

A reassessment of historical records of avian introductions to Australia: no case for propagule pressure

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Abstract Introduced species are widely believed to represent a significant threat to conservation of biological diversity. A better understanding of the ecological factors associated with successful species establishment should lead to improved management and mitigation of these introductions. The “propagule pressure hypothesis”, implying a greater chance of successful introduction with greater numbers introduced, has been widely accepted as a principal ecological factor in explaining establishment of exotic species. The historical record of bird introductions in a few locations, including the state of Victoria in Australia, has been advanced as the principal quantitative support for the hypothesis. We compiled lists of bird species introductions into Australia from several sources, and discovered inconsistencies in the records of introductions. In a series of comparisons, we found that the historical record of passerine introductions to Australia does not support the propagule pressure hypothesis unless superfluous introductions of already successful species are included. An additional problem with previous analyses is the inclusion of unsuccessful haphazard cage escapes.

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Introduction

Several authors have argued that propagule pressure is the primary determinant of the outcomes of species introductions (Griffith et al. 1989; Veltman et al. 1996; Cassey et al. 2004, 2005; Lockwood et al. 2005; Blackburn et al. 2009; Simberloff 2009). The essence of the propagule pressure hypothesis is that the more individuals released in an introduction—the propagule—the greater the chance that the introduction will be successful. The hypothesis is tested by asking if successful introductions involved the release of more individuals than unsuccessful introductions.

Although most species introductions are unsuccessful (e.g. Long 1981; Williamson 1996), from a conservation perspective it would be valuable to understand clearly the ecological factors that influence the outcome of species introductions. Such an understanding is essential to developing conservation practices to identify potentially harmful invasive species. Numerous examples exist of species introductions that have led to serious ecological and economic consequences (e.g. Savidge 1987; Willson et al. 2011). These consequences may include disruption of fire regimes, disease and pest problems, loss of harvested natural resources and indirect effects (Mooney 2005). Additionally an understanding of the introduction process can aid in promoting re-introductions of extirpated populations (e.g. Cassey et al. 2008; Van Houtan et al. 2009).

As noted by Duncan et al. (2003), at least three levels of factors can influence the outcome of introductions. These include species-level, site-level and event or human-level factors. Species-level factors include variables such as size of native range as an index of ecological plasticity (Moulton and Pimm 1986a, 1986b), behavioral flexibility (Sol and Lefebvre 2000), response to sexual selection (McLain et al. 1995, 1999; Moulton et al. 2009; Sorci et al. 1998), and relative brain size (Sol et al. 2005). Site-level factors include extent of habitat disturbance (e.g. Elton 1958; Diamond and Veitch 1981; Smallwood 1994; Case 1996), or the presence of competitors (e.g. Moulton and Pimm 1983, 1987; Moulton 1985, 1993; Lockwood and Moulton 1994; Gamarra et al. 2005), or predators (Wilson 1858; Thomson 1922; Blackburn et al. 2009).

Propagule pressure only represents one component of human influence on species introductions. Humans decide which species to introduce, as well as when, how and where to introduce them. A reliance only on propagule size could mislead analyses of potential invasive species. Indeed, several successful invaders originated from small propagules (e.g., Simberloff 2009; Van Houtan et al. 2009; Willson et al. 2011) and other species failed to become established despite releases of large numbers (e.g. Labisky 1961; Peacock and Abbott 2010). Such examples suggest that the propagule pressure hypothesis may lack general applicability.

For birds, three main cases have fueled support for the propagule pressure hypothesis. The first involves repeated reports that perhaps the most successful introduced bird in the world, the House Sparrow (*Passer domesticus*), required three separate introductions in the 1850s totaling to more than 100 individuals to Brooklyn, New York to gain a toehold in the New World (e.g. Robbins 1973; Long 1981; Simberloff and Boecklen 1991; Simberloff 2009). The second case deals with the introduced birds in New Zealand (e.g. Veltman et al. 1996; Duncan 1997; Green 1997). The third case involves the analysis of avian introductions to Australia (Newsome and Noble 1986).

The paradigmatic example of the importance of propagule pressure in deciding the fate of avian introductions involves the House Sparrow to North America (Simberloff and Boecklen 1991; Simberloff 2009). However, a more careful analysis has shown that the historical record does not support the usual story (Moulton et al. 2010; Schrey et al. 2011). Perhaps as few as 16 individuals may have been sufficient for the initial establishment of House Sparrows in New York, USA.

