2011

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Biodivers Conserv (2011) 20:607–623
DOI 10.1007/s10531-010-9969-8

ORIGINAL PAPER

A reassessment of the role of propagule pressure in influencing fates of passerine introductions to New Zealand

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Received: 10 November 2010 / Accepted: 15 December 2010 / Published online: 28 December 2010

Abstract Several studies have argued that principal factor in determining the fate of bird introductions is introduction effort. In large part, these studies have emerged from analyses of historical records from a single place—New Zealand. Here we raise two concerns about these conclusions. First, we argue that although many bird species were introduced repeatedly to New Zealand, in many cases the introductions apparently occurred only after the species were already successfully naturalized. The inclusion of such seemingly superfluous introductions may exaggerate the importance of propagule pressure. And second, we question the reliability of the records themselves. In many cases these records are equivocal, as inconsistencies appear in separate studies of the same records. Our analysis indicates that species were successful not because they were introduced frequently and in high numbers, but rather it is likely that they were introduced frequently and in high numbers because the initial releases were successful.

Keywords Introduced passerines · Propagule pressure · New Zealand · Historical records

Introduction

Why do some introductions to new locations succeed and others fail? Is it because the individuals released possess some species-specific trait that prevents their success? Could it

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be that the new environment is too inhospitable or that it supports too many competitors or predators for them to survive? Or could it simply be that too few individuals were introduced and the few that were released were unable to find mates?

The ability to predict the outcomes of species introductions would be of great practical importance for conservation biologists. Introduced species have the potential to devastate native ecosystems (e.g. Savidge 1987). Populations of introduced birds, for example, may provide a reservoir for pathogens such as *Mycoplasma gallisepticum* (Farmer et al. 2005) seen in introduced populations of House Finches (*Carpodacus mexicanus*) in the eastern United States. Warner (1968) found evidence that a sample of introduced House Finches on the Hawaiian island of Kauai showed symptoms of current or past bird pox viral infection, and so introduced species could serve as a reservoir for bird pox. In addition to their potential to carry and transmit diseases, in some cases introduced species might also interbreed with native species. Thus Munoz-fuentes et al. (2007) reported that introduced ruddy-ducks (*Oxyura jamaciensis*) hybridized with rare white-headed ducks (*Oxyura leucocephala*) in Spain, and Rhymer et al. (1994) and Rhymer and Simberloff (1996) summarized reports of interbreeding between introduced mallards (*Anas platyrhynchos*) and Pacific grey ducks (*Anas superciliosa*); introduced Mallards and Mottled Ducks (*Anas fulvigula*); and Hawaiian Ducks (*Anas wyvilliana*).

Unfortunately, it is not always clear on first appearance, what impacts any introduced species might eventually have. Thus, efforts to determine the forces that influence the fates of introductions are of critical importance to conservation.

The notion that success or failure of introductions depends ultimately on introduction effort or propagule pressure, has become in-grained in the introduced species literature (See review by Simberloff 2009; Duncan et al. 2003; Cassey et al. 2004; Lockwood et al. 2005). Of course it has long been known that introductions of very small numbers of individuals have reduced chances for success (e.g. Phillips 1928), although there are numerous examples of successful species introductions of only a few individuals. Thus, Munoz-fuentes et al. (2007) note that the founder population for Ruddy Ducks in Europe consisted of just seven individuals. Demographic analyses indicate that introduced vertebrate populations can achieve positive growth rates with small founder populations (Van Houtan et al. 2009; Wilson et al. in press).

Despite this newfound enthusiasm for propagule pressure we note that several other ecological variables and processes have been shown to influence establishment success. These include factors from two other levels: the site-level (e.g. Elton 1958; Diamond and Veitch 1981; Smallwood 1994; Case 1996; Moulton and Lockwood 1992; Lockwood et al. 1993; Moulton and Pimm 1983, 1986a, b, 1987; Brooke et al. 1995; Lockwood and Moulton 1994; Lockwood et al. 1996; Moulton 1985, 1993), and the species-level including factors such as size of native range (Moulton and Pimm 1986b), response to sexual selection (McLain et al. 1995, 1999; Moulton et al. 2009; Sorci et al. 1998), behavioral flexibility (Sol and Lefebvre 2000), overall colonization ability (Simberloff and Boecklen 1991) and perhaps even relative brain size (Sol et al. 2005).

Supporters of the propagule pressure model for avian introductions have relied heavily on information from historical records of bird introductions. Thus, Lockwood et al. (2005) listed 10 published studies dealing exclusively with birds that purport to show evidence for a positive effect of propagule pressure in birds, and six of these dealt with introductions of birds to New Zealand. Similarly, Blackburn et al. (2009) listed 18 avian introduction studies that reported a positive impact of propagule pressure 13 of which dealt at least in part with birds introduced to New Zealand.

Here we argue that the propagule pressure model is based on an over-generalization of historical records from a highly limited geographical area, namely New Zealand. Moreover, the potential conservation consequences of placing faith in the propagule pressure model are not trivial. The assumption that the fates of introductions depend primarily on the numbers of individuals released or the number of releases, could imply that assessments of site-level factors and species-level factors of potential introduced pests are of lesser, or even no, importance. Also, introductions consisting of just a few individuals, by this model, might be ignored as they would be assumed to be doomed to fail. Simberloff (2009) details instances of species successfully invading following the release of relatively small numbers. Although there are numerous other potentially important interacting ecological factors, some have argued that propagule pressure should form the basis for null models in the field of biological invasions (Colautti et al. 2006), and others have even claimed that introduced species policies based on propagule pressure could represent an important prevention strategy (Reaser et al. 2008).

