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Is propagule size the critical factor in predicting introduction outcomes in passeriform birds?

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Abstract Influential analyses of the propagule pressure hypothesis have been based on multiple bird species introduced to one region (e.g. New Zealand). These analyses implicitly assume that species-level and site-level characteristics are less important than the number of individuals released. In this study we compared records of passerine introductions with propagule size information across multiple regions (New Zealand, Australia, and North America). We excluded species introduced to just one of the three regions or with significant uncertainty in the historical record, as well as species that succeeded or failed in all regions. Because it is often impossible to attribute success to any single event or combination of events, our analysis compared randomly selected propagule sizes of unsuccessful introductions with those of successful introductions. Using Monte Carlo repeated sampling we found no statistical support for the propagule pressure hypothesis, even when using assumptions biased toward showing an effect.

Keywords Introduced species · Passeriforms birds · Propagule pressure

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Introduction

Several authors have argued that propagule pressure, commonly defined as the total number of individuals introduced in a new place, is the primary determinant of the outcome of the introduction (e.g. Duncan 1997; Green 1997; Lockwood et al. 2005, 2009; Blackburn et al. 2009a, b, 2011; Simberloff 2009). In a series of recent papers, Moulton et al. (2010, 2011, 2012a, b) argued that a more straightforward alternative interpretation of the historical record of passeriform introductions fails to support the propagule pressure hypothesis.

On the surface, the idea that propagule size is the primary determinant of introduction outcomes is compelling for two reasons. First, small populations are believed to be more vulnerable to extinction, although many examples exist of successful introductions from small founder populations indicating that the actual risk is variable and likely a function of species' characteristics, site characteristics, and health and condition of the introduced individuals

(Simberloff 2009). Second, tests of the propagule pressure hypothesis have involved simply tallying the total number of individuals of a species released over multiple introduction events or the number of releases of that species in a place. The assumption here is that all the introductions were required for establishment. Potentially significant species-level and site-level factors have not been properly assessed through analyses of historical reports. Unfortunately, except for species introduced to New Zealand, there is very little information on the number of individuals released or on the number of releases of most passeriform introductions (Blackburn et al. 2009a). Moreover, what information does exist comes primarily from just three regions: New Zealand (Veltman et al. 1996; Duncan 1997; Green 1997); Australia (Newsome and Noble 1986); and North America, meaning the United States and Canada (Phillips 1928; Long 1981).

Newsome and Noble (1986) reported that successfully introduced birds in Australia had been introduced in higher numbers than unsuccessful species. Veltman et al. (1996), Duncan (1997) and Green (1997) reported a similar pattern for birds introduced to New Zealand. Duncan (1997) went two steps further in his analysis of introduced New Zealand passeriforms. First, he argued that introduction effort (propagule pressure) was not just associated with, but rather a determinant of, introduction outcomes for passeriform birds released in New Zealand. Second, he claimed that competitive patterns reported among introduced passeriform birds in the Hawaiian Islands (Moulton and Pimm 1983, 1986a, b, 1987; Moulton 1985, 1993; Moulton and Lockwood 1992), Bermuda (Lockwood and Moulton 1994), Tahiti (Lockwood et al. 1993), and Saint Helena (Brooke et al. 1995) could merely be the result of differences in introduction effort.

The analyses of Veltman et al. (1996), Duncan (1997), and Green (1997) have been repeatedly interpreted as supporting the propagule pressure hypothesis for birds. Cassey et al. (2004, 2005), Lockwood et al. (2005, 2009), Blackburn et al. (2009a), and Simberloff (2009) all argued that increased numbers of individuals released per species increases the chances for establishment success. Further supporting evidence supposedly has come from the oft-cited account of the earliest House Sparrow (*Passer domesticus*) introductions to North America (e.g. Simberloff and Boecklen 1991, Simberloff 2009), a story shown to be unsupported by the historical record (Moulton et al. 2010), and by genetic analysis (Schrey et al. 2011).