In the second case, Moulton et al. (2011) re-examined analyses of the historical records for passerine introductions to New Zealand (Veltman et al. 1996; Duncan 1997; Green 1997) and found that a clearly predominant role for propagule pressure in these studies could only be construed under a very restricted and unrealistic set of assumptions.

This leaves the record of avian introductions to Australia by Newsome and Noble (1986) as a principal support for the propagule pressure model. The propagule pressure hypothesis assumes that species introduced in high numbers were successful due to relatively large propagule sizes. However, many of the passerine introductions to New Zealand, occurred after species were already established (Moulton et al. 2011). Could this be the case in Australia as well? If so, it would argue against the notion that propagule pressure played a central role in deciding the fate of introductions. Testing this hypothesis depends on accurate data and inference from sources typically more than 100 years old.

In conjunction with this problem is the phenomenon of releasing very small numbers of a species, either as accidental escapes or as intentional releases. For example, just two Nightingales (*Luscinia megarhynchos*) were released in Victoria (Wilson 1858). Such small releases risk including individuals of just one sex (in the case of monochromatic species), extinction by predation such as described by Wilson (1858), or release of individuals in sub-optimal health. Newsome and Noble (1986) included a number of species that were either accidental escapes or introduced in extremely small numbers in their analysis. Moreover, because Newsome and Noble (1986) did not categorize introductions by location or state, it is impossible to assess whether all of the introductions were spatially and temporally associated, or needed for the establishment of introduced species in Australia. For a given species, the historical record often includes records of releases widely separated in space and time.

Here we present a detailed re-examination of early introductions of passerine birds to Australia. We show that the report by Newsome and Noble (1986), based on historical records of bird introductions to Australia, contains numerous inconsistencies and inaccuracies with respect to the numbers of individuals released/species, the dates of introduction, and in some cases even the identities of the species released. Moreover, a re-analysis shows that, as in New Zealand (Moulton et al. 2011), the introduced passerines of Australia fail to support the propagule pressure model except when questionable data and assumptions form the basis of the analysis.

Materials and methods

A principal concern in assessing support for the propagule pressure model is the inclusion of superfluous releases—those that had no bearing on the outcome of the introduction. In New Zealand, for example, it is not clear if introductions were successful because large numbers of birds were released or if large numbers were released because the early releases were successful (Moulton et al. 2011). Thus, if colonists believed that a species from their home country could be a control agent for insect pests they would likely be motivated to release additional individuals.

Newsome and Noble (1986) relied on the compendium of Long (1981) for compiling their list of passerine species introduced to Australia, adjacent islands, and distant territories. Newsome and Noble (1986) apparently summed for each species the numbers of individuals released throughout Australia. Thus, it is possible that many of the releases included in these sums were not needed for a species to be successful.

We compiled lists of passerine introductions presumably released into the wild by state, from several sources. We started with Long (1981), who included the mainland of Australia, adjacent offshore islands and Tasmania. We also consulted Jenkins (1977), Ryan (1906), and Balmford (1978), as these studies were cited frequently by Long (1981). Jenkins (1977) limited his analysis to acclimatization societies in Victoria, South Australia, Western Australia, New South Wales, Queensland and Tasmania, whereas Balmford (1978) and Ryan (1906) limited their studies to the state of Victoria. In addition, we examined records from other references cited by Newsome and Noble (1986) and Long (1981), including Wilson (1858), Hardy (1928), Lawson (1949), Tarr (1950), and McCance (1962). For all scientific names, we followed the Howard and Moore checklist of birds of the world (Dickinson 2003).

We compared numbers of successful species with those of unsuccessful species using Kruskal–Wallis tests. Exact numbers were not listed for 22 of the 29 species listed by Newsome and Noble (1986). There was no numerical information for eight species and estimates for 14 species. To account for this, we scored the estimates of the numbers of individuals released following the system used by Green (1997), Cassey et al. (2005) and Moulton et al. (2011). We scored the sums/species within each state. In this scheme, propagules of 2–10 individuals are assigned a score of 0; those of 11–100 individuals are scored as 1; and those with more than 100 are scored as 2.

Results

We re-analyzed Newsome and Noble (1986) using just their passerine species (Table 1). For this analysis, following Newsome and Noble (1986), we excluded three species: the House Crow (*Corvus splendens*), on grounds that the species was likely eradicated; the Redpoll (*Carduelis flammea*), as it was only on distant Macquarie Island (Selkirk et al. 1990); and the Wood Lark (*Lullula arborea*), as these may not have actually been released (Long 1981).

