Are introduced birds unimportant mutualists? A case study of frugivory in European blackbirds (*Turdus merula*)

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Abstract: Many types of birds regularly consume fleshy fruits and, as seed dispersers, perform important mutualistic services for plants. Some frugivorous birds have recently been introduced to geographic locales beyond their native range. Are non-native birds important frugivores in their introduced range? To answer this question, I observed native and introduced birds foraging for fruits in a New Zealand forest at approximately 5-day intervals for 5 years. I then compared fruit consumption patterns of European blackbirds (*Turdus merula*) to native New Zealand birds to determine whether blackbirds are important frugivores in New Zealand. I also compared the fruit diets of blackbirds to previously published dietary records from similar latitude forests in the United Kingdom. Results showed that blackbirds were among the most common frugivores at both New Zealand sites. They exhibited similar levels of dietary diversity to native bird species and consumed an unusually broad composition of fruit species. Introduced blackbird populations also exhibited remarkably similar patterns in dietary diversity and composition to populations in their native range. Results suggest that introduced birds can form important mutualistic partnerships with native plants, as seed dispersers, in the absence of contemporary coevolution.

Keywords: coevolution; fruit; frugivore; New Zealand; United Kingdom

Introduction

Nearly half of New Zealand's avifauna has gone extinct since the arrival of humans 750 years ago (Tennyson & Martinson 2006). Although hunting by humans and forest fragmentation have contributed to this loss, introduced predatory mammals (e.g. cats, rats and mustelids) are the main cause of avian declines. Concomitant with the decline and extinction of native bird species, various bird species that are native to other parts of the world have been introduced to New Zealand. As a result, introduced birds have replaced native birds in many New Zealand forests (Innes et al. 2010). Unfortunately, this situation is not unique to New Zealand. The endemic avifaunas of isolated islands across the globe have suffered similar fates (Blackburn et al. 2004).

Many New Zealand birds are important pollinators and seed dispersers (Clout & Hay 1989). Therefore, the decline and extinction of native birds could lead to reproductive failure in native plants (Kelly et al. 2010; Anderson et al. 2011; Wotton & Kelly 2011). Many introduced bird species provide important mutualistic services for plants in their native ranges, so introduced birds could now serve as surrogate mutualists for native plants in the absence of native birds (see Davis et al. 2011; Wenny et al. 2011).

The capacity of introduced birds to perform mutualistic services for native plants hinges on how mutualisms are structured evolutionarily (see Johnson & Steiner 2000; Kiers et al. 2010; Wenny et al. 2011). Some mutualisms are characterised by fine-tuned coevolutionary adjustments between particular species (e.g. Compton et al. 2010). Other types of mutualisms are comprised of large numbers of unrelated species that interact interchangeably (e.g. Burns 2006). If seed dispersal mutualisms are characterised by finetuned coevolutionary adjustments between particular fruit and frugivore species, the extinction of native bird species may leave native plants without effective seed dispersers (Templeton 1977; Hansen & Müller 2009; Kaiser-Bunbury et al. 2010). On the other hand, frugivores could forage for fruit more or less indiscriminately, leading to highly unspecialised associations (Zamora 2000; Herrera 2002).

The European blackbird (*Turdus merula*) is a common seed disperser in many parts of Europe (see Jordano 1993). Blackbirds were introduced to New Zealand over a century ago and are now one of the most common bird species inhabiting New Zealand forests (Innes et al. 2010). If effective seed dispersal mutualisms do not require fine-tuned coevolutionary adjustments, blackbirds could be important seed dispersal mutualists in New Zealand and provide surrogate mutualistic services to native plants as seed dispersers. However, dietary overlap between blackbirds and native frugivores has yet to be documented adequately, so the importance of blackbirds as seed dispersal mutualists in New Zealand is unknown.

At approximately 5-day intervals for five consecutive years, I observed fruit consumption by both native and introduced birds in 'Zealandia', a forest reserve surrounded by a special fence designed to exclude introduced mammals. Many rare and endangered native birds have been translocated into the reserve over the past decade. As a result, Zealandia now supports one of the largest assemblages of native New Zealand birds in addition to large populations of many introduced bird species.