Moulton et al. (2011, 2012b) recently showed that reports of passeriform bird introductions to New Zealand (Veltman et al. 1996; Duncan 1997; Green 1997; Blackburn et al. 2011), using the data sets published in each study, fail to support the propagule pressure hypothesis except when additional, and likely superfluous, introductions following successful establishment are included in the summed propagules. Moreover, several questionable assumptions must be made regarding which species were actually introduced in order for a significant propagule pressure effect to occur. Moulton et al. (2012b) made essentially the same case questioning the role of propagule pressure based on the historical record reported for Australia, as presented by Newsome and Noble (1986).

Perhaps an equally serious problem with the abovementioned analyses for New Zealand and Australia is that they tout the singular influence of propagule pressure, but only use interspecific comparisons within a single region, thus assuming that any particular propagule size affects the probability of success of all species equally.

A more direct test of the propagule pressure hypothesis involves comparing the outcomes of individual species released into multiple areas. If propagule pressure is indeed the most important consideration then species that succeed in some places but not others, should be most likely to succeed in those places where they were released in higher numbers.

Materials and methods

Ideally for our analysis we would compare propagule sizes for as many species as possible across as many locations as possible. Unfortunately, it is soon apparent among passerine birds that most introduction events have no propagule size information. A second complication is that for several species there were multiple introduction events and it is impossible in most cases to evaluate the outcomes of the individual releases. Moreover, different authors for the different regions commonly reported different propagule information for the same species (Moulton et al. 2011, 2012b).

Limitations of the data

The limitations of the data are clearly visible on inspection of the compendium authored by Long (1981), who listed approximately 1,048 introduction events for 208 species of passeriform birds around the world. We say 'approximately' for several reasons. First, Long (1981) pooled introductions of some species at some sites. For example, for the European Starling (*Sturnus vulgaris*) in New Zealand, Long (1981) simply stated that at least 653 individuals were released by the Nelson, Canterbury, Otago, Auckland, and Wellington acclimatization societies between 1862 and 1883. Second, Long (1981) sometimes listed the same vague record under more than one species. Thus, Long (1981) includes the 300 'sparrows' reportedly brought to New Zealand in 1859 (Hargreaves 1943) under the species accounts for both the Hedge Sparrow (*Prunella modularis*) and the House Sparrow. Third, Long (1981) listed several species that he was not certain were actually released. In fact, Green (1997), using Long (1981) as his primary reference for historical introductions to New Zealand, included just 28 of the 42 passeriform species listed by Duncan (1997). Long (1981) also listed introductions of a single individual for some species (e.g. *Sturnus nigricollis* to Oahu), which would not represent true introductions. Finally, as many historical records included only common names, Long (1981) sometimes incorrectly guessed the actual identity of the species (Moulton et al. 2012b).

Long (1981) listed information on propagule size for just 57 of the 208 introduced passeriform species (Table 1). These 57 species account for 291 of the total 1,048 releases (27.7 %) he listed. To this list we added an additional release of the Rook (*Corvus frugilegus*), which was apparently introduced to Victoria, Australia (Jenkins 1977) as well as to New Zealand. Of the resulting 292 releases, 268 (91.7 %) include propagule information and involved just three regions (Table 1): New Zealand (155 releases of 33 species); Australia (70 releases of 23 species) and North America (United States and southwestern British Columbia, 43 releases of 18 species).

As noted above, more than one author compiled lists of species and propagule sizes within each region. Thus, for New Zealand we used compilations by Thomson (1922), Lamb (1964) and Duncan 1997. For Australia, we used Jenkins (1977), Balmford (1978)

Table 1 A list of 57 passeriform species with propagule information according to the compilation of Long (1981) and Moulton et al. (2011, 2012b)