We also excluded the Hawfinch (*Coccothraustes coccothraustes*), as we were unable to find corroborating evidence for this introduction in any reference other than McCance (1962). There are newspaper reports of sightings this species and the Bullfinch (The Sydney Morning Herald 10.4.1909, 11; The Sydney Morning Herald 26.3.1910, 8; The West Australian 11.12.1935, 16), but the first two of these reports apparently refer to captive individuals and the last to a single dead individual. The Hermit Thrush (Newsome and Noble 1986) was probably never introduced to Australia—Jenkins (1977) stated that “Virginian Nightingales” had been introduced to Victoria, and whereas Long (1981) imagined these could be Hermit Thrushes, Coues (1875) noted that “Virginian Nightingales” was the common name used for Northern Cardinals (*Cardinalis cardinalis*). Thus, Newsome and Noble (1986) apparently counted a single unsuccessful species twice. We further argue that the Red-billed Leiothrix (*Leiothrix lutea*), introduced to Western Australia (Jenkins 1977) and the Rook (*Corvus frugilegus*), introduced to Victoria and Queensland (Chisolm 1919; Jenkins 1977) should be included.

Table 1 List of 29 introduced passerine species from Newsome and Noble (1986)

Species	Fate	Number	Score
<i>Alauda arvensis</i>	1	>700	2
<i>Pycnonotus jocosus</i>	1	?	0
<i>Pycnonotus cafer</i>	0	?	0
<i>Erithacus rubecula</i>	0	47	1
<i>Luscinia megarhynchos</i>	0	2	0
<i>Catharus guttatus</i> ^a	0	3	0
<i>Turdus merula</i>	1	>150	2
<i>Turdus philomelos</i>	1	>70	1
<i>Emberiza citrinella</i>	0	>15	1
<i>Emberiza hortulana</i>	0	16	1
<i>Cardinalis cardinalis</i>	0	?	0
<i>Fringilla coelebs</i>	0	<200	2
<i>Fringilla montifringilla</i>	0	<80	1
<i>Serinus canaria</i>	0	18	1
<i>Carduelis chloris</i>	1	<150	2
<i>Carduelis spinus</i>	0	80	1
<i>Carduelis carduelis</i>	1	<500	2
<i>Carduelis flammea</i> ^b		?	–
<i>Carduelis cannabina</i>	0	<50	1
<i>Pyrrhula pyrrhula</i>	0	14	1
<i>Passer domesticus</i>	1	>>100	2
<i>Passer montanus</i>	1	>70	1
<i>Euplectes orix</i>	0	?	0
<i>Euplectes albonatus</i>	0	?	0
<i>Lonchura punctulata</i>	1	?	0
<i>Lonchura malacca</i>	0	?	0
<i>Lonchura oryzivora</i>	0	>>100	2
<i>Sturnus vulgaris</i>	1	>450	2
<i>Acridotheres tristis</i>	1	>350	2

Number is the number of individuals listed by Newsome and Noble (1986). A ‘?’ indicates that the authors believed the species was released but the propagule size was unknown, so assumed to be <10. Fate: successful = 1;

unsuccessful = 0; “Score” is 0 for 2–10 individuals released; 1 for 11–100 individuals; 2 for >100 individuals. Scientific names follow Dickinson (2003)

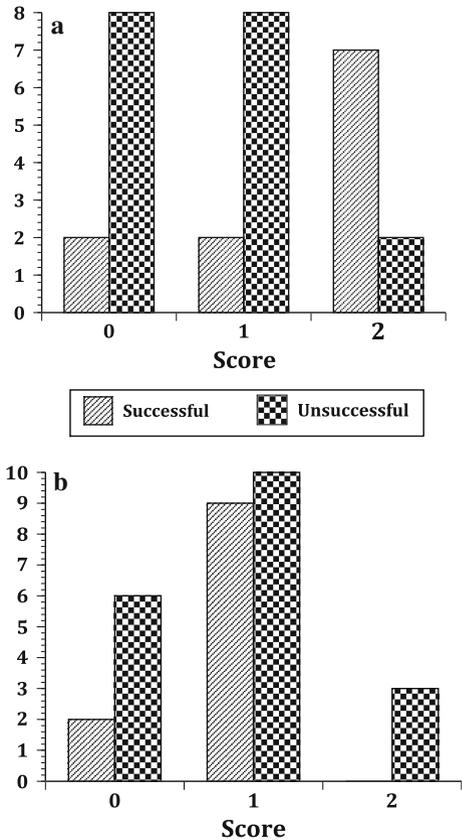
^a Misidentified actually refers to *Cardinalis cardinalis*

^b Not introduced to mainland Australia, Tasmania, or adjacent islands

In our first test, we compared the scores of successful to unsuccessful species listed in Newsome and Noble (1986) (Fig. 1a). The result of this comparison supported a positive effect of propagule pressure (Lockwood et al. 2005, Blackburn et al. 2009). Of the 29 species, 18 were unsuccessful and 11 successful (Newsome and Noble 1986). Here we also assigned a score of ‘0’ to each of the eight species with no propagule information. The mean score for unsuccessful species was less than half that of the successful species (0.67—unsuccessful; 1.45—successful), a statistically significant difference (Kruskal–Wallis approximate $X^2 = 6.14$, $P = 0.013$).