The New Zealand records form the bulk of the supporting data for the propagule pressure among birds, yet these focus just on the introduction efforts of various acclimatization societies (Thomson 1922). Acclimatization Societies were formed throughout New Zealand in the latter part of the nineteenth century with the expressed goal of bringing species for reasons ranging from sport to nostalgia to pest control (Druett 1983). Members of these societies paid annual dues and these funds were then used to purchase individuals of various species for ultimate acclimatization in New Zealand (Dunlap 1997). These acclimatization societies were not the only parties involved in species introductions as private individuals were also involved (Thomson 1922). However, the records of such efforts are not available. And as Thomson (1922) noted the efforts of the acclimatization societies in New Zealand were often haphazard and, in fact, some were "very careless" when it came to keeping records. With this in mind, we re-examined the data presented in influential papers by Veltman et al. (1996), Duncan (1997), and Green (1997). We show that even though these authors drew their data from the same basic sources, they do not agree on which species were actually released, nor do they agree on the numbers of individuals released for all species. Moreover, the record does not support the assumption that multiple introductions of a species were required to ensure introduction success to New Zealand. In contrast, our reanalysis supports an alternative explanation for the association between elevated levels of introduction success and introduction effort (See Fig. 1).

Materials and methods

We compiled a master list (see Appendix) of species using Thomson (1922, 1926) and Long (1981) and then compared our list to the lists of Veltman et al. (1996), Duncan (1997), and Green (1997). Veltman et al. (1996) point out the remarkable similarity between Thomson (1922) and Long (1981) and suggest that this correspondence somehow strengthens the foundation of their analyses. However, this similarity is hardly surprising as Long (1981) cited Thomson (1922) as his reference for 172 of the 181 New Zealand non-native passerine introductions in his book. Two of the remaining nine introductions occurred after publication of Thomson's (1922) book. The remaining exceptions list references that, in turn, cite Thomson (1922) as their reference.

The studies by Green (1997) and Veltman et al. (1996) treated New Zealand as a single location, whereas Duncan (1997) looked at the outcomes at four separate acclimatization societies: Auckland and Wellington on the North Island; Canterbury and Otago on the

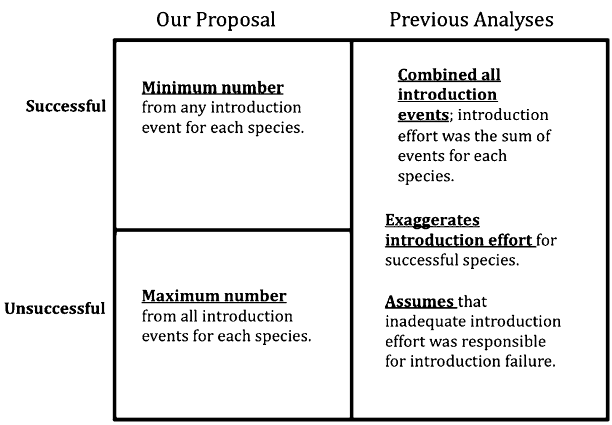

Fig. 1 Contrasting methods for assessing introduction effort and success of passerine birds to New Zealand

South Island. Ecological heterogeneities and size differences among the regions covered by the acclimatization societies; support Duncan's (1997) and Duncan and Forsyth's (2006) decision to conduct their analyses at the society level. The Canterbury district alone encompassed roughly 38,850 km^2 (Wall 1927), which is roughly twice the area of the entire Hawaiian archipelago (Juvik and Juvik 1998).

Tables 1 and 2 include the numbers of individuals released per species at each of the four Acclimatization Societies according to Duncan (1997). We scored each species/society combination as successful or unsuccessful following Duncan (1997). Generally, introductions are considered successful if they generate a 'persistent or probably persistent

Table 1 Numbers of individuals of successful species released by four Acclimatization Societies

Species	Cby (SI)	Ota (SI)	Wel (NI)	Auc (NI)
Alauda arvensis	434	100 (1)	108	**62** (**1**)
Carduelis carduelis	265	118 (2)	177	**55** (**1**)
Carduelis chloris	**32** (**1**)	–	–	51 (1)
Carduelis flammea	326	81 (1)	**2** (**0**)	209
Corvus frugilegus	**36** (**1**)	–	–	66 (1)
Emberiza cirlus	0	7 (0)	**4** (**0**)	0
Emberiza citrinella	236	**39** (**1**)	–	345 (2)
Fringilla coelebs	**16** (**1**)	99	126	113 (2)
Gymnorhina tibicen	313	81 (1)	260	**10** (**0**)
Passer domesticus	44	**14** (**1**)	200	49 (1)
Prunella modularis	210	98 (1)	50	**46** (**1**)
Sturnus vulgaris	125 (2)	169	298	**109** (**2**)
Turdus merula	477	**138** (**2**)	–	170 (2)
Turdus philomelos	299	145 (2)	**8** (**0**)	125

