snow 1958). Blackbirds must then feed outside their territories so that territory size is a conservative measure of the potential seed dispersal distance. They also roost outside their territories, many prefering bush patches up to 1.6 km away (Gurr, 1954). Ivy (Hedera helix) was recovered beneath a blackbird roosting site 800 m from source (Théry, 1989).

Likely role of blackbirds in weed invasion

The capacity of blackbirds to consume large numbers of fruit greater than 7–8 mm diameter, i.e. greater than commonly eaten by silvereyes, places blackbirds in a potentially important position as dispersers in a range of habitats. Their foraging behaviour, especially their use of open ground, "stepping stones" such as fences, and shrubby vegetation characteristic of successional vegetation, makes it likely they will position seeds in a range of potential sites for seedling establishment. Both the behaviour and preferred habitats of blackbirds means they are ideally placed to move seeds of exotic species from cultivation into the wild, and once these are naturalised, to spread them from semi-natural areas to remote mountain valleys. This is likely to be mainly via short distance "diffusion" dispersal (*sensu* Davis and Thompson, 2000) of 50–100m. Occasional longdistance gap-crossing 'saltation' dispersal events (Davis and Thompson, 2000), such as when blackbirds move outside their territories, are likely to result in new invasive loci are up to 2 km distant from the seed source.

In the least modified tracts of vegetation the fleshy-fruited component of early successional vegetation is dominated by native bird-dispersed woody species. Blackbirds contribute to their dispersal (Baylis, 1986; Lee *et al.*, 1991; Burrows, 1994) although at a national scale their contribution is probably minor (Kelly *et al.*, 2003; Kelly *et al.*, *in press*). This applies less in fragmented landscapes because blackbirds consumed similar quantities of native and naturalised fruit in forest remnants near Nelson city (Williams and Karl, 1996). Blackbirds were also considered to be more important than native birds in moving seeds of native species between islands in the Three Kings Islands group (Baylis, 1986).

In highly modified landscapes, especially those in eastern South Island with relatively low densities of native fleshy-fruited woody species, and few endemic birds (Bull et al., 1985, Burrows, 1994), extensive new communities dominated by naturalised fleshy-fruited species are developing e.g., Darwin's barberry (Berberis darwinii) (Allen and Lee, 1992), bone seed (Chrysanthemoides monilifera) (Partridge, 1994), elderberry (Sambucus nigra) (Williams, 1983), wild currant (Ribes sanguineum) (Williams, 1984), and hawthorn (Crataegus monogyna) (Williams and Buxton, 1986). The fruit of these species appears to be of only minor importance to endemic birds but of major importance to silver eyes and introduced birds. The resulting plant communities are more suited to the dietary requirements of the birds responsible for their spread, than to endemic birds (Williams and Karl, 1996, p. 143). How important are blackbirds to this process in view of other potential dispersers?

Possums have some involvement in seed dispersal (Dungan *et al.*, 2002) but birds are more important (Kelly *et al.*, *in press*), even for relatively large fruit (Williams, 2003). While thrushes take fruit, and starlings may be important locally, the two most widespread and abundant frugivorous birds in highly modified landscapes are silvereyes and blackbirds. Some inferences can be made concerning the relative contribution of these two species to seed dispersal beyond urban areas. Studies in forest remnants at Nelson show that naturalised fruit plays a less important part in the diet of silvereyes than it does of blackbirds (Williams and Karl, 1996). Moreover, for naturalised species with fruit approaching 10 mm diameter e.g., Prunus spp., and hawthorn, blackbirds are likely to be the principle disperser in the absence of native pigeons. Recent field observations of a Canterbury hawthorn population described by Williams and Buxton (1986) confirms that possums are of minimal importance to its dispersal, silvereyes only peck at the fruit, whereas blackbirds swallow fruit whole (B.Karl, Landcare Research, Nelson, pers. obs.) in accordance with the overseas literature. While not underestimating the importance of silvereyes, some naturalised plant species may be especially dependant on blackbirds for dispersal in New Zealand.

Many exotic fleshy-fruited plants have yet to naturalise in New Zealand and very few naturalised species have reached their potential range at even a provincial scale (Williams and Cameron, in press). Local dispersal of some fleshy-fruited species seems particularly slow e.g., hawthorn studied by Williams and Buxton (1986) appears to have extended only a few square kilometres in 20 years (Buxton and Williams, unpublished) despite the pomes having a near optimum balance of food to ballast ratio (Herrera, 1981). Similarly rowan (Sorbus aucuparia) and sweet cherry (Prunus avium) have also spread relatively slowly at several eastern South Island localities (Webb et al., 1988). This may be partly because of the relative youth of their founding populations and intrinsically slow growth. It may also reflect the predominance of short distance dispersal and the rarity of long distance dispersal of plant species dependant largely on blackbirds.

Directions for research and management

While we know a great deal about the behaviour of blackbirds overseas, their precise role in any New Zealand ecosystem is poorly understood. The relationship between native and naturalised plants and native and naturalised birds, particularly in early successional vegetation, warrants closer study to better understand weed invasions and restoration of indigenous landscapes. The most important question concerns the relative contribution of silvereyes and blackbirds to dispersal of both native and naturalised plant species, particularly in parts of eastern South Island where there are few other avian seed dispersers (Burrows, 1994). Knowledge of where blackbirds make only a minor contribution to native plant dispersal compared with a major role in weed invasions may help clarify the potential of controlling blackbirds in specific locations, as for example pigs are controlled in Hawaii to slow the spread of passion vine (Passiflora sp.) (LaRosa, 1992).

Acknowledgements

Thanks to Doug Armstrong, David Dawson, Phil Cowan, Kris French, Margaret Stanley, and Colin Meurk for helpful comments.

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