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BRIEF COMMUNICATION

Historical records of passerine introductions to New Zealand fail to support the propagule pressure hypothesis

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Abstract Blackburn et al. (Biodiver Conserv 20:2189–2199, 2011) claim that a reanalysis of passerine introductions to New Zealand supports the propagule pressure hypothesis. The conclusions of Blackburn et al. (2011) are invalid for three reasons: First, the historical record is so flawed that there is no sound basis for identifying the mechanisms behind extinction following introduction, or whether species were successful because they were introduced in large numbers or were introduced in large numbers because earlier releases succeeded. Second, the GLIMMIX analysis of Blackburn et al. (2011) is biased in favor of the propagule pressure hypothesis. Third, the population viability analysis presented by Blackburn et al. (2011) is based on unjustified and questionable assumptions. It is likely that the outcome of passerine bird introductions to New Zealand depended on species characteristics, site characteristics, and human decisions more than on a simple summing of the numbers introduced.

Keywords Propagule pressure · Introduced birds · Historical records

Introduction

Following their assessment of our paper (Moulton et al. 2011) on passerine introductions to New Zealand, Blackburn et al. (2011) claim to have conducted a "robust" analysis and

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found a positive effect of propagule pressure on establishment success. As we showed previously (Moulton et al. 2011), and will show in more detail here, however, the propagule pressure hypothesis for bird species is not strongly supported by previous analyses. In fact, the propagule pressure hypothesis as proposed, cannot predict the fate of any New Zealand bird species following an introduction event. In this paper we address three critical flaws in the arguments of Blackburn et al. (2011). Specifically we deal with problems with the historical record, their statistical analyses, and finally their population viability analysis.

Problems with historical records

Blackburn et al. (2011) agree with our contention that the historical records for New Zealand are inaccurate. However, we did not simply point out differences in the numbers of individuals introduced or possibly introduced (Moulton et al. 2011). As we noted, using the same sources, Green (1997) listed 28 passerines whereas Duncan (1997) included 41. The historical records for New Zealand are not just inaccurate, they are also incomplete as noted by Thomson (1922) who stated that the Acclimatization Societies were "very careless in the matter [of keeping records]". Thomson (1922) was the principal source for most of the records analyzed for New Zealand by Duncan (1997) and Veltman et al. (1996). Duncan (1997) also cited Thomson (1926). Green (1997) used Long (1981) as the primary source for his analysis of New Zealand bird introductions, but Long (1981) essentially used Thomson (1922, 1926) or others who in turn used Thomson (1922). These records may actually be wildly inaccurate, as shown in our comparison of various authors' records for one society (i.e. Canterbury; Moulton et al. 2011, Table 3).

It is difficult to infer ecological mechanisms associated with the fates of introduced birds using compilations, made long after the events (e.g. Thomson 1922), of fragmentary reports of bird introductions. It is impossible to evaluate these hypotheses, when event level data are not even reported in the cited literature. Blackburn et al. (2011) in their Table 2 claim that Cassey et al. (2004) provided data for a classification of *Passer domesticus* success following introduction to North America. Neither Cassey et al. (2004), or Cassey (2002), cited by Cassey et al. 2004), provide any event-level propagule size data for this species that could be used to evaluate these claims.

A "robust" analysis hardly seems appropriate for the poor quality of the records Thomson (1922) presents. He notes, for example, that "a number of those [people] who were concerned with the introduction of small birds in the early days of acclimatization activity did not know a hedge-sparrow from a common sparrow…". He also indicates that one person reported to him that the three introductions of European robins (*Erithacus rubecula*) in the Otago district amounting to 100 individuals in a two-year span included only "cocks". Similarly, for the Linnet (*Carduelis cannabina*), Thomson (1922) reported that according to one observer all the linnets might have belonged to "all or nearly all of a one sex".