The score using Green's (1997) system is shown in parentheses for each of the two islands (NI and SI). The score used for the combined island test is shown in boldface. For successful species we used the minimum propagule that Duncan (1997) listed as successful

Cby Canterbury, *Ota* Otago, *Wel* Wellington, *Auc* Auckland, *SI* South Island

Table 2 Numbers of individuals of unsuccessful species released by four Acclimatization Societies

Species	Cby (SI)	Ota (SI)	Wel (NI)	Auc (NI)
Acridotheres tristis	18 (1)	–	**70** (**1**)	–
Agelaius phoeniceus	–	–	–	**2** (**0**)
Carduelis cannabina	**119** (**2**)	2	22	42 (1)
Carduelis flavirostris	21	**38** (**1**)	–	–
Carduelis spinus	**52** (**1**)	–	2 (0)	–
Corvus monedula	**5** (**0**)	–	–	–
Emberiza hortulana	–	–	**6** (**0**)	–
Emberiza schoeniclus	**7** (**0**)	4	–	–
Erithacus rubecula	–	**62** (**1**)	10 (0)	9
Fringilla montifringilla	**117** (**2**)	–	3 (0)	–
Lonchura castaneothorax	12 (1)	–	–	**27** (**1**)
Lonchura oryzivora	–	–	–	**6** (**0**)
Lonchura punctulata	–	–	–	**8** (**0**)
Lullula arborea	–	–	–	**5** (**0**)
Malurus cyaneus	–	–	–	**12** (**1**)
Manorina melanocephala	200* (2)	80	**224** (**2**)	–
Manorina melanophrys	–	–	**2** (**0**)	–
Neochmia temporalis	–	4 (0)	–	**12** (**1**)
Passer montanus	–	2 (0)	–	**12** (**1**)
Piranga rubra	–	–	–	**2** (**0**)
Pyrrhula pyrrhula	**2** (**0**)	–	–	–
Stagonopleura bella	–	–	**8** (**0**)	2
Stagonopleura guttata	–	–	**12** (**1**)	–
Sturnella neglecta	–	–	–	**2** (**0**)
Sylvia atricapilla	–	–	–	**5** (**0**)
Sylvia communis	–	–	–	**2** (**0**)
Taeniopygia guttata	–	–	**12** (**1**)	–
Grallina cyanoleuca	–	–	–	–
Luscinia megarhynchos				
Parus caeruleus	–	–	–	–

The score using Green's (1997) system is shown in parentheses for each of the two islands (NI and SI). The score used for the combined island test is shown in boldface. For unsuccessful species we used the maximum propagule that Duncan (1997) listed as unsuccessful

Cby Canterbury, *Ota* Otago, *Wel* Wellington, *Auc* Auckland, *SI* South Island

*Thomson (1922) listed 200 pairs (=400)

population', and unsuccessful otherwise (Cassey et al. 2005). However, we used the minimum propagule size listed by Duncan (1997) for each successfully introduced species for any of the four acclimatization societies, and the maximum number Duncan (1997) listed for any one of the four Acclimatization Societies for each unsuccessfully introduced species. Our reasons for these two assumptions are simple. First, we agree with the idea of treating the four societies separately. Second, species would be considered successfully introduced to New Zealand so long as they succeeded in any one of the four acclimatization districts. Additional releases of successful species would therefore be superfluous, and additional establishment events, all with propagule numbers above the minimum threshold for success, tell us little about the importance of initial propagule size. Species would be considered unsuccessfully introduced to New Zealand if every attempt to introduce the species in the four districts ended in failure. Clearly, for successfully introduced species the smallest successful propagule in any of the districts listed by Duncan (1997) must have been adequate for the species to be considered successfully introduced to New Zealand. And, it must also be true that even the largest propagule in any of the four districts for unsuccessful species was inadequate for the species to be successful.

To compensate for differences across studies (Veltman et al. 1996; Duncan 1997) in the numbers of individuals released per species, we followed Green (1997) and Cassey et al. (2005) and assigned scores to propagule sizes using the following scoring scheme: 0 = 2–10 individuals; 1 = 11–100 individuals; 2 = >100 individuals. We compared scores for successful versus unsuccessful species using Duncan's (1997) list (42 species) and Green's (1997) list (28 species). We did our tests combining the North and South Islands, as well as just within the North and South islands. Our reasons for conducting separate tests for the two main islands stems from the fat that they differ in climatic factors such as mean annual rainfall and temperature (Coulter 1973) as well as in terms of soils, landforms and natural vegetation (Cochrane 1973) all of which could impact introduction fates.

We also performed the combined island tests and for the North Island tests, treating the Common Myna as successful and additionally as unsuccessful. Duncan (1997) listed that the Common Myna as unsuccessful in Canterbury, Wellington and Otago, whereas Green (1997) listed the Common Myna as successfully introduced to New Zealand. We used Kruskal–Wallis tests for all of our comparisons.