Thus, at first glance the data appear to support the propagule pressure model that species introduced in higher numbers have increased chances for successful establishment (Cassey et al. 2004, Lockwood et al. 2005). However, by using sums of all introductions to all of Australia for each species Newsome and Noble (1986) likely included introductions that occurred after a species was successfully established. For instance, the 265 Eurasian Skylarks (*Alauda arvensis*) introduced by the South Australia Acclimatization Society starting in 1879 probably were unneeded for establishing this species. In fact, Balmford

Fig. 1 a Comparison of categories for numbers of individuals released (0 2–10, 1 11–100, 2 >100) for successfully and unsuccessfully introduced species listed by Newsome and Noble (1986). **b** Comparison of categories for numbers of successfully and unsuccessfully introduced passerines from the expanded list (see text): scores as in (a)



(1978) suggested Eurasian Skylarks, as well as other species, were likely already established in Victoria following introductions in the 1850s. Also, Newsome and Noble (1986) counted both the Hermit Thrush and Northern Cardinal in their list of 29 passerines, but as noted above, Hermit Thrushes were likely not introduced to Australia.

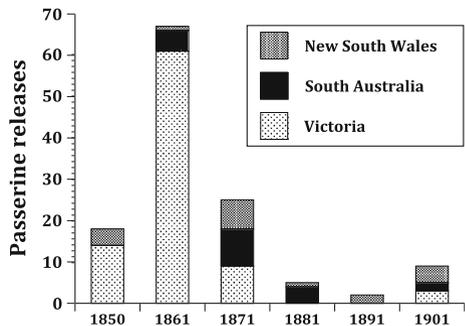
In our second test, we attempted to compare successful and unsuccessful species in each of the different states (Table 2; Appendices 1, 2). When listed by state however, it becomes clear that most of the introductions and most species were released in Victoria (Table 2). Moreover, in most cases, introductions to Victoria preceded those in other states (Lucas and Le Souef 1911; Fig. 2).

Given these data, in this test we compared numbers of successfully versus unsuccessfully introduced species in Victoria alone. No species that was unsuccessful in Victoria was successful in any other state (Jenkins 1977; Long 1981). Although the analyses of Balmford (1978); Jenkins (1977) and Ryan (1906) presumably were based on the same acclimatization society records, they frequently did not agree on the numbers of individuals released and identities of certain species (Table 3). Thus, Balmford (1978) included just 14 species; Ryan (1906) listed 16; and Jenkins (1977) 17 species. Ryan (1906) listed the Ortolan Bunting (*Emberiza hortulana*) as did Lucas and Le Souef (1911). However, neither Balmford (1978) nor Jenkins (1977) included this species. Newsome and Noble (1986) included the Ortolan Bunting as well as the Hawfinch (*Coccothraustes coccothraustes*) but we excluded the latter species because we could find no corroborating evidence

Table 2 Numbers of species and releases of passerines in seven states in Australia from Long (1981)—numbers in parentheses from Jenkins (1977)

State	Releases	Species
VIC	88 (58)	26 (18)
SA	19 (36)	14 (12)
NSW	19 (18)	13 (7)
QLD	9 (12)	7 (9)
WA	6 (5)	6 (5)
ACT	2 (NA)	1 (NA)

States are: *VIC* Victoria, *SA* South Australia, *NSW* New South Wales, *QLD* Queensland, *WA* Western Australia, *ACT* Australian Capital Territory

Fig. 2 Passerine releases by decade for Victoria, South Australia and New South Wales

for this introduction—moreover their reference for this listing was McCance (1962) who actually listed ‘Chinese Hawfinch’, not *Coccothraustes coccothraustes*, so the true identity of the species is uncertain. Neither Jenkins (1977) nor Ryan (1906) included the Nightingale (*Luscinia megarhynchos*) of Newsome and Noble (1986) although Balmford (1978) reported that five individuals were listed in the Melbourne Argus as having been imported in 1857. Wilson (1858) detailed the fate of five Nightingales that could refer to the record listed by Newsome and Noble (1986) and Balmford (1978). Based on Wilson’s (1858) report we included the Nightingale in our expanded list (see below).