Species	AU	NZ	NA	Other
Group A				
Alauda arvensis	9	11	12	0
Sturnus vulgaris	6	1	3	1
Turdus merula	6	12	2	0
Turdus philomelos	5	10	1	0
*Erithacus rubecula**	3	7	2	0
*Passer domesticus***	6	7	3	3
Passer montanus	2	2	1	0
Fringilla coelebs	3	8	3	0
Carduelis chloris	4	4	1	0
*Carduelis spinus**	3	1	1	0
Carduelis carduelis	4	5	3	0
*Carduelis cannabina**	2	1	1	0
Group B				
Corvus frugilegus	1	6	0	0
Acridotheres tristis	4	2	0	3
*Lonchura oryzivora**	1	1	0	0
*Fringilla montifringilla**	1	4	0	0
*Pyrrhula pyrrhula**	1	0	1	0
Emberiza citrinella	2	6	0	0
*Emberiza hortulana**	1	1	0	0
Group C				
Menura novaehollandidae	3	0	0	0
Leiothrix lutea	1	0	0	1
Luscinia megarhynchos	1	0	0	0
Serinus canaria	1	0	0	1
Group D				
Xenicus longipes	0	1	0	0
Lonchura castaneothorax	0	4	0	0
Malurus cyaneus	0	1	0	0
Prunella modularis	0	13	0	0
Carduelis flammea	0	8	0	0
Carduelis flavirostris	0	2	0	0
Emberiza cirlus	0	3	0	0
Emberiza schoeniclus	0	1	0	0
Piranga rubra	0	1	0	0
Corvus monedula	0	1	0	0
Sylvia communis	0	1	0	0
Stagonopleura guttata	0	2	0	0
Gymnorhina tibicen	0	4	0	0
Manorhina melanocephala	0	5	0	0
Philesturnus carunculatus	0	19	0	0

Table 1 continued

Species	AU	NZ	NA	Other
Group E				
Lullula arborea	0	0	2	0
Sylvia atricapilla	0	0	2	0
Mimus polyglottos	0	0	2	0
Turdus iliacus	0	0	2	0
Loxia pytyopsittacus	0	0	1	0
Group F				
Pitangus sulphuratus	0	0	0	1
Paradisaea apoda	0	0	0	1
Pycnonotus cafer	0	0	0	1
Gracula religiosa	0	0	0	1
Sturnus nigricollis	0	0	0	1
Sialia mexicana	0	0	0	1
Copsychus saularis	0	0	0	1
Foudia sechellarum	0	0	0	1
Amandava amandava	0	0	0	1
Erythrura gouldiae	0	0	0	1
Telespyza cantans	0	0	0	2
Telespyza ultima	0	0	0	1
Zonotrichia capensis	0	0	0	1
Euphonia musica	0	0	0	1

The number of releases with propagule information is given for each species in various regions (*AU* Australia, *NZ* New Zealand, *NA* North America, Other = places other than Australia, New Zealand or North America) by group: Group A—species released in all three regions; Group B—species in two of the three regions; Group C—species just in Australia; Group D—species just in New Zealand; Group E—species just in Canada and the USA; Group F—species with information from elsewhere. Species marked with a single asterisk failed in all regions, a double asterisk indicates the species succeeded in all regions

and Ryan (1906). For North America we used Phillips (1928), Sprot (1937), Pfluger (1896a, b, c, d, e, f, g, 1897), Cleaveland (1866), and Forbush (1915).

Within regions, different authors examining presumably the same records reported different propagule sizes for the same species. In the absence of agreement among the various sources, and uncertainty over which releases were necessary for establishment, we opted for a repeated sampling analysis. We listed all the reported introductions and propagules sizes for species within region by author and then removed all obvious duplicate listings.

As our goal was to compare the propagule sizes of the same introduced species across three major geographic area we excluded 14 species with propagule information from somewhere other than Australia, New Zealand or North America (Table 1, Group F). We also excluded species with propagule information for just one of the three regions (Table 1; Groups C, D, E), and species that either always succeeded or failed regardless of propagule size. The most parsimonious explanation of species that always succeeded or always failed is that site-level or species-level characteristics were more important than the numbers released.