Results

The lists of species used by, Long (1981), Veltman et al. (1996), Green (1997) and Duncan (1997) did not agree (See Appendix). The numbers of individuals released per species also did not agree. Thomson (1922) listed 47 passerine species, but he noted that one of these (*Serinus canaria*) was a common cage bird and likely not the subject of any serious introduction attempts. Two additional species (*Hirundo neoxena* and *Zosterops lateralis*) listed by Thomson (1922) presumably could have arrived in New Zealand (from Australia) without human assistance. If we exclude these three species Thomson's (1922) list comes to 44 species. To this roster, Long (1981) added two species: *Malurus cyaneus*—released in 1923 (Westerskov 1953), and *Pycnonotus cafer*—reported in the 1950s (Oliver 1955). As the government of New Zealand took steps to eradicate *Pycnonotus cafer* (Oliver 1955), Veltman et al. (1996), Duncan (1997) and Green (1997) did not include it in their analyses. Both these latter species were released after publication of Thomson's (1922) book, and these bring the master list to 46 species. All the studies (Long 1981; Veltman et al. 1996; Duncan 1997; Green 1997) excluded Thomson's (1922) 'Australian Shrike' (as the species was unknown), Long (1981), Veltman et al. (1996) and Green (1997) also excluded '*Zonaeginthus bella*' (=*Stagonopleura bella*).

Veltman et al. (1996) included 39 passerine species in their analyses and Duncan (1997) included 41. Duncan (1997) listed *Parus caeruleus* but as he had no data for this species, he excluded it from his analyses. In contrast, Green (1997) included just 28 passerine species. Veltman et al. (1996) excluded four species in addition to the Australian Shrike: *Parus caeruleus*; *Malurus cyaneus*; *Pycnonotus cafer*; and *Stagonopleura bella*, and they included *Luscinia megarhynchos*, although Green (1997) and Duncan (1997) did not.

Green (1997) used essentially the same references (Long 1981) as Duncan (1997) and excluded 14 species from Duncan's (1997) list of 42 species. For 10 of the species Green (1997) excluded, Long (1981) reported that there was evidence that the species were not actually released into the wild: *Agelaius phoeniceus*; *Lonchura punctulata*; *Lonchura oryzivora*; *Lullula arborea*; *Manorina melanophrys*; *Neochmia temporalis*; *Parus caeruleus*; *Sturnella neglecta*; *Sylvia atricapilla*; and *Taeniopygia guttata*. Green (1997) also excluded three species: *Corvus monedula*; *Pyrrhula pyrrhula*; and *Stagonopleura guttata*. And Green (1997) likely excluded (*Stagonopleura bella*) as Long (1981) did not include it.

Fifteen species succeeded in New Zealand on one or both of the main islands and as many as 27 failed (Tables 1, 2). With one exception (*Acridotheres tristis*), species either always succeeded or always failed on both the North and South Islands. Thus, 14 species succeeded on both islands in all four acclimatization districts used by Duncan (1997). Veltman et al. (1996) summed the numbers of individuals listed for each species for all of New Zealand and used this sum as their metric of introduction effort. Green (1997) used the largest number of individuals released in a single event within a 10-year period. Duncan (1997) limited his study to passerine introductions in each of four acclimatization districts: two on the North Island (Auckland, and Wellington) and two on the South Island (Canterbury and Otago).

Since Green (1997) did not use raw numbers, we cannot directly compare his results to those of Veltman et al. (1996) or Duncan (1997). However, we can compare the numbers used by Veltman et al. (1996) with those of Duncan (1997). For 26 species of 42 species (62%), the number released listed by Veltman et al. (1996) and Duncan (1997) do not agree, although in most cases they are very close (Tables 3, 4).

The expectation in this comparison would be that any differences between the two studies would be in the direction of more individuals in the study by Veltman et al. (1996) as those authors included all of New Zealand, whereas Duncan (1997) limited his analyses to the introductions of just four Acclimatization Societies. Indeed, Veltman et al. (1996) list more individuals than Duncan (1997) for only 13 of the 26 species that differed. However, for the other 13 species Duncan (1997) reported more individuals being released by the four Acclimatization Societies than Veltman et al. (1996). If the same scoring

Table 3 Scores (Green 1997) and numbers of individuals for successfully introduced passerine species used by Duncan (1997) the sum of the four columns, Veltman et al. (1996)

Species	Green	Duncan[a]	Veltman
Alauda arvensis	2	704	391
Carduelis carduelis	2	615	626
Carduelis chloris	1	83	65
Carduelis flammea	2	618	607
Corvus frugilegus	2	102	182
Emberiza cirlus	0	11	29
Emberiza citrinella	2	620	656
Fringilla coelebs	2	354	449
Gymnorhina tibicen	2	664	448
Passer domesticus	2	307	416
Prunella modularis	2	404	245
Sturnus vulgaris	2	701	653
Turdus merula	2	785	596
Turdus philomelos	2	577	343

[a] Duncan (1997) performed his analyses using separate Acclimatization Societies. The number shown here is the sum over the four societies he used and presented here only for comparative purposes

Table 4 Scores (Green 1997) and numbers of individuals for unsuccessfully introduced passerine species used by Duncan (1997) the sum of the four columns in, Tables 1 and 2, Veltman et al. (1996)