Differences between median numbers of successful and unsuccessful species listed by Balmford (1978) and Ryan (1906) for Victoria were not significant although for the list of Jenkins (1977) the difference was nearly significant (Table 4).

In a third test, we expanded the list to include introductions of species to Australia outside of Victoria. In this test, we compared the median of the minimum propagule sizes of successful species with the median of maximum propagule sizes for unsuccessful species (Table 6). The reasoning here is that for successful species clearly the minimum propagule was sufficient for establishment success whereas the maximum propagule sizes of unsuccessfully introduced species were presumably not large enough (Moulton et al. 2011).

In compiling this expanded list, we noted that Jenkins (1977) also reported that 100 Eurasian Skylarks and 200 European Goldfinches were unsuccessfully introduced to Western Australia in 1899. Since these introductions were widely separated from introductions of these species in South Australia and Victoria, these introductions should be counted independently. Elsewhere, Jenkins (1959) reported that the first successful

Table 3 Comparison of introduction records for passerines to Victoria: R = Ryan (1906); B = Balmford (1978); J = Jenkins (1977)

Species	Fate	R	B	J
<i>Acridotheres tristis</i>	1	152	70	170
<i>Alauda arvensis</i>	1	140	39	141
<i>Cardinalis cardinalis</i> ^a	0	*	*	?
<i>Carduelis cannabina</i>	0	*	*	19
<i>Carduelis carduelis</i>	1	54	*	12
<i>Carduelis chloris</i>	1	110	20	20
<i>Carduelis spinus</i>	0	60	20	20
<i>Corvus frugilegus</i>	0	*	*	3
<i>Emberiza citrinella</i>	0	30	15	15
<i>Emberiza hortulana</i>	0	16	*	*
<i>Erithacus rubecula</i>	0	11	31	47
<i>Fringilla coelebs</i>	0	130	40	40
<i>Lonchura oryzivora</i>	0	535	255	255
<i>Passer domesticus</i>	1	345	65	130
<i>Passer montanus</i> ^b	1	65	20	60
<i>Serinus canaria</i>	0	18	18	18
<i>Sturnus vulgaris</i>	1	77	12	168
<i>Turdus merula</i>	1	45	28	50
<i>Turdus philomelos</i>	1	28	30	67

A “*” means that the species was not mentioned; a “?” indicates that the species was recorded but the propagule size was not listed

^a Jenkins (1977) listed “Virginian Nightingales”

^b Ryan (1906) and Balmford (1978) all identified “chinese sparrows” as *Passer montanus*

Table 4 Comparison of the number of individuals introduced to Victoria for successful and unsuccessful species

	B	R	J
Mean unsuccessful (<i>n</i>)	63.2 (6)	114.3 (7)	52.1 (8)
Mean successful (<i>n</i>)	35.5 (8)	124 (9)	90.9 (9)
χ^2	0.02	1.75	3.17
$P > \chi^2$	0.90	0.19	0.07

B Balmford (1978), R Ryan (1906), J Jenkins (1977)

European Goldfinches in Western Australia appeared in 1933 and concluded that these birds had come from aviary escapes. We have excluded this record from our analyses in keeping with our view that it represents an extemporaneous introduction, as at least 60 years had passed since the European Goldfinches had been successfully introduced to Australia. With this in mind, we conducted statistical tests on our expanded list with and without these two introductions. In the first case (including the two Western Australia introductions), the median for successful species was not significantly different from that of the unsuccessful species (Table 5, Case 1). In the next test of this list, we excluded the unsuccessful introductions of the 200 European Goldfinches and 100 Eurasian Skylarks

Table 5 Comparison of the number of individuals introduced for successful and unsuccessful species from the expanded list of passerine introductions to Australia

	Case 1	Case 2
Mean unsuccessful (n)	90.1 (15)	80.9 (13)
Mean successful (n)	32.9 (9)	32.9 (9)
χ^2	0.70	0.11
$P > \chi^2$	0.40	0.74

Case 1 includes introductions of 100 Eurasian Skylarks and 200 European Goldfinches to Western Australia, case 2 excludes these two introductions

to Western Australia. In this case the medians also were not significantly different (Table 5, Case 2).

Discussion

There are two general results from our analysis of passerine introductions to Australia. First, the historical record for Australia, as in New Zealand, is riddled with inconsistencies and errors. Second, the record of passerine introductions to Australia does not support the propagule pressure model unless all introductions for each species are summed, ignoring sizable intervening gaps between introductions in time and space.