In addition to inconsistencies in the numbers reported, Thomson (1922) also noted that there was confusion over which species were actually involved. Thomson (1922) suggested that some (or all?) of the Australian Minahs (*Manorina melanocephala)* might in fact have been Common Mynas (*Acridotheres tristis*). He also expressed uncertainty over the species identification of "Nutmeg Sparrows". Thomson (1922) identified "Diamond Sparrows" as *Emblema guttata* but notes that the individuals might actually have belonged to *Pardalotus punctatus* (Hutton 1871), and he expressed uncertainty about reports of Bullfinches

(*Pyrrhula pyrrhula*) that, at least in some cases, might actually have been Chaffinches (*Fringilla coelebs*). Before judging the merit of any analyses, one must recognize that these historical records are in many cases mere rumors and impressions, and not actual "data" in any sense.

Statistical analyses

Blackburn et al. (2011) claim our analysis (Moulton et al. 2011) was biased toward not showing an effect of propagule pressure. Species that were repeatedly introduced for biocontrol or cultural reasons after they were successfully established would have large propagule sizes based on the summing of introductions. This bias in favor of the hypothesis is consistent with the definition of propagule pressure proposed by Blackburn et al. (2011). Unsurprisingly, the GLIMMIX analysis of Blackburn et al. (2011) has the same bias in favor of the propagule pressure hypothesis. As stated in our paper (Moulton et al. 2011), the question we addressed was, "Were introductions of passerine species successful because they were introduced in high numbers or were they introduced in high numbers because they were desirable and initially successful?"

To answer this we ignored the poor quality of the historical records and simply used the numbers Duncan (1997) listed for four acclimatization societies in New Zealand: two on the North Island–Auckland and Wellington; and two on the South Island–Otago and Canterbury. The degree to which the use of sums biases the results is easily seen with a glance at the listing in the Appendix Table 1. Thus, for the Auckland district we used Duncan's (1997) sum of 345 Yellowhammers (*Emberiza citrinella*), even though 312 of these individuals were released 3 years after four earlier releases of 8, 4, 5 and 16 individuals in the years 1865, 1867, 1868, and 1870. Of course, the species could have been successful following the release of the first eight–Simberloff (2009) lists several examples of successful introductions involving very tiny propagules. To help readers see the situation more clearly we list the passerine records of Thomson (1922) in the Appendix Table 1. As we noted (Moulton et al. 2011) for three of the Acclimatization Societies (Auckland, Wellington and Otago) the numbers Duncan (1997) used are virtually identical to those of Thomson (1922). By using sums of all introductions of a species in a district, our analysis was biased in the direction of showing an effect of propagule pressure. Our analysis is also biased because it ignores differences in time. For example, 40 Common Mynas (*Acridotheres tristis*) released in Wellington in 1876 might well have been unnecessary for successful establishment as 30 had been released just the year before. One year is hardly sufficient time to judge the fate of an introduction.

Blackburn et al. (2011) note that other authors, namely Veltman et al. (1996); Green (1997); Duncan (1997); Sol and Lefebvre (2000); and Duncan et al. (2006), have reported a positive effect of propagule pressure based on analyses of New Zealand's historical records. There is just one avifauna in New Zealand and repeated analyses of the same inaccurate, incomplete records from the same second-hand (e.g. Thomson 1922, 1926) or third-hand (e.g. Long 1981) sources hardly bolsters support for the propagule pressure hypothesis.

There are very few unambiguous examples of mixed success for passerines introduced to New Zealand across the separate districts (the all-or-none hypothesis of Simberloff and Boecklen (1991) does a better job of predicting introduction outcomes in New Zealand than the propagule pressure hypothesis). Blackburn et al. (2011) concluded the introduction failure of *Fringilla coelebs* in Otago (ultimately successfully established

throughout New Zealand) could be inferred from Thomson (1922, 1926). Thomson (1922, 1926) actually reported that this species became rare after large-scale poisoning (a site-level factor), but didn't report local extinction. Similarly, we find no evidence in Thomson (1922) that the *Gymnorhina tibicen* introduction to Auckland failed. Moreover, in our paper we followed the interpretations of Duncan (1997) who claimed these introductions were successful.