Species	Green	Duncan[a]	Veltman
Acridotheres tristis[b]	1	88	88
Agelaius phoeniceus	0	2	2
Carduelis cannabina	1	185	209
Carduelis flavirostris	1	59	61
Carduelis spinus	0	54	54
Corvus monedula	–	5	3
Emberiza hortulana	0	6	6
Emberiza schoeniclus	0	11	9
Erithacus rubecula	1	81	123
Fringilla montifringilla	–	120	121
Lonchura castaneothorax	1	39	45
Lonchura oryzivora	–	6	6
Lonchura punctulata	–	8	8
Lullula arborea	–	5	5
Malurus cyaneus	1	12	–
Manorina melanocephala[c]	2	504	80
Manorina melanophrys	–	2	2
Neochmia temporalis	–	16	14
Passer montanus	1	14	14
Piranga rubra	0	2	2
Pyrrhula pyrrhula	–	2	NA
Stagonopleura bella	–	10	–
Stagonopleura guttata	–	12	112
Sturnella neglecta	–	2	2
Sylvia atricapilla	–	5	5
Sylvia communis	0	2	2
Taeniopygia guttata	–	12	12
Grallina cyanoleuca	–	–	NA
Luscinia megarhynchos	–	–	7
Parus caeruleus[d]	–	NA	–

[a] See Table 1

[b] Green (1997) and Veltman et al. (1996) treated *Acridotheres tristis* as successful

[c] Thomson (1922) lists 200 pairs = 400 individuals but Duncan (1997) and Lamb (1964) reported the number to be 200 individuals

[d] Duncan (1997) listed *Parus caeruleus* as having been introduced to New Zealand but no numbers were available

–, Not included in analyses

NA Listed but not included in analysis

system used by Green (1997) is applied to the raw numbers listed in Veltman et al. (1996) and Duncan (1997) many of the differences are eliminated. The scores assigned using Green's (1997) system are unchanged for all 15 of the successfully introduced species (assuming that *Acridotheres tristis* was successful), but for five of the 28 (=18%)

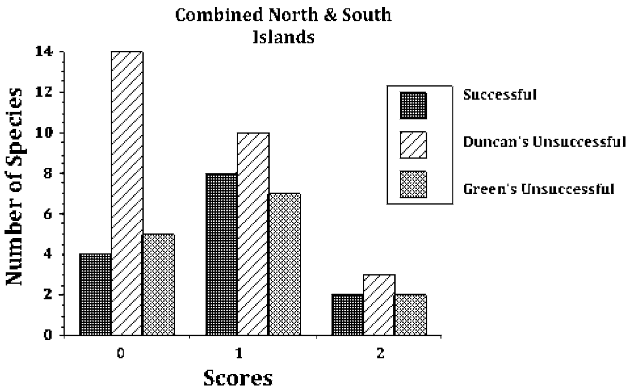

Fig. 2 Combined island distribution of scores for successful and unsuccessful introductions using scores based on numbers from Duncan (1997) and Green (1997); *0* 2–10 individuals, *1* 11–100 individuals, *2* >100 individuals

unsuccessful species (*Emberiza schoeniclus*, *Erithacus rubecula*, *Manorina melanocephala*, *Stagonopleura guttata*, *Luscinia megarhynchos*) the scores are not the same (Tables 3, 4).

In our first set of tests (Fig. 2) we used the overall list of 41 species analyzed by Duncan (1997). Recall that Duncan (1997) included one species (*Parus caeruleus*) in his list of 42 species, but had no data for it, so his analysis is limited to 41 species. The scores for the minimum successful propagule sizes for the combined North and South Islands did not differ significantly from the maximum propagule sizes for the unsuccessful species (Kruskal–Wallis, approximate $\chi^2 = 1.61$, $P > \chi^2 = 0.20$). When we conducted the test on the shortened list of 28 species used by Green (1997) the scores were also not significantly different (Kruskal–Wallis, approximate $\chi^2 = 0.06$, $P > \chi^2 = 0.80$).

We then tested to see if a pattern appeared within the North or South Islands when treated separately. For the North Island (Fig. 3), using Duncan's (1997) list the scores were significantly different (Kruskal–Wallis, approximate $\chi^2 = 5.00$, $P > \chi^2 = 0.03$), but were not significantly different when we used Green's (1997) list (Kruskal–Wallis, approximate $\chi^2 = 1.92$, $P > \chi^2 = 0.17$). For the South Island (Fig. 4), the scores were marginally different when we used Duncan's (1997) list (Kruskal–Wallis, approximate $\chi^2 = 2.89$, $P > \chi^2 = 0.09$), but not when we used Green's (1997) list (Kruskal–Wallis, approximate $\chi^2 = 0.67$, $P > \chi^2 = 0.41$) (Fig. 4).