We found numerous inconsistencies in the historical record of introductions to Australia (Tables 3 and 6). The studies by Balmford (1978), Ryan (1906) and Jenkins (1977) only agree on the number of individuals released for one species (*Serinus canaria*). For all other species, their numbers are different, and sometimes very different. These differences coupled with discrepancies in the roster of species that were actually introduced paint a rather different picture regarding the clarity of the introduction record that has become paradigmatic (i.e. Blackburn et al. 2009). Additionally, Balmford (1978) challenged introductions listed by Ryan (1906) and noted that numerous introductions to Victoria occurred before the acclimatization society formed. Indeed, she noted that it might be impossible to say with certainty when any of the successful species were first released.

Duncan et al. (2003) listed three main categories of variables that could influence the outcome of species introductions: species-level traits, location-level traits and event-level traits. To this, we suggest the addition of a fourth category: individual-level traits. This level encompasses the condition of the actual individuals that are released. In the nineteenth century, birds that were imported to Australia from afar came by ship. The death rate for birds in transit was often staggering. Jenkins (1977) recounts that of the first recorded shipment of House Sparrows in 1862 all 60 birds perished en route. Chisolm (1919) noted that all the individuals in two consignments of “English Wood-Pigeons” died en route through the Suez Canal and Red Sea. Wilson (1858) describes health issues among Nightingales intended for release in Victoria. Such examples suggest that the health and physical condition of the birds that arrived by sea was important in influencing the fates of introductions, regardless of how many individuals were shipped, how embracing the new environment was, or how pre-adapted the species might have been for the new environment.

Finally, we emphasize that the only possible way we could find to interpret the historical record of passerine introductions to Australia as supporting the propagule pressure model

Table 6 Expanded list of species and propagule sizes for three studies of avian introductions to Victoria

Species	Fate	R	B	J
<i>Acridotheres tristis</i>	1	152	70	170
<i>Alauda arvensis</i>	1	140	39	141
<i>Alauda arvensis</i> (WA) ^a	0	–	–	100
<i>Cardinalis cardinalis</i> ^b	0	–	–	?
<i>Carduelis cannabina</i>	0	–	–	19
<i>Carduelis carduelis</i>	1	54	–	12
<i>Carduelis carduelis</i> (WA) ^a	0	–	–	200
<i>Carduelis chloris</i>	1	110	20	20
<i>Carduelis spinus</i>	0	60	20	20
<i>Corvus frugilegus</i>	0	–	–	3
<i>Emberiza citrinella</i>	0	30	15	15
<i>Emberiza hortulana</i>	0	16	–	–
<i>Euplectes albonotatus</i> (NSW) ^c	0	–	–	?
<i>Euplectes orix</i> (SA) ^d	0	–	–	?
<i>Erithacus rubecula</i>	0	11	31	47
<i>Fringilla coelebs</i>	0	130	40	40
<i>Fringilla montifringilla</i> (SA) ^a	0	–	–	78
<i>Leiothrix lutea</i> (WA) ^a	0	–	–	100
<i>Lonchura malacca</i> (NSW) ^c	0	–	–	?
<i>Lonchura oryzivora</i>	0	535	255	255
<i>Lonchura punctulata</i> (QLD, NSW) ^{a,c}	1	–	–	?
<i>Luscinia megarhynchos</i> ^{e,f}	0	–	–	2
<i>Passer domesticus</i>	1	345	65	130
<i>Passer montanus</i>	0	65	20	60
<i>Prunella modularis</i> (QLD) ^a	0	–	–	?
<i>Pycnonotus jocosus</i> (NSW) ^a	1	–	–	?
<i>Pycnonotus cafer</i> ^{g,h}	0	–	–	?
<i>Pyrrhula pyrrhula</i> (SA) ^a	0	–	–	14
<i>Serinus canaria</i>	0	18	18	18
<i>Sturnus vulgaris</i>	1	77	12	168
<i>Turdus merula</i>	1	45	28	50
<i>Turdus philomelos</i>	1	28	30	67

'Fate' is the introduction outcome. *B* Balmford (1978), *R* Ryan (1906), *J* Jenkins (1977). All introductions are for Victoria, except where indicated in parentheses after the species name: WA = Western Australia; SA = South Australia; NSW = New South Wales; QLD = Queensland. A '?' indicates that the species was likely introduced in small (i.e. < 10 individuals). A '–' indicates that the author did not record the species

^a Jenkins (1977)

^b Jenkins listed only the common name "Virginian Nightingales"

^c Tarr (1950)

^d Condon (1962)

^e Wilson (1858)

^f Hardy (1928)

^g Le Souef (1918)

^h Lendon (1952)

was to include superfluous introductions of successful species and to inflate the roster of unsuccessful species by including accidental escapes and releases of very small numbers of individuals (as listed in Table 1). Our results argue that future analyses of introductions should more carefully evaluate the role of propagule pressure in influencing introduction outcomes. Moreover, consistent methodologies for tabulating releases are essential.