Here, I use these data to compare the diversity and composition of fruits consumed by blackbirds to those consumed by native bird species. Using analogous datasets from the United Kingdom and another site in New Zealand, I also compare the fruit diets of blackbirds in Zealandia to their diets in other biogeographic locales. Comparisons were made using a series of null model simulations and multivariate analyses

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that control for variation in sampling effort and differences in the diversity of fruit communities, to answer three questions:

- 1. Do blackbirds consume fewer fleshy-fruited plant species than New Zealand bird species?
- 2. Do blackbirds consume fewer fruit species in their introduced range (New Zealand) than in their native range (United Kingdom)?
- 3. Does the composition of blackbird fruit diets differ from the dietary composition of native birds and do patterns in dietary composition differ between geographic locales?

Methods

All data were collected in Zealandia, which is located at the southern tip of the North Island of New Zealand (41°18.3'S, 174°44.8'E). Zealandia experiences a mild, temperate climate and supports conifer-broadleaved forest comprised of evergreen trees, tree ferns and lianas, which is still undergoing succession after being cleared for agriculture in the late 19th century (Blick et al. 2008). Zealandia is surrounded by a specially designed, predator-resistant fence and therefore houses one of the largest assemblages of extant New Zealand birds. Since the construction of this fence, many rare and endangered frugivores have been translocated within its boundaries, including the bellbird (Anthornis melanura), kākā (Nestor meridionalis), saddleback (Philesturnus carunculatus), stitchbird (Notiomystis cincta) and whitehead (Mohua albicilla). The tūī (Prosthermadera novaeseelandiae) and kererū (Hemiphaga novaeseelandiae) were the only endemic avian frugivores present within the reserve prior to construction of the fence. The waxeye (Zosterops lateralis) is a self-introduced, native frugivore that colonised New Zealand from Australia in the recent past (< 200 years ago). Several species of introduced frugivores also occur in Zealandia, including the European starling (Sturnus vulgaris), songthrush (Turdus philomelos) and mallard (Anas platyrhynchos); the European blackbird (Turdus merula) was the most common introduced frugivore species. It was brought to New Zealand by European colonists in the late 19th century and rapidly spread throughout the North and South Islands.

I quantified the diets of frugivorous birds in Zealandia by observing birds foraging for fruits along a circular trail that took me approximately one hour to traverse. Observations were made approximately every 5 days for five consecutive years (2006–2010). Accurate observations of the total number of fruits consumed during foraging bouts were infeasible logistically, due to the often rapid movements of birds in dense foliage. Therefore, I quantified bird-plant interactions more broadly following Snow & Snow (1988) and Burns (2006). I scored a feeding 'observation' when a bird approached a plant and consumed at least one fruit. To avoid multiple observations of the same bird during each census period, observations were halted after each observation and resumed 10 m down the trail. Across the observation period (1 h), a total of 2857 foraging observations were observed for 12 species of avian frugivores and 33 species of fleshy-fruited plants.

O'Donnell and Dilks (1994) observed 15 species of birds foraging for 32 species of fruit on the north-west coast of New Zealand's South Island. They recorded a total of 2033 observations of foraging by frugivorous birds on fleshy-fruited plants, between 1983 and 1985. Snow and Snow (1988) observed 19 species of birds forage for 35 species of fruit in Buckinghamshire, south-central England. They recorded a total of 5355 foraging observations between 1980 and 1985. Sorensen (1981) observed 14 species of birds forage for 12 fruit species in Wytham forest, south-central England. He observed a total of 7434 foraging observations between 1979 and 1980. Data from Snow & Snow (1988) and Sorensen (1981) were retrieved from the Interaction Web Database (http://www.nceas.ucsb.edu/interactionweb/).

I conducted two analyses to assess patterns in dietary diversity (i.e. the total number of fruit species consumed throughout the observation period). First, total dietary diversity was regressed against the total number of foraging observations for each species (i.e. sampling effort). Analyses were conducted on natural-logarithm-transformed axes and sample sizes were determined by the total number of species observed at each study site. Positive relationships would indicate that uncorrected dietary diversity estimates increase passively with sampling effort.

Second, I conducted rarefaction analyses to test whether effort-corrected dietary diversity estimates differed between blackbirds and other frugivore species at each site, as well as between blackbirds in New Zealand and the UK. To obtain unbiased estimates of dietary diversity, I conducted a bootstrapping analysis wherein individual observations were randomly selected from the total pool observed at each study site and the total number of fruit species was tallied (see Gotelli & Colwell 2001).