The GLIMMIX analysis conducted by Blackburn et al. (2011) is unconvincing as a test of propagule pressure. It assumes that the districts are natural eco-geographical units with respect to the different species, and that errors in the data are inevitable and can therefore be ignored. These districts can be very large (e.g. Canterbury encompassed more than 38,000 km^2–Wall 1927), and it is arbitrary to assume that multiple introductions by multiple agents as noted by Thomson (1922) within a district across many years represents a single population of introduced birds. Often the birds were distributed to the members who may have lived, and therefore released the birds, in distant localities (Thomson 1922).

Population viability analysis

We are also not convinced by the population viability analysis presented by Blackburn et al. (2011). The assumed mechanism for local species extinction associated with the propagule pressure hypothesis is through demographic stochasticity (there appears to be no evidence of the unsimulated species-level Allee effects for the passerine species introduced to New Zealand). The Vortex simulations were based on the assumption that fecundity and survivorship are fixed properties of the species (no environmental stochasticity). However, large inter-annual variation of bird population sizes in native habitats (Pimm 1991) and direct estimates of fecundity variation (Grant et al. 2000, Etterson et al. 2011) demonstrate that demographic parameters are functions of the environment. If the actual fecundity and survivorship of bird species in the novel New Zealand environment reduced λ to less than one, demographic stochasticity would not be relevant to the ultimate fate.

Blackburn et al. (2011) assumed a hypothetically long-lived (11 year maximum female reproductive age) passerine, with high biotic potential ($\lambda = 1.105$) and an equal sex ratio, to represent all of the bird introductions to New Zealand. The Vortex simulations report probabilities for extinction over a period of 100 years. If one accepts the Vortex simulations, the unsuccessfully introduced Linnet with 119 individuals (Duncan 1997) in the Canterbury district (or 185 individuals if one sums separate districts and assume a single population) or the 224 'Australian Minahs' that failed in the Wellington District (Duncan 1997) would have a 100% chance of establishment (Fig. 2 in Blackburn et al. 2011). The historical record does not support the idea that a 100-year simulation is appropriate for comparing failed New Zealand bird introductions to the hypothetical species. It would be interesting to examine the distribution of extinction times presumably to some (unreported by Blackburn et al. 2011) quasi-extinction threshold. Thomson (1922) lists numerous examples of species for which there is no record following their release. Birds that never reproduced in New Zealand did not become extinct due to demographic stochasticity.

Given the poor quality and incompleteness of the historical records, it is puzzling that Blackburn et al. (2011) claim to have shown a positive effect of propagule pressure on establishment success. We stand behind our previous conclusions that most of the releases of individuals of successfully introduced passerine species were superfluous and had no bearing on the fate of the species in New Zealand. The answer to our question of whether species were successful because they were introduced in large numbers or if they were

introduced in large numbers because they were successful seems clear. And, as Blackburn et al. (2011) state, "Moreover, there is growing evidence for effects on success of the characteristics of the avian species introduced (e.g. habitat or dietary generalism, migratory tendency) and the novel environment encountered, independent of propagule pressure…".

Appendix

See Table 1.

Table 1 A list of passerine introductions taken from Thomson (1922)