These exclusions (Table 1, Groups A and B) left just 11 species that showed a mixed outcome across the three regions. Two species (*Acridotheres tristis* and *Passer montanus*) failed in New Zealand but succeeded in either Australia or North America. Three species (*Corvus frugilegus, Emberiza citrinella and Fringilla coelebs*) failed either in Australia or North America, but succeeded in New Zealand. Three species (*Carduelis chloris, Turdus merula, and Turdus philomelos*) all failed in North America but succeeded in Australia and New Zealand. Within Australia, *Carduelis carduelis* and *Alauda arvensis* failed in Western Australia, but succeeded in Victoria (Jenkins 1977). Within North America, the Eurasian Skylark failed in the New York City area and in California, but succeeded on Vancouver Island (Sprot 1937). Also within North America, *Sturnus vulgaris* failed in the Portland, Oregon area (Jewett and Gabrielson 1929; Lord 1902) but succeeded in the New York (Forbush 1915).

Propagule information was available for just one species (Eurasian Skylark) on Vancouver Island (Sprot 1937) and we were unable to find any propagule size information for any of the species supposedly introduced to the Cincinnati, Ohio area even though Phillips (1928) and Long (1981) reported that several introductions occurred there in the late nineteenth century. Phillips (1928) lists failed introductions of "about 200" Skylarks to Santa Cruz County California and 150 ("75 pairs") to San Jose 12 years earlier. For introductions to the Greenwood Cemetery in Brooklyn, New York we included reports by Cleaveland (1866), and for Portland, Oregon we used the series of reports by Pfluger (1896a, b, c, d, e, f, g, 1897), as well as Jewett and Gabrielson (1929) and Lord (1902).

Because the historical record does not allow us to attribute success to any single event or combination of events, we used repeated (100,000) sampling of randomly chosen introduction events for each species, from the list of successful and from unsuccessful introductions.

We conducted our analysis in two ways. First, we randomly selected a single release for each species from the pool of all successful reported releases for that species, and one from the pool of all reported unsuccessful releases. We excluded six events of a single individual release, although it is possible that the excluded individual successfully bred with individuals from other release events. For each iteration, we conducted a Kruskal–Wallis test and calculated the associated approximate X^2. If propagule pressure is truly an important force, we would expect a large proportion of these random X^2 values to be significantly greater than expected by chance (i.e. $p > X^2 < 0.05$). Our first test assumed that a single introduction event of more than a single individual per species could determine establishment fate. Other authors have argued that propagule pressure involves all the introductions of a species. Therefore as a second test, we repeated our analysis using subsets from the propagule reports within regions (Australia, New Zealand, and North America). Each species entry in the comparison table (Table 2) could be randomly selected as an individual event or as a sum of any two up to all of the individual events within a region (Figs. 1, 2).

Results

For the eleven species included, 185 releases were reported as successful and 33 as unsuccessful (Table 2). Unfortunately, in most cases it is not possible to determine the outcomes of individual releases. Thus, for unsuccessfully introduced species in a region we treated all releases of that species as unsuccessful and for successfully introduced species with multiple releases to a region, we treated each release as successful.

In our first test, we generated 100,000 randomizations by selecting a single introduction event for each species for both successful and unsuccessful introductions. For each randomization we calculated a Kruskal–Wallis approximate X^2. Of the 100,000