A useful evaluation of potential invasive species should be part of a risk-consequence analysis framework. A simplified model of the invasion process that overemphasizes the risk from large introduction events, or underemphasizes the risk from small introduction events, makes rational management of invasive species more difficult. There is more to the invasion process, and much more to predicting establishment success, than can be found by simply summing propagule sizes.

Appendix 1

See Table 7.

Table 7 List of passerines introduced to Australia and surrounding islands, from Long (1981)

Species	Place	Number	Fate	Date
ACT				
<i>Turdus philomelos</i>	Canberra	?	0	1935
<i>Turdus philomelos</i>	Canberra	?	4	?
NSW				
<i>Acridotheres tristis</i>	Sydney	?	1	<1896
<i>Alauda arvensis</i>	Sydney	?	1	1866
<i>Alauda arvensis</i>	Sydney	?	1	1880
<i>Alauda arvensis</i>	Sydney	?	1	1870–1872
<i>Carduelis cannabina</i>	?	?	0	1880
<i>Carduelis carduelis</i>	?	?	1	<1886
<i>Carduelis chloris</i>	?	?	1	<1896
<i>Emberiza citrinella</i>	?	?	3	1880
<i>Euplectes albonotatus</i>	?	?	4	1931
<i>Lonchura malacca</i>	Sydney	?	0	<1929
<i>Lonchura punctulata</i>	?	?	1	<1960
<i>Pycnonotus cafer</i>	Sydney	?	5	1917
<i>Pycnonotus jocosus</i>	?	?	1	1880
<i>Turdus merula</i>	Sydney	?	1	1857
<i>Turdus merula</i>	Sydney	?	1	1858
<i>Turdus merula</i>	Sydney	?	1	1859
<i>Turdus merula</i>	Sydney	?	1	1860
<i>Turdus merula</i>	?	?	0	1872
<i>Turdus philomelos</i>	Sydney	?	0	1872
QLD				
<i>Acridotheres tristis</i>	?	?	1	1883
<i>Alauda arvensis</i>	?	?	0	1869

Table 7 continued

Species	Place	Number	Fate	Date
<i>Lonchura punctulata</i>	Townsville	?	1	1950
<i>Lonchura punctulata</i>	Innisfail	?	1	1955
<i>Lonchura punctulata</i>	Brisbane	?	1	<1937
<i>Passer domesticus</i>	Brisbane	?	1	1869–1870
<i>Sturnus vulgaris</i>	Brisbane	?	6	1869–1870
<i>Turdus merula</i>	?	?	3	1869
<i>Turdus philomelos</i>	Brisbane	?	0	1869
SA				
<i>Carduelis cannabina</i>	?	?	0	1879
<i>Alauda arvensis</i>	Enfield	18	1	1879
<i>Alauda arvensis</i>	Dry Creek	44	1	1879
<i>Alauda arvensis</i>	?	147	1	1881
<i>Carduelis carduelis</i>	Adelaide	43	1	1879
<i>Carduelis carduelis</i>	Adelaide	110	1	1881
<i>Carduelis chloris</i>	Royal Park	20	1	1863
<i>Carduelis spinus</i>	Royal Park	20	0	1866
<i>Euplectes orix</i>	?	?	4	1926
<i>Fringilla coelebs</i>	?	?	0	1879
<i>Fringilla montifringilla</i>	?	78	0	1879
<i>Passer domesticus</i>	?	?	1	1863
<i>Pycnonotus jocosus</i>	?	?	1	<1950
<i>Pyrrhula pyrrhula</i>	?	14	0	1879
<i>Sturnus vulgaris</i>	Adelaide	89	1	1881
<i>Turdus merula</i>	?	?	1	1863
<i>Turdus merula</i>	?	4	1	1879
<i>Turdus merula</i>	?	45	1	1881
<i>Turdus philomelos</i>	Adelaide	?	0	1879
TAS				
<i>Acridotheres tristis</i>	?	?	0	1900
<i>Acridotheres tristis</i>	?	?	6	1914
<i>Alauda arvensis</i>	?	36	1	1899
<i>Alauda arvensis</i>	?	?	1	1862
<i>Alauda arvensis</i>	?	?	1	1887
<i>Carduelis carduelis</i>	?	?	1	1827
<i>Carduelis chloris</i>	?	?	6	<1945
<i>Passer domesticus</i>	?	?	1	1863–1873
<i>Passer montanus</i>	?	?	0	<1950
<i>Sturnus vulgaris</i>	?	75	1	1860
<i>Turdus merula</i>	?	?	6	1919
VIC				
<i>Acridotheres tristis</i>	Melbourne	100+	1	1862
<i>Acridotheres tristis</i>	Melbourne	42	1	1863
<i>Acridotheres tristis</i>	Melbourne	40	1	1864