Species	Place	Number	Date
Acridotheres tristis	All centers	?	?
Acridotheres tristis	Canterbury	18	1870
Acridotheres tristis	Otago	?	1870s
Acridotheres tristis	Nelson	?	1877
Acridotheres tristis	Wellington	30	1875
Acridotheres tristis	Wellington	40	1876
Agelaius phoeniceus	Auckland	2	1869
Alauda arvensis	Nelson	20	1864
Alauda arvensis	Otago	4	1867
Alauda arvensis	Otago	35	1868
Alauda arvensis	Otago	61	1869
Alauda arvensis	Private dealers	?	1869a
Alauda arvensis	Canterbury	13	1867
Alauda arvensis	Canterbury	18	1871
Alauda arvensis	Auckland	10	1867
Alauda arvensis	Auckland	52	1874
Alauda arvensis	Wellington	52	1874
Alauda arvensis	Wellington	56	1875
Australian Shrike	Wellington	14	1877
Australian Shrike	Wellington	15	1878
Carduelis cannabina	Nelson	7	1862
Carduelis cannabina	Otago	2	1867
Carduelis cannabina	Otago	18	1868
Carduelis cannabina	Canterbury	20	1867
Carduelis cannabina	Canterbury	3	1868
Carduelis cannabina	Canterbury	?	1869
Carduelis cannabina	Canterbury	?	1875
Carduelis cannabina	Auckland	8	1865
Carduelis cannabina	Auckland	14	1867
Carduelis cannabina	Auckland	20	1868
Carduelis cannabina	Auckland	?	1869
Carduelis cannabina	Wellington	22	1882
Carduelis carduelis	Nelson	10	1862

Table 1 continued

Species	Place	Number	Date
Carduelis carduelis	Auckland	11	1867
Carduelis carduelis	Auckland	44	1871
Carduelis carduelis	Canterbury	95	1871
Carduelis carduelis	Canterbury	?	1875
Carduelis carduelis	Otago	3	1867
Carduelis carduelis	Otago	30	1868
Carduelis carduelis	Otago	54	1869
Carduelis carduelis	Otago	31	1871
Carduelis carduelis	Wellington	1	1877
Carduelis carduelis	Wellington	52	1880
Carduelis carduelis	Wellington	22	1881
Carduelis carduelis	Wellington	103	1883
Carduelis chloris	Nelson	5	1862
Carduelis chloris	Canterbury	2	1863
Carduelis chloris	Auckland	?	1865
Carduelis chloris	Auckland	18	1867
Carduelis chloris	Auckland	33	1868
Carduelis chloris	Otago	8	1868
Carduelis flammea	Nelson	2	1862
Carduelis flammea	Otago	10	1868
Carduelis flammea	Otago	71	1871
Carduelis flammea	Canterbury	14	1868
Carduelis flammea	Canterbury	120	1871
Carduelis flammea	Canterbury	?	1875
Carduelis flammea	Auckland	1	1871
Carduelis flammea	Auckland	209	1872
Carduelis flammea	Wellington	2	1875
Carduelis flavirostris	Nelson	2	1862
Carduelis flavirostris	Otago	38	1871
Carduelis spinus	Wellington	2	1876
Carduelis spinus	Canterbury	?	1879
Carduelis spinus	All centers	?	
Corvus frugilegus	Nelson	3	1862
Corvus frugilegus	Canterbury	?	<1870
Corvus frugilegus	Canterbury	?	1870
Corvus frugilegus	Auckland	2	1869
Corvus frugilegus	Auckland	64	1870
Corvus frugilegus	Canterbury	5	1871
Corvus frugilegus	Canterbury	35	1873
Corvus monedula	Otago	?	1867
Corvus monedula	Canterbury	1	1868
Corvus monedula	Canterbury	?	<1872
Emberiza cirlus	Otago	7	1871
Emberiza cirlus	Taranaki	?	?