Table 2 Reported releases for 11 passerine species to three regions

Species	Fate	Release reports
Alauda arvensis		
Nelson (Thomson 1922)	1	20;
Otago (Thomson 1922)	1	4; 35; 61
Canterbury (Lamb 1964)	1	(13); (15)
Canterbury (Thomson 1922)	1	13; 18
Auckland (Thomson 1922)	1	10; 52
Wellington (Thomson 1922)	1	52; 56
Victoria (Jenkins 1977)	1	6: 12; 6: 4; 4; 4; 25; 80
South Australia (Jenkins 1977)	1	18: 44; 18; 147; 36; 2
Western Australia (Jenkins 1977)	0	100
Victoria (Ryan 1906)	1	(*80*); 30; 30; 100
Victoria (Balmford 1978)	1	*(6); (4); (4); (25)*
Victoria (Balmford—Argus)	1	7; 3; 43
Brooklyn (Cleaveland 1866)	0	48
New York; Brooklyn (Phillips 1928)	0	74; 100
Oregon (Phillips 1928)	0	*(100)*
California (Phillips 1928)	0	200; 150
Oregon (Pfluger 1897)	0	100
Vancouver (Sprot 1937)	1	100
Fringilla coelebs		
Nelson (Thomson 1922)	1	23
Otago (Thomson 1922)	1	27; 6; 66
Canterbury (Lamb 1964)	1	11
Canterbury (Thomson 1922)	1	*(11);* 5
Auckland (Thomson 1922)	1	45; 68
Wellington (Thomson 1922)	1	70; 36; 20
Victoria (Jenkins 1977)	0	*(40)*
South Australia (Jenkins 1977)	0	3
Australia, Victoria (Ryan 1906)	0	50; *(40);* 40
Australia, Victoria (Balmford 1978)	0	40
New York City (Phillips 1928)	0	60
Oregon (Pfluger 1896g)	0	80; 40; 40
Cardeulis carduelis		
Nelson (Thomson 1922)	1	10
Otago (Thomson 1922)	1	3; 30; 54; 31
Canterbury (Lamb 1964)	1	60; 95; 110
Canterbury (Thomson 1922)	1	*(95)*
Auckland (Thomson 1922)	1	11; 44
Wellington (Thomson 1922)[a]	1	1; 52; 22; 103
Victoria (Jenkins 1977)	1	12
South Australia (Jenkins 1977)	1	5; 43; 30; 50; 30
Western Australia (Jenkins 1977)	0	200

Table 2 continued

Species	Fate	Release reports
Victoria (Ryan 1906)	1	34; 20
Brooklyn (Cleaveland 1866)	0	48
Oregon (Pfluger 1896g)	0	80
Sturnus vulgaris		
Nelson (Thomson 1922)	1	17
Otago (Thomson 1922)	1	3; 81; 85
Canterbury (Lamb 1964)	1	20; 32; 40; 33
Canterbury (Thomson 1922)	1	*(20); (40)*
Auckland (Thomson 1922)	1	12; 15; 82
Wellington (Thomson 1922)	1	60; 90; 14; 100; 34
Victoria (Jenkins 1977)	1	6; 36; 120; 6
South Australia (Jenkins 1977)	1	44; 45
Australia, Victoria (Ryan 1906)	1	*(36); (6);* 15; 20
Australia, Victoria (Balmford 1978)	1	*(6); (6)*
New York City (Forbush 1915)	1	80; 40
Portland, Oregon (Pfluger 1896e)	0	70
Turdus merula		
Nelson (Thomson 1922)	1	26
Otago (Thomson 1922)	1	2; 6; 39; 21; 70
Canterbury (Lamb 1964)	1	46; 153; 95; 62; 117
Canterbury (Thomson 1922)	1	2; *(46); (152); (62)*
Auckland (Thomson 1922)	1	8; 30; 132
Victoria (Jenkins 1977)	1	18; 4; 10; 6; 12
South Australia (Jenkins 1977)[a]	1	1;2;2;15
Victoria (Ryan 1906)	1	*(6); (17);* 22
Victoria (Balmford 1978)	1	*(18); (6)*
Victoria (Balmford—Argus)	1	37; 2; 36
Brooklyn (Cleaveland 1866)	0	12
Portland, Oregon (Pfluger 1896c)	0	70
Turdus philomelos		
Nelson (Thomson 1922)	1	5
Otago (Thomson 1922)	1	2; 4; 49; 48; 42
Canterbury (Lamb 1964)	1	36; 24; 43; 28; 74; 96
Canterbury (Thomson 1922)	1	*(36); (24)*
Auckland (Thomson 1922)	1	30; 95
Wellington (Thomson 1922)	1	8
Victoria (Jenkins 1977)	1	14; 4; 24; 6;9;2;4
South Australia (Jenkins 1977)[a]	1	4;1;20;1;2
Victoria (Ryan 1906)	1	28