The total number of observations obtained for blackbirds differed among study sites. Therefore, effort-corrected dietary diversity was compared across a range of sampling efforts that were shared among study sites. For sites where blackbirds were observed on 60 or more occasions, dietary diversity was rarefied down to 30 observations. For sites where blackbirds were observed on 100 or more occasions, dietary diversity was rarefied down to 50 observations. Sites with 500 or more observations were rarefied down to 250 observations. All other frugivore species were treated similarly. One thousand simulation replicates were conducted for each site and average dietary diversity (\pm 95% confidence limits) was obtained.

The total number of fruit species available to blackbirds differed among study sites (Zealandia = 33, Sorensen = 12, Snow & Snow = 35, O'Donnell & Dilks = 32). As a result, rarefied estimates of dietary diversity vary asymptotically among sites according to the total pool of fruit species available. To remove this confounding effect, rarefied estimates of dietary diversity were corrected (scaled) for the total number of fruit species present at each site. Therefore, rarefaction analyses yielded estimates of the proportion of available fruit species that were consumed by each bird species. To determine whether the dietary diversity of blackbirds differed from native bird species at each study site, the same procedure was applied to all native frugivore species at each site.

The analyses described above evaluate patterns in dietary diversity, or the total number of fruit species consumed, regardless of species composition. To evaluate differences between the composition of fruit species consumed by blackbirds and the species composition of fruits consumed by co-occurring native bird species, I used non-metric multidimensional scaling to ordinate the diets of all bird species at each site. This technique generates a two-dimensional graphical representation of dietary differences between species wherein points that are situated close together represent frugivore species with similar fruit diets. So if blackbirds consume different types of fruit than other frugivore species, blackbirds will be widely separated from other bird species in ordination space. To test whether blackbirds were situated more distantly from co-occurring frugivore species in ordination space, Euclidean distances between blackbirds and all other bird species were averaged and compared to average Euclidean distances for all other frugivore species with a single-sample *t*-test. To remove the influence of observation rates on results and restrict analyses to dietary composition alone, data were converted to proportions prior to analyses, such that the total number of observations summed to one for each frugivore species. Analyses were conducted in the R statistical and programming environment (R Development Core Team 2011).

Results

The number of fruit species dispersed by birds was positively related to the number of times they were observed in three out of four study sites (Fig. 1). In Zealandia, dietary diversity increased with sampling effort ($R^2=0.932$, P<0.001); blackbirds consumed more fruit species than any other frugivore species and registered the second highest number of observations. On the South Island of New Zealand (O'Donnell & Dilks 1996), dietary diversity increased with sampling effort ($R^2 = 0.778$, P < 0.001); blackbirds consumed the third highest number of fruit species, but were observed in only 3% of foraging observations. In Snow and Snow's (1988) study in the UK, dietary diversity again increased with sampling effort ($R^2 = 0.666$, P < 0.001); blackbirds had the highest number of observations and interaction partners. Sorensen's (1981) study in the UK yielded somewhat different results. Dietary diversity was unrelated to sampling

173

effort ($R^2 = 0.075$, P = 0.177), yet blackbirds were tied for the highest number of fruit species consumed and had the third highest number of observations.

Effort-corrected estimates of dietary diversity in blackbirds did not differ between New Zealand and the UK. Blackbirds had similar values of dietary diversity to native bird species in New Zealand, but they had higher dietary diversity than several native species in the UK (Table 1). Dietary diversity of blackbirds in Zealandia was similar to that of all native bird species (N =11 comparisons). Similarly, no differences in dietary diversity were observed in the O'Donnell & Dilks (1994) dataset (N =4 comparisons). In the Sorensen (1981) dataset, blackbirds displayed greater dietary diversity in 7 out of 11 comparisons. Blackbirds had higher dietary diversity than redwings, field fares and great tits in rarefied estimates of 30 observations, and higher dietary diversity than redwings and field fares in rarefied estimates of both 100 and 500 observations. In the Snow & Snow (1988) dataset, blackbirds displayed greater dietary diversity in 13 out of 25 comparisons. Blackbirds had higher dietary diversity than redwings, fieldfares, magpies, carrion crows and wood pigeons in rarefied estimates of 30 observations. They had higher dietary diversity than starlings, redwings, fieldfares and wood pigeons in rarefied estimates of 100 observations and they had higher dietary diversity than mistle-thrushes, starlings, redwings and fieldfares in rarefied estimates of 500 observations.