In our first set of tests, we followed Duncan (1997) and treated *Acridotheres tristis* as having been unsuccessfully introduced to both Canterbury and Otago (South Island) and Wellington (North Island). However, both Veltman et al. (1996) and Green (1997) listed *Acridotheres tristis* as successful on the North Island, as did Heather and Robertson (1997), thus we repeated our North Island tests assuming the species was successful. For the combined islands test the scores between successful and unsuccessful species did not differ significantly using Duncan's (1997) list (Kruskal–Wallis, approximate $\chi^2 = 2.08$, $P > \chi^2 = 0.15$) or Green's (1997) list (Kruskal–Wallis, approximate $\chi^2 = 0.03$, $P > \chi^2 = 0.86$). We also compared scores for the North Island separately using both lists. When we used Duncan's (1997) list the scores for the North Island were significantly different (Kruskal–Wallis, approximate $\chi^2 = 5.90$, $P > \chi^2 = 0.01$). However, when we used Green's

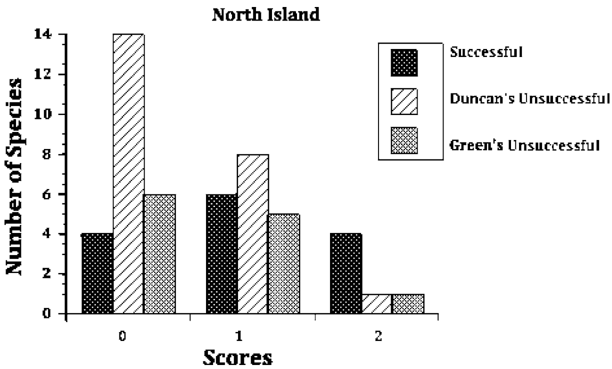

Fig. 3 North Island distribution of scores for successful and unsuccessful introductions using scores based on numbers from Duncan (1997) and Green (1997); *0* 2–10 individuals; *1* 11–100 individuals; *2* >100 individuals

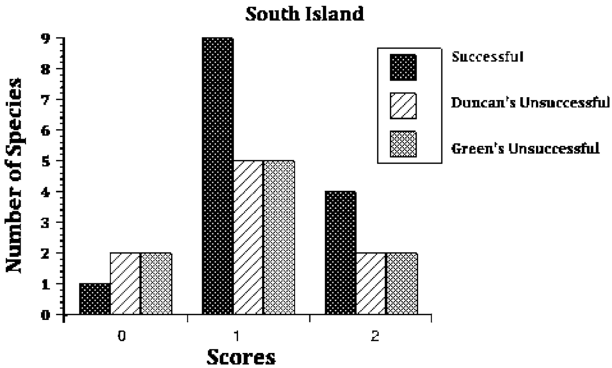

Fig. 4 South island distribution of scores for successful and unsuccessful introductions using scores based on numbers from Duncan (1997) and Green (1997); *0* 2–10 individuals; *1* 11–100 individuals; *2* >100 individuals

(1997) list the North Island scores were not significantly different (Kruskal–Wallis, Approximate $\chi^2 = 2.36$, $P > \chi^2 = 0.12$).

Scores on the South Island was marginally significantly when we used Duncan's (1997) list (Kruskal–Wallis, approximate $\chi^2 = 2.89$, $P > \chi^2 = 0.09$) but not when we used Green's (1997) list (Kruskal–Wallis, Approximate $\chi^2 = 0.67$, $P > \chi^2 = 0.41$).

Clearly the outcome of these tests approached significance only when we followed Duncan's (1997) expanded list including the 14 species that Green (1997) excluded due to lack of evidence for introduction, and only when we analyzed North Island separately, whether we treated *Acridotheres tristis* as successful or unsuccessful. Thus in summary, our 10 tests yielded one marginally significant and two clearly significant differences—*and* all three involved comparisons just within the North Island.

All three authors (Veltman et al. 1996; Duncan 1997; Green 1997) ultimately relied on a single reference—Thomson (1922). In a comparison of Duncan's (1997) data with that of Thomson (1922) we found no major differences in the Otago Society lists. For the Auckland Society Duncan (1997) reported that there were two releases and a total of 12 individuals of *Neochmia temporalis* released, but Thomson (1922) reported just one introduction in the Auckland district of four individuals. For the Wellington Society, Duncan (1997) included a release of four individuals of *Emberiza cirlus*, apparently citing Thomson (1926), but Thomson (1922) did not mention this release. Duncan (1997) also incorporated a release of 200 *Passer domesticus* in 1866 by the Wanganui Acclimatization Society under his Wellington roster. It is true that Buller (1888) stated that the Wanganui Society, of which he was then secretary of the society, advertized a premium for 100 pairs of this species to be delivered alive to Wanganui, and that "both the 'circular' (i.e., the advertisement) and the introduction were successful". Duncan (1997) assumed from this quotation in Buller (1888) that in fact 200 House Sparrows were indeed released in Wanganui. However, 20 years earlier Buller (1868) stated that the advertisement had not been successful after 2 years, as it apparently led to the introduction of just four *Passer domesticus*, but he noted that these individuals had nested successfully. Thus, it remains to be shown that any additional releases would have been needed for the establishment of this species or even if any were more were even released. Clearly alternative interpretations exist.

There were several differences between Duncan (1997) and Thomson (1922) for the Canterbury Society. Differences in numbers released per species between Duncan (1997), Thomson (1922) and Lamb (1964) are listed in Table 5 and differences in the dates of first introduction in Table 6.

Discussion

As with other historical reports (e.g., *Passer domesticus* in North America; Moulton et al. 2010), the records of passerine introductions to New Zealand are open to alternative interpretations. Passerine introductions to different acclimatization districts in New Zealand often involved species that had already been successfully introduced to other districts in New Zealand. Moreover, the birds were typically distributed among the members of the Acclimatization Societies and potentially released over a large area (Thomson 1922, 1926; Lamb 1964; Andersen 1916). We found that by using the minimum number of individuals released by any of the four acclimatization societies as listed as successful by Duncan (1997), and the maximum number for species he listed as unsuccessful, the relationship between propagule size and introduction outcome in New Zealand is not supported except under the very limited conditions of the questionably expanded list of 41 species and when the North Island is treated separately.