Table 2 continued

Species	Fate	Release reports
Victoria (Balmford 1978)	1	*(14); (4); (4); (6); (2)*
Victoria (Balmford—Argus)[a]	1	36; 1; 37
Brooklyn (Cleaveland 1866)	0	12
Oregon (Pfluger 1896b)	0	70
Carduelis chloris		
Nelson (Thomson 1922)	1	5
Otago (Thomson 1922)	1	8
Canterbury (Thomson 1922)	1	2
Auckland (Thomson 1922)	1	18; 33
Victoria (Jenkins 1977)	1	20
South Australia (Jenkins 1977)	1	4; 10
Victoria (Ryan 1906)	1	50; 40 *(20)*
Victoria (Balmford 1978)	1	*(20)*
Oregon (Pfluger 1896f)	0	30
Passer montanus		
Otago (Thomson)	0	2
Auckland (Thomson 1922)	0	3; 9
Victoria (Jenkins 1977)	1	*(20); (40)*
Victoria (Ryan 1906)	1	45; 20
Victoria (Balmford 1978)	1	*(20)*
Missouri (Phillips 1928)	1	24
Emberiza citrinella		
Nelson (Thomson 1922)	1	3
Otago (Thomson 1922)	1	8; 31
Canterbury (Lamb 1964)[a]	1	1; 34; 180; 22
Canterbury (Thomson 1922)	1	*(1); (34)*
Auckland (Thomson 1922)	1	8;4;5;16; 312
Victoria (Jenkins 1977)	0	15
Victoria (Ryan 1906)	0	*(15);* 15
Victoria (Balmford 1978)	0	*(15)*
Acridotheres tristis		
Canterbury (Thomson 1922)	0	18
Wellington (Thomson 1922)	0	30; 40
Victoria (Jenkins 1977)	1	100: 50; 20
Victoria (Ryan 1906)	1	42; 40; 70
Victoria (Balmford 1978)	1	*(20); (50)*
Corvus frugilegus		
Nelson (Thomson 1922)	0	3
Canterbury (Lamb 1964)	1	(4); (32)
Canterbury (Thomson 1922)	1	5; 35
Auckland (Thomson 1922)	1	2; 64

Table 2 continued

Species	Fate	Release reports
Victoria (Jenkins 1977)	0	3

New Zealand sites: Nelson; Otago; Canterbury; Wellington; and Auckland. Australian sites: Victoria; South Australia; Western Australia; North American sites: Portland, Oregon; New York City; Brooklyn (Greenwood Cemetery). Italicized numbers in parentheses represent reports deemed to be duplicates and thus were excluded from all simulations

[a] Releases of a single individual are reported here but were excluded from our analyses

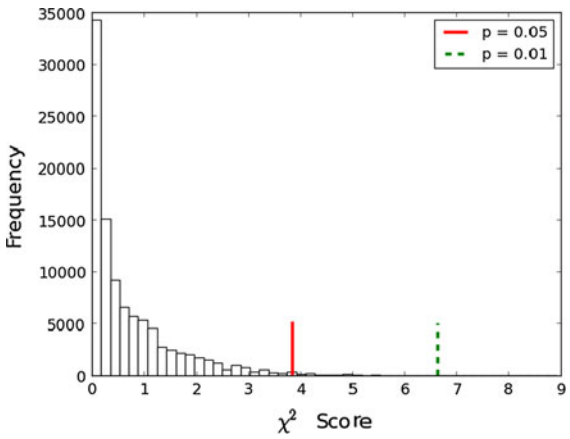

Fig. 1 Distribution of random X^2 values from 100,000 random simulations. Each value was calculated after randomly selecting a single introduction event for each species from the list of successful and unsuccessful introductions

simulations, only 864 (0.864 %) of the approximate X^2 were significant and almost all of these 812 (94 %) were significant in the direction opposite that predicted by the propagule pressure hypothesis. In other words, propagules of successful introductions were significantly smaller than those from unsuccessful ones.