Comparisons of dietary composition illustrated that blackbirds had similar diets to other birds in all four sites (Fig. 2). Non-metric multidimensional scaling analyses yielded a robust two-dimensional depiction of dietary relationships between species in Zealandia (normalised raw stress = 0.036). The average Euclidian distance between blackbirds



Figure 1. Relationships between the total number of fruit species included in the diets of frugivorous birds (dietary diversity, *y*-axis) and the total number of foraging observations (sampling effort, *x*-axis) observed for frugivorous bird species in four geographic locales. Each point represents a single bird species and blackbirds (*Turdus merula*) are illustrated as black points. Positive relationships were observed on the North Island of New Zealand (top left, data from this study), the South Island of New Zealand (top right, data from O'Donnell & Dilks 1994), and southern England (bottom left, data from Snow & Snow 1988). Solid lines represent best-fit regression lines for significantly positive relationships. Dashed lines are 95% confidence intervals. Dietary diversity was unrelated in a second site in southern England (bottom right, Sorensen 1981).

Table 1. Rarefaction analyses of the diets of frugivorous birds inhabiting two sites in New Zealand (Zealandia, North Island, this study; South Island, O'Donnell & Dilks 1994) and two sites in southern England (Oxford, Sorensen 1981; Wytham, Snow & Snow 1988). The proportion of fruit species consumed (\pm 95% confidence intervals) are shown in the third, fourth and fifth columns. The third column shows the results for species that were observed more than 60 times, which were rarefied down to 30 observations. The fourth and fifth columns illustrate species that were observed more than 100 and 500 times, which were rarefied down to 50 and 250 observations, respectively.

Study	Bird species	> 60, 30	> 100, 50	> 500, 250
Zealandia	Blackbird (<i>Turdus merula</i>) Waxeye (<i>Zosterops lateralis</i>) Tūī (<i>Prosthemadera novaeseelandiae</i>) Stitchbird (<i>Notiomystis cincta</i>) Saddleback (<i>Philesturnus carunculatus</i>) Whitehead (<i>Mohua albicilla</i>)	0.284 (0.188–0.380) 0.294 (0.210–0.378) 0.310 (0.227–0.394) 0.287 (0.205–0.369) 0.261 (0.181–0.340) 0.254 (0.196–0.313)	0.354 (0.251–0.458) 0.341 (0.259–0.424) 0.362 (0.280–0.448) 0.339 (0.260–0.418) 0.322 (0.240–0.404) –	0.627 (0.529–0.724) 0.488 (0.407–0.570) 0.525 (0.455–0.596) – –
O'Donnell & Dilks (1994)	Blackbird (<i>Turdus merula</i>) Waxeye (<i>Zosterops lateralis</i>) Bellbird (<i>Anthornis melanura</i>) Kākā (<i>Nestor meridionalis</i>) Tūī (<i>Prosthemadera novaeseelandiae</i>)	0.286 (0.230–0.335) 0.346 (0.244–0.448) 0.385 (0.286–0.483) 0.197 (0.131–0.264) 0.188 (0.117–0.259)	- 0.428 (0.324-0.533) 0.485 (0.379-0.591) 0.230 (0.166-0.295)	_ 0.678 (0.598–0.758) 0.766 (0.725–0.806)
Snow & Snow (1988)	Blackbird (<i>Turdus merula</i>) Robin (<i>Erithacus rubecula</i>) Songthrush (<i>Turdus philomelos</i>) Blackcap (<i>Sylvia atricapilla</i>) Mistlethrush (<i>Turdus viscivorus</i>) Starling (<i>Sturnus vulgaris</i>) Redwing (<i>Turdus iliacus</i>) Fieldfare (<i>Turdus pilaris</i>) Magpie (<i>Pica pica</i>) Carrion crow (<i>Corvus corone</i>) Woodpigeon (<i>Columba palumbus</i>)	$\begin{array}{c} 0.354 \ (0.259-0.449) \\ 0.346 \ (0.252-0.440) \\ 0.290 \ (0.197-0.348) \\ 0.321 \ (0.233-0.410) \\ 0.286 \ (0.188-0.347) \\ 0.199 \ (0.136-0.261) \\ 0.203 \ (0.150-0.255) \\ 0.131 \ (0.079 \ 0.182) \\ 0.191 \ (0.133-0.248) \\ 0.149 \ (0.112-0.185) \\ 0.109 \ (0.088-0.131) \end{array}$	0.433 (0.335-0.530) 0.431 (0.331-0.532) 0.358 (0.264-0.453) 0.390 (0.300-0.482) 0.315 (0.239-0.391) 0.228 (0.164-0.293) 0.226 (0.182-0.270) 0.150 (0.097-0.203) - - 0.134 (0.105-0.122)	0.646 (0.562-0.730) 0.679 (0.602-0.756) 0.585 (0.500-0.670) 0.588 (0.521-0.654) 0.443 (0.383-0.520) 0.317 (0.256-0.378) 0.276 (0.22-0.331) 0.215 (0.158-0.273)
Sorensen (1981)	Blackbird (<i>Turdus merula</i>) Willow tit (<i>Poecile montanus</i>) Blue tit (<i>Cyanistes caeruleus</i>) Redwing (<i>Turdus iliacus</i>) Fieldfare (<i>Turdus pilaris</i>) Great tit (<i>Parus major</i>)	0.421 (0.294–0.549) 0.428 (0.301–0.554) 0.210 (0.105–0.315) 0.171 (0.086–0.256) 0.166 (0.157–0.175) 0.209 (0.046–0.209)	0.462 (0.344-0.579) 0.470 (0.359-0.582) 0.236 (0.125-0.347) 0.194 (0.111-0.276) 0.167 (0.167-0.167) -	0.557 (0.479–0.634) - 0.240 (0.186–0294) 0.167 (0.167–0.167) -