People have long recognized that the chances for introduction success in very small propagules are remote (e.g. Phillips 1928; Caughley 1983). However, evidence for the idea that the release of larger numbers of individuals of a species increases the chances for introduction success of that species (Lockwood et al. 2005; Simberloff 2009) is equivocal at best. Instead, we agree with Pimm (1991) who analyzed introductions of game birds to the United States and found a threshold in propagule size below which introductions inevitably failed and above which introductions had positive chances for success.

This begs the question as to why people in New Zealand in the nineteenth century would continue to release more individuals of species that had already been acclimatized? One reason was nostalgia (Thomson 1922) and another was the desperate need for biological control (Drummond 1907). Beyond this was the possibility that additional birds may well have been ordered before people knew that earlier releases of a species had been successful already.

Table 5 A comparison of the total number individuals reportedly released by the Canterbury Acclimatization Society according to Duncan (1997), Thomson (1922) and Lamb (1964)

Species	Duncan	Thomson	Lamb
Turdus merula	477	262	473
Corvus frugilegus	36	40	36
Alauda arvensis	434	31	28
Carduelis chloris[a]	32	–	–
Turdus philomelos	299	60	301
Gymnorhina tibicen	313	86	–
Lonchura castaneothorax	12	12	–
Stagonopleura guttata	X	–	–
Fringilla coelebs	16	16	11
Carduelis carduelis	265	95	265
Sturnus vulgaris	125	60	125
Carduelis cannabina	119	23	130[a]
Carduelis flammea	326	134	326
Prunella modularis	210	50	208
Passer domesticus	44	45	44
Fringilla montifringilla	117	8	117
Acridotheres tristis	18	18	–
Corvus monedula	5	1	5
Emberiza citrinella	236	35	237
Emberiza schoeniclus	7	0	7
Parus caeruleus	X	X	–
Pyrrhula pyrrhula	2	2	–
Erithacus rubecula	X	X	1
Manorina melanocephala[b]	200	400	–
Carduelis spinus	52	X	52
Carduelis flavirostris	21	0	21

An ‘X’ indicates that the author acknowledged an introduction but was unable to ascertain the propagule size

[a] Thomson (1922) says there is no record of this release in the Canterbury Society records

[b] See note in Table 2

Insect outbreaks were evidently a serious threat to agriculture in New Zealand. Drummond (1907) reported that a train was stopped after it had crushed so many caterpillars that the rails became too slick for the train to move. Drummond (1907) further related that a farmer used a flock of 1,600 sheep to crush an advancing army of caterpillars. Faced with such an onslaught of insects and their larvae, colonists had little alternative but to introduce birds from England and elsewhere that fit the criteria laid out by Drummond (1907); namely species with high reproductive rates, that did not migrate in winter, and above all else, that ate insects. But why did they release so many individuals in so many places? We believe that this would occur simply because of human perceptions. Thus, if a species was thought to eat insects in one district, people in other districts likely would have been eager to bring that species directly to their district. Why wait for what could be years

Table 6 A comparison of the first known dates of introduction for the Canterbury Acclimatization Society

Species	Th	An	La	Wi	Du
Turdus merula	1865	1872	1867	1865	1861[a]
Corvus frugilegus	1862	1871	1868	1862	1862
Alauda arvensis	1867	1863	1867	1863	1863
Carduelis chloris	1871	–	–	1863	1863
Turdus philomelos	1867	1863	1867	1866	1863
Gymnorhina tibicen	1864	–	–	1864	1864
Lonchura castaneothorax	1864	–	–	–	1864
Stagonopleura guttata	1864	–	–	–	1864
Fringilla coelebs	1867	–	1867	1865	1865
Carduelis carduelis	1871	1873	1872	1865	1865
Sturnus vulgaris	1867	1871	1867	1867	1867
Carduelis cannabina	1867	1873	1867	–	1867
Carduelis flammea	1868	1873	1868	1867	1868
Prunella modularis	1868	1873	1867[b]	1868	1868
Passer domesticus	1867	1877[c]	1868	1868	1868
Fringilla montifringilla	1868	–	1868	–	1868
Acridotheres tristis	1870	–	–	–	1871
Corvus monedula	1872?	–	1872	–	1872
Emberiza citrinella	1871	1875	1868	1866	1873
Emberiza schoeniclus	–	–	1873	–	1873
Parus caeruleus	1874	–	–	–	1874
Pyrrhula pyrrhula	1875	–	–	–	1875
Erithacus rubecula	1879	–	–	–	1879
Manorina melanocephala	1879	–	–	–	1879
Carduelis spinus	1879	–	1880	–	1879
Carduelis flavirostris	–	–	1880	–	1880

[a] The earliest date we could find for *Turdus merula* in any of the references Duncan (1997) listed was 1865

[b] A single *Prunella modularis* landed in 1867 (Williams 1969; Duncan 1997) ignored releases of single individuals

[c] Andersen's (1916) date here refers only to the first observation of *Passer domesticus* in South Canterbury

Th Thomson (1922), *An* Andersen (1916), *La* Lamb (1964), *Wi* Williams (1969), *Du* Duncan (1997)

–, No information

for the species to spread to their district? And why would people on the North Island risk the chance that beneficial birds introduced to the South Island might not cross to the North Island?