In our second test, using sums of events, very large numbers (i.e. >100) of individuals were often associated with species' successes. To some extent this reflects the assumption by other authors of propagule pressure studies (e.g. Newsome and Noble 1986; Veltman et al. 1996; Duncan 1997; Cassey et al. 2004; Blackburn et al. 2011) that the total number of individuals released from all events is the necessary propagule size. So our second analysis is biased toward supporting these previous results. However, as noted by Blackburn et al. (2009b) when more than 100

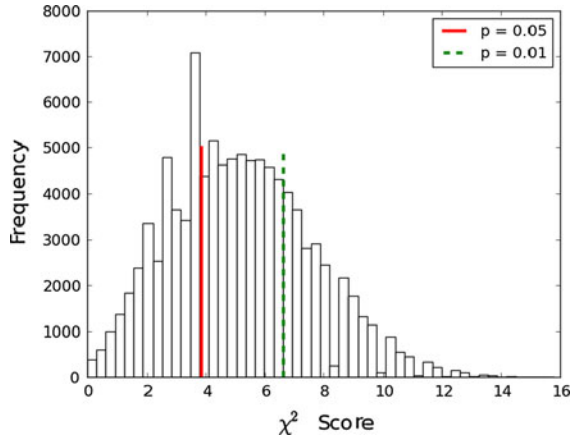

Fig. 2 Distribution of random X^2 values from 100,000 random simulations. Each value was calculated by randomly combining from one to all propagules for each species from the lists of successful and unsuccessful introductions

individuals of a species are released, "success is no longer determined by numbers". Despite the bias of including successful propagules well in excess of 100 individuals, only 67,603 of 100,000 produced a significant X^2 value ($p = 0.05$). It is not possible to determine which introduction event or combination of events was responsible for any successful establishment. We do know that the sum of all introductions for unsuccessful species was insufficient for establishment. Repeating the analysis with all unsuccessful propagule sizes summed yields only 47,283 significant X^2 values ($p = 0.05$), and 25,490 values significant at $p = 0.01$.

Blackburn et al. (2011) argued that the most appropriate way to analyze propagule pressure data is through the use of generalized linear mixed models with introduction outcome as the response variable distributed as a binomial. By this approach propagule sizes are transformed to their common logarithms and serve along with regions as predictor variables. Different regions and species in this model are treated as class variables. When we entered all the log transformed introduction sizes into a generalized linear mixed model (Glimmix) our linear estimate was not significant (estimate 0.28 ± 0.53, $t = 0.54$, $p > t = 0.59$). Indeed using this analysis, the estimate was significant only when we log-transformed the sum of all introductions for each species, with each fate, within each region (estimate 2.16 ± 0.92, $t = 2.35$, $p > t = 0.03$). Of course this last analysis assumes

that all the introductions were needed for successful establishment, an assumption that the historical record does not support (Moulton et al. 2011, 2012a, b).

Discussion

We believe that analyses that use the sums of all introductions of a species to a certain region are inherently flawed. The acclimatization societies had many reasons for introducing birds (Moulton et al. 2011), but conducting experiments in propagule pressure was not among them. Thus these introductions were not controlled for site-level or species-level differences. Since the outcomes of individual releases for successfully introduced species are unknown we believe that the repeated sampling approach we used is more appropriate.

With this in mind, our results are compelling despite the small number of species included. Previous analyses were based on sums of numbers released for each species including those that failed everywhere in the region where they were released (e.g. *Fringilla montifringilla*) and others that succeeded everywhere (e.g. *Passer domesticus*). Differences in propagules sizes for such species (those that always succeed or always fail) provide no test of the importance of propagule pressure. In contrast, our analyses included only those species introduced to multiple regions, with differential success across the three regions. Of course, our results make no evaluative assumptions regarding differences in propagules sizes reported by different authors. Despite assertions to the contrary (e.g. Blackburn et al. 2009a), the historical record is often barely lucid enough to ascertain the identities of the species that were introduced, let alone how many individuals of each were released, how many releases of each species occurred, or even if any individuals were ever released at all.