Table 1 continued

Species	Place	Number	Date
Emberiza cirlus	Stewart Island	18	1879
Emberiza citrinella	Nelson	3	1862
Emberiza citrinella	Auckland	8	1865
Emberiza citrinella	Auckland	4	1867
Emberiza citrinella	Auckland	5	1868
Emberiza citrinella	Auckland	16	1870
Emberiza citrinella	Auckland	312	1871
Emberiza citrinella	Canterbury	1	1867
Emberiza citrinella	Canterbury	34	1871
Emberiza citrinella	Otago	8	1868
Emberiza citrinella	Otago	31	1871
Emberiza citrinella	Stewart Island	32	1879
Emberiza hortulana	Wellington	6	1885
Emberiza schoeniclus	Otago	4	1871
Emblema guttata	Canterbury	?	1864
Emblema guttata	Wellington	12	1874
Emblema guttata	Nelson	?	?
Emblema guttata	Kawau	100	?
Erithacus rubecula	Nelson	1	1862
Erithacus rubecula	Auckland	3	1868
Erithacus rubecula	Auckland	3	1871
Erithacus rubecula	Auckland	3	1872
Erithacus rubecula	Canterbury	?	1879
Erithacus rubecula	Wellington	10	1883
Erithacus rubecula	Otago	40	1885
Erithacus rubecula	Otago	20	1886
Erithacus rubecula	Otago	2	1899
Erithacus rubecula	Otago	1	1900
Fringilla coelebs	Nelson	23	1862
Fringilla coelebs	Auckland	?	1864
Fringilla coelebs	Auckland	45	1867
Fringilla coelebs	Auckland	68	1868
Fringilla coelebs	Auckland	?	1869
Fringilla coelebs	Canterbury	11	1867
Fringilla coelebs	Canterbury	5	1868
Fringilla coelebs	Canterbury	?	1871
Fringilla coelebs	Otago	27	1868
Fringilla coelebs	Otago	6	1869
Fringilla coelebs	Otago	66	1871
Fringilla coelebs	Wellington	70	1874
Fringilla coelebs	Wellington	36	1876
Fringilla coelebs	Wellington	20	1877
Fringilla coelebs	Wellington	?	?
Fringilla coelebs	Private	?	?

Table 1 continued

Species	Place	Number	Date
Fringilla coelebs	Stewart Island	70	1879
Fringilla montifringilla	Canterbury	2	1868
Fringilla montifringilla	Canterbury	6?	1871
Fringilla montifringilla	Wellington	3	1874
Fringilla montifringilla	Wellington	1	1871
Grallina cyanoleuca	West Coast NI	?	?
Gymnorhina tibicen	Canterbury	8	1864
Gymnorhina tibicen	Canterbury	4	1866
Gymnorhina tibicen	Canterbury	32	1867
Gymnorhina tibicen	Canterbury	18	?
Gymnorhina tibicen	Canterbury	24	1871
Gymnorhina tibicen	Canterbury	?	1870
Gymnorhina tibicen	Otago	3	1865
Gymnorhina tibicen	Otago	20	1866
Gymnorhina tibicen	Otago	32	1867
Gymnorhina tibicen	Otago	20	1868
Gymnorhina tibicen	Otago	6	1869
Gymnorhina tibicen	Auckland	10	1867
Gymnorhina tibicen	Auckland	1	1870
Gymnorhina tibicen	Wellington	260	1874
Gymnorhina tibicen	Kawau Island	?	<1867
Lonchura castaneothorax	Nelson	6	<1864
Lonchura castaneothorax	Auckland	25	1867
Lonchura castaneothorax	Auckland	2	1871
Lonchura castaneothorax	Canterbury	12	1864
Lonchura oryzivora	Nelson	?	1862
Lonchura oryzivora	Auckland	6	1867
Lonchura punctulata	Auckland	8	1868
Lullula arborea	Auckland	5	1872
Luscinia megarhynchos	Canterbury	1	1879
Manorina melanocephala	Nelson	?	1870s
Manorina melanocephala	Wellington	184	1874
Manorina melanocephala	Wellington	8	1876
Manorina melanocephala	Wellington	12	1877
Manorina melanocephala	Wellington	20	1878
Manorina melanocephala	Canterbury	400	1879
Manorina melanocephala	Otago	80	1880
Manorina melanophrys	Wellington	2	1874
Neochmia temporalis	Otago	4	1867
Neochmia temporalis	Auckland	4	1871
Parus caeruleus	Canterbury	?	1874
Passer domesticus	Canterbury	5	1867
Passer domesticus	Wanganui	?	1866
Passer domesticus	Auckland	2	1865