The historical record of bird introductions to New Zealand, however, doesn't support the primacy of propagule pressure, or rather, as characterized by Duncan et al. (2003), event-level factors over site-level factors or species-level factors. Our results support the alternative idea that non-native passerine species were successful in New Zealand not because they were introduced in large numbers, but rather species were introduced in high numbers because the initial releases were perceived to be successful and useful.

Our conclusions are compelling for two reasons. First the historical record of bird introductions to New Zealand as set out by Thomson (1922) has been highly touted (e.g.

Blackburn et al. 2009) as ‘unusually thorough and clear’. Indeed it is this very record of New Zealand introductions that has fueled the widespread and apparently uncritically accepted notion (e.g. Blackburn et al. 2009; Lockwood et al. 2005) that propagule pressure is more important than any species-level or site level factors. But as we have shown the record is open to other interpretations. Secondly, we argue that a potential danger lies in ignoring other factors including species-level characters such as relative brain size (Sol et al. 2005), demographic factors (Wilson et al. in press) or site-level factors such as food web structure (e.g. Baiser et al. 2010) or interspecific competition (Gamarra et al. 2005).

Acknowledgments We thank Stuart Pimm, Kyle Van Houtan and anonymous reviewers for very helpful comments on the manuscript.

Appendix

See Table 7.

Table 7 Lists of passeriform species introduced to New Zealand from five studies

Species	A	B	C	D	E
Acridotheres tristis	Yes	Yes	Yes	Yes	Yes
Agelaius phoeniceus	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Alauda arvensis	Yes	Yes	Yes	Yes	Yes
‘*Australian Shrike*’	***Yes***	***No***	***No***	***No***	***No***
Carduelis cannabina	Yes	Yes	Yes	Yes	Yes
Carduelis carduelis	Yes	Yes	Yes	Yes	Yes
Carduelis chloris	Yes	Yes	Yes	Yes	Yes
Carduelis flammea	Yes	Yes	Yes	Yes	Yes
Carduelis flavirostris	Yes	Yes	Yes	Yes	Yes
Carduelis spinus	Yes	Yes	Yes	Yes	Yes
Corvus frugilegus	Yes	Yes	Yes	Yes	Yes
Corvus monedula	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Emberiza cirlus	Yes	Yes	Yes	Yes	Yes
Emberiza citrinella	Yes	Yes	Yes	Yes	Yes
Emberiza hortulana	Yes	Yes	Yes	Yes	Yes
Emberiza schoeniclus	Yes	Yes	Yes	Yes	Yes
Erithacus rubecula	Yes	Yes	Yes	Yes	Yes
Fringilla coelebs	Yes	Yes	Yes	Yes	Yes
Fringilla montifringilla	Yes	Yes	Yes	Yes	Yes
Grallina cyanoleuca	**Yes**	**Yes**	**No**	**Yes**	**No**
Gymnorhina tibicen	Yes	Yes	Yes	Yes	Yes
Hirundo neoxena[a]	Yes	No	No	No	No
Lonchura castaneothorax	Yes	Yes	Yes	Yes	Yes
Lonchura oryzivora	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Lonchura punctulata	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Lullula arborea	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Luscinia megarhynchos	**Yes**	**Yes**	**No**	**Yes**	**No**

Table 7 continued

Species	A	B	C	D	E
Malurus cyaneus	**No**	**Yes**	**Yes**	**No**	**Yes**
Manorina melanocephala	Yes	Yes	Yes	Yes	Yes
Manorina melanophrys	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Neochmia temporalis	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Parus caeruleus	**Yes**	**Yes**	**No**	**No**	**Yes**
Passer domesticus	Yes	Yes	Yes	Yes	Yes
Passer montanus	Yes	Yes	Yes	Yes	Yes
Piranga rubra	Yes	Yes	Yes	Yes	Yes
Poephila guttata	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Prunella modularis	Yes	Yes	Yes	Yes	Yes
Pycnonotus cafer	**No**	**Yes**	**No**	**No**	**No**
Pyrrhula pyrrhula	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Serinus canaria (caged only?)	**Yes**	**No**	**No**	**No**	**No**
Stagonopleura bella	**Yes**	**No**	**No**	**No**	**Yes**
Stagonopleura guttata	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Sturnella neglecta	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Sturnus vulgaris	Yes	Yes	Yes	Yes	Yes
Sylvia atricapilla	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Sylvia communis	Yes	Yes	Yes	Yes	Yes
Turdus merula	Yes	Yes	Yes	Yes	Yes
Turdus philomelos	Yes	Yes	Yes	Yes	Yes
Zosterops lateralis[b]	Yes	No	No	No	No

Bold text indicates that the different studies do not agree

[a] Thomson (1922) believed the records of *Hirundo neoxena* involved natural visitors

[b] Thomson (1922) believed that *Zosterops lateralis* was likely a "comparatively modern natural introduction" from Australia

A Thomson (1922), *B* Long (1981), *C* Green (1997), *D* Veltman et al. (1996), *E* Duncan (1997)

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