The historical record consists of published reports made by acclimatization societies, and, to an unknown extent, private individuals. The imported individuals were at least sometimes distributed among the members of a society (e.g. Jenkins 1977; Ashby 1967). Unfortunately, as Phillips (1928) noted, "The early history of the introduction of foreign birds into this country is mostly clothed in darkness." Indeed, in constructing his compendium of introduced birds in North America, Phillips (1928) relied, in part, on "inquiring letters" sent to game commissioners, sportsmen and ornithologists, as well as on the "comparatively recent files of sportsmen's periodicals". As Phillips (1928) noted, the potential for error here is enormous. Elsewhere, Moulton et al. (2010) detailed errors in the record of the earliest House Sparrow introductions in North America, and Teale (2011) detailed misinterpretations of the historical record regarding the introduction and establishment of the Mute Swan (*Cygnus olor*) in North America.

Our analyses clearly show that the number of individuals released alone does not predict introduction outcomes for passeriform birds. These simulations included introduction events that were widely spaced (e.g. Western Australia and Victoria, Australia), sometimes spanning many years. Summing propagules from multiple introduction events to represent the founding population, as we did in the second sampling method, creates a bias *in favor* of the propagule pressure hypothesis. Additionally, a classification of introduction events based only on ultimate success or failure does not properly account for species that persisted for many decades before local extinction, or those that were extirpated by humans.

If propagule pressure is not the critical factor in deciding the outcomes of introductions what could be? One possibility, suggested by Simberloff and Boecklen (1991), is that species-level characteristics could produce an All-or-None pattern where species either always succeed or always fail when introduced to new environments. Seven species in our study always failed despite 32 introductions across the three regions (Table 1), this could be the result of species-level characteristics. Blackburn et al. (2009b) also suggested that species level traits may play an important role in establishment outcome. Our results suggest, on the other hand, that site-level characteristics might better explain the pattern seen among the 11 species with mixed outcomes analyzed here.

Several authors have argued that site-level factors could explain the historical pattern. Case (1996) found a positive relationship between the number of native bird extinctions and the number of successfully introduced birds on islands, and Smallwood (1994) found that proximity to disturbed habitats with reduced native mammalian richness facilitated non-native species invasion of California nature reserves. Gullion (1965) decried the Foreign Game Bird Importation Program, emphasizing that site-level

characteristics were far more important than sheer numbers when it came to introduction success. Elsewhere other authors have championed life history and other species-level variables as being of secondary importance to propagule pressure (e.g. Duncan and Forsyth 2006; Sol et al. 2005; Blackburn et al. 2009b). However, such variables would seem to be of less importance if the introduced individuals cannot find sufficient food, face too many enemies, or simply find the new environment climatically inhospitable.

It is unfortunate that birds have been used so extensively as a primary example of the importance of propagule pressure for understanding success or failure of introductions. The foundation for asserting that propagule pressure determines success or failure for introduced birds was built on incomplete, inaccurate, and inconsistent accounts from secondary and tertiary sources 100–150 years old. Critical review and parsimonious alternative analyses of these avian introduction records have consistently revealed no support for the propagule pressure model, except under special and unrealistic circumstances.

In assessing the success of grouse introductions to North America, Bump (1963, p. 857) observed:

> The success or failure of a species in a new environment is determined by many factors. Some, such as habitat, climate, food and water, general habits, and reproductive capacity, are characteristic of a species. Others are associated with the actual attempt at introduction. Among these are the suitability of the release area, the source from which the birds came, their age at release, their physical and psychological condition, the number of liberations attempted, the number of birds involved, and the time and method of release. While exact proof is lacking, the probability is that successful introductions occur only when all or nearly all these factors are in productive conjugation.

At best, at a given time and place, propagule pressure is but one of many factors that could influence the fate an introduction. The claim that "the primary determinant of establishment success is propagule pressure" (Lockwood et al. 2009, p. 904) trivializes the nature of an important, complex ecological process.

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