Table 1 continued

Species	Place	Number	Date
Passer domesticus	Nelson	1	1864
Passer domesticus	Canterbury	40	1867
Passer domesticus	Auckland	47	1867
Passer domesticus	Nelson	6	1871
Passer domesticus	Otago	3	1868
Passer domesticus	Otago	11	1869
Passer montanus	Otago	2	1868
Passer montanus	Auckland	3	1868
Passer montanus	Auckland	9	1871
Piranga rubra	Auckland	2	1868
Poephila guttata	Wellington	12	<1885
Prunella modularis	Auckland	300	1859
Prunella modularis	Auckland	1	1867
Prunella modularis	Auckland	2	1868
Prunella modularis	Auckland	7	1872
Prunella modularis	Auckland	19	1874
Prunella modularis	Auckland	18	1875
Prunella modularis	Otago	18	1868
Prunella modularis	Otago	80	1871
Prunella modularis	Canterbury	9	1868
Prunella modularis	Canterbury	41	1871
Prunella modularis	Christchurch	?	1875
Prunella modularis	Hawke's Bay	?	1876
Prunella modularis	Wellington	4	1880
Prunella modularis	Wellington	26	1881
Prunella modularis	Wellington	20	1882
Pyrrhula pyrrhula	Nelson	6	?
Pyrrhula pyrrhula	Canterbury	2	1875
Pyrrhula pyrrhula	Hawke's Bay	?	?
Stagonopleura bella	Auckland	2	1870
Stagonopleura bella	Wellington	8	1885
Sturnella neglecta	Auckland	2	1869
Sturnus vulgaris	Nelson	17	1862
Sturnus vulgaris	Otago	3	1867
Sturnus vulgaris	Otago	81	1868
Sturnus vulgaris	Otago	85	1869
Sturnus vulgaris	Canterbury	20	1867
Sturnus vulgaris	Canterbury	40	1871
Sturnus vulgaris	Auckland	12	1865
Sturnus vulgaris	Auckland	15	1867
Sturnus vulgaris	Auckland	82	1868
Sturnus vulgaris	Wellington	60	1877
Sturnus vulgaris	Wellington	90	1878
Sturnus vulgaris	Wellington	14	1881

Table 1 continued

Species	Place	Number	Date
Sturnus vulgaris	Wellington	100	1882
Sturnus vulgaris	Wellington	34	1883
Sturnus vulgaris	Private	?	?
Sylvia atricapilla	Auckland	5	1872
Sylvia communis	Auckland	2	1868
Turdus merula	Nelson	26	1862
Turdus merula	Otago	2	1865
Turdus merula	Otago	6	1867
Turdus merula	Otago	39	1868
Turdus merula	Otago	21	1869
Turdus merula	Otago	70	1871
Turdus merula	Canterbury	2	1865
Turdus merula	Canterbury	46	1867
Turdus merula	Canterbury	152	1868
Turdus merula	Canterbury	62	1871
Turdus merula	Canterbury	?	1875
Turdus merula	Auckland	8	1865
Turdus merula	Auckland	30	1867
Turdus merula	Auckland	132	1868
Turdus merula	Auckland	?	1869
Turdus philomelos	Nelson	5	1872
Turdus philomelos	Otago	2	1865
Turdus philomelos	Otago	4	1867
Turdus philomelos	Otago	49	1868
Turdus philomelos	Otago	48	1869
Turdus philomelos	Otago	42	1871
Turdus philomelos	Canterbury	36	1867
Turdus philomelos	Canterbury	24	1868
Turdus philomelos	Canterbury	?	1871
Turdus philomelos	Canterbury	?	1875
Turdus philomelos	Auckland	30	1867
Turdus philomelos	Auckland	95	1868
Turdus philomelos	Wellington	8	1878

Species names are from Dickinson (2003), place refers to an Acclimatization Society if known

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