and all other bird species (0.684) was lower than for the rest of the community $(0.876 \pm 0.228 \text{ SD}, \text{T} = 2.57, P = 0.048)$, indicating elevated dietary similarity to other bird species. Similar results were obtained for the O'Donnell & Dilks (1996) dataset (normalised raw stress = 0.028), where the average Euclidian distance between blackbirds and all other bird species (0.6721) was also lower than for the rest of the community (0. 903 \pm 0.205 SD, T = 4.832, P < 0.001). In the Snow & Snow (1988) dataset, the average Euclidian distance between blackbirds and all other bird species (0.668) was again lower than the distribution of average values for the rest of the community (0.888 \pm 0.228 SD, T = 24.123, P < 0.001, normalised raw stress = 0.050). Different results were obtained in the Sorensen (1981) dataset, where the average Euclidian distance between blackbirds and all other bird species (0.825) was similar to the distribution of average values for the rest of the community $(0.869 \pm 0.258 \text{ SD}, T = 0.210, P = 0.838)$ normalised raw stress = 0.050).

Discussion

Field observations showed that European blackbirds consumed a greater total number of fruit species than all native New Zealand bird species. They also dispersed a similar number

of plant species per foraging bout than native birds. These results were strikingly similar to analogous field observations in the UK. Results also showed that the composition of blackbird fruit diets was strongly undifferentiated from co-occurring bird species, both in their native and introduced ranges. Therefore, blackbirds appear to be highly efficient frugivores in the introduced range, where they may serve as surrogate mutualists for missing native birds.

Although most statistical comparisons of blackbird fruit diets failed to detect dietary differences, blackbirds foraged for fruits at different rates in the two New Zealand study sites. Observations in Nothofagus forests on the South Island (Burns & Lake 2009; Burns pers. obs.) suggest they are far less abundant in this forest type than in conifer-broadleaved forest on the North Island. Therefore, differences in total observation rates between field observations and O'Donnell & Dilks' (1994) data may result from geographic variation in blackbird population sizes. Blackbirds showed similar levels of dietary diversity to native bird species in both New Zealand sites but they dispersed greater numbers of fruit species per foraging observation than several species of native birds in England. Additional long-term observations in other geographic locales are needed to pinpoint the processes responsible for the differences in fruit diets observed and to confirm the generality of results reported here.



Figure 2. Results from non-metric multidimensional scaling analyses of the diets of frugivorous birds in four geographic locales. Top left is the North Island of New Zealand (data from this study), top right is from the South Island of New Zealand (data from O'Donnell & Dilks 1994), bottom left is from southern England (data from Snow & Snow 1988), bottom right is from a second site in southern England (data from Sorensen 1981). Each point represents a single bird species and blackbirds (*Turdus meruula*) are illustrated as black points.

Williams (2006) reviewed the literature on the diet of European blackbirds both in New Zealand and across their native range. The general consensus was that blackbirds consume a wide range of fruit species and appear to be important seed dispersers throughout their native and introduced ranges. However, Williams (2006) also concluded that blackbirds are particularly important dispersers of invasive plant species. Gleditsch and Carlo (2011) also showed that native birds commonly disperse introduced fruit species in North America. There are few introduced plant species in Zealandia that produce fleshy fruits, aside from Japanese dogwood (*Cornus kousa*). So the observations from Zealandia cannot be used to test whether blackbirds preferentially disperse introduced plant species.

Seed dispersal is a multi-stage process and patterns arising at initial stages may be overridden in later stages (see Schupp et al. 2010). Results presented here relate only to the initial stage of seed dispersal and blackbirds may interact differently with plants at later stages (e.g. germination). For example, seeds ingested by blackbirds could have lower germination rates than through native bird species, or blackbirds may disperse seeds over smaller spatial scales, reducing probabilities of establishment. Future work on the relative roles introduced birds play in avian seed dispersal mutualisms would benefit from investigating how blackbirds influence later stages of plant recruitment.

In a similar study, Kelly et al. (2006) compiled previously published data on frugivory by native and introduced bird species in New Zealand. Based on these data, they conclude that introduced birds are unimportant frugivores, in sharp contrast to those reported here. Differences between studies may result from the use of different analytical techniques, as Kelly et al. (2006) analyse their data using percentages instead of using rarefaction techniques. Significant among-site variation in bird abundances or fruit consumption patterns might also explain this discrepancy. Additional data from other localities and comparative analytical procedures are clearly needed to understand better how introduced birds interact with native plants, as seed dispersers. Future work might also benefit from investigating whether blackbirds compete with native birds for food resources.

Burns and Lake (2009) showed that bird-fruit interactions in New Zealand are size related, with bigger birds generally consuming bigger fruits and smaller birds consuming smaller fruits. Blackbirds have intermediate body size, so their diverse, unspecialised fruit diet may arise as a result of their body size. The largest species of avian frugivore in New Zealand, the kererū (New Zealand pigeon Hemiphaga novaeseelandiae), appears to be the only native frugivore capable of dispersing several large-seeded native plant species (Kelly et al. 2010). Wotton and Kelly (2011) recently showed that without the dispersal services of this frugivore species, several largeseeded plant species are likely to suffer seed dispersal and regeneration failure. However, kererū were rarely observed in Zealandia. So while available data indicate that blackbirds show similar levels of dietary diversity and composition to the native bird species, it seems doubtful that blackbirds can replace kererū functionally as seed dispersers.

Even though blackbirds share no evolutionary history with the New Zealand flora, they have rapidly developed important partnerships with native plants as frugivores in Zealandia. Furthermore, patterns in blackbird frugivory are similar to those maintained by native bird species. Many native frugivores in Zealandia belong to genera (e.g. Mohua spp.) or families (e.g. New Zealand wattlebirds, Callaeidae) that are endemic to New Zealand. These species have therefore had ample time to develop more specialised, co-evolutionary relationships with New Zealand plants. However, patterns in frugivory are remarkably unspecialised. Results are therefore consistent with the generalisation that seed dispersal mutualisms are often comprised of unrelated species that interact interchangeably and do not require reciprocal co-evolutionary adjustments (Herrera 1998, 2002; Levey & Benkman 1999; Zamora 2000; Burns 2006).

Davis et al. (2011) recently called for a reappraisal of the commonly held belief that introduced species are universally harmful. They argue that non-native species are now permanent features of most 'natural' ecosystems worldwide so they should be judged based on their functioning within the ecosystems to which they have been introduced. In this case, blackbirds appear to consume a similar range of fruits to native New Zealand birds and may provide effective seed dispersal services in their absence. Although the European blackbirds will never compensate for loss of endemic New Zealand birds, they may help to make the best of a bad situation.

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