Table 7 continued

Species	Place	Number	Fate	Date
<i>Acridotheres tristis</i>	Melbourne	?	1	1866
<i>Acridotheres tristis</i>	Melbourne	70	1	1872
<i>Alauda arvensis</i>	Melbourne	7	1	1854
<i>Alauda arvensis</i>	?	32	1	1866
<i>Alauda arvensis</i>	?	30	1	1870
<i>Alauda arvensis</i>	?	100	1	1874
<i>Alauda arvensis</i>	?	80	1	1863–1867
<i>Alauda arvensis</i>	?	?	1	1950a
<i>Cardinalis cardinalis</i>	?	?	0	1860s?
<i>Carduelis cannabina</i>	?	19	0	1865
<i>Carduelis cannabina</i>	?	7	0	1860s
<i>Carduelis carduelis</i>	Melbourne	?	1	1857
<i>Carduelis carduelis</i>	Melbourne	?	1	1858
<i>Carduelis carduelis</i>	Melbourne	20	1	1863
<i>Carduelis carduelis</i>	Melbourne	34	1	1864
<i>Carduelis chloris</i>	Melbourne	50	1	1863
<i>Carduelis chloris</i>	Melbourne	40	1	1864
<i>Carduelis chloris</i>	Melbourne	20	1	1872
<i>Carduelis chloris</i>	?	?	1	1860s
<i>Carduelis spinus</i>	?	40	3	1864
<i>Carduelis spinus</i>	?	20	3	1872
<i>Coccothraustes coccothraustes</i>	?	?	3	1860
<i>Corvus splendens</i>	?	?	v	1960s
<i>Emberiza citrinella</i>	Melbourne	15	0	1863
<i>Emberiza citrinella</i>	Melbourne	15	0	1864
<i>Emberiza hortulana</i>	Melbourne	16	0	1863
<i>Erithacus rubecula</i>	?	16	0	1863
<i>Erithacus rubecula</i>	?	14	0	1866
<i>Erithacus rubecula</i>	?	17	0	1870
<i>Fringilla coelebs</i>	Melbourne	40	0	1863
<i>Fringilla coelebs</i>	Melbourne	220	0	1864
<i>Fringilla coelebs</i>	Melbourne	235	0	1872
<i>Catharus guttatus</i>	?	?	0	1860s?
<i>Lullula arborea</i>	?	?	3	1857
<i>Luscinia megarhynchos</i>	?	2	0	1857
<i>Luscinia megarhynchos</i>	?	?	0	1858
<i>Lonchura oryzivora</i>	Melbourne	235	0	1863
<i>Passer domesticus</i>	Melbourne	120	1	1863
<i>Passer domesticus</i>	G. Sprigg	80	1	1863
<i>Passer domesticus</i>	?	30	1	1863
<i>Passer domesticus</i>	Melbourne	125	1	1864
<i>Passer domesticus</i>	Melbourne	?	1	1866
<i>Passer domesticus</i>	Ararat	14	1	1867

Table 7 continued

Species	Place	Number	Fate	Date
<i>Passer domesticus</i>	Ballarat	?	1	1867
<i>Passer domesticus</i>	Beechworth	?	1	1867
<i>Passer domesticus</i>	Benalla	?	1	1867
<i>Passer domesticus</i>	Castlemaine	?	1	1867
<i>Passer domesticus</i>	Daylesford	?	1	1867
<i>Passer domesticus</i>	Geelong	?	1	1867
<i>Passer domesticus</i>	Gisborne	?	1	1867
<i>Passer domesticus</i>	Heathcote	?	1	1867
<i>Passer domesticus</i>	Kyneton	?	1	1867
<i>Passer domesticus</i>	Maryborough	?	1	1867
<i>Passer domesticus</i>	Melbourne	?	1	1867
<i>Passer domesticus</i>	Meredith	?	1	1867
<i>Passer domesticus</i>	Portland	?	1	1867
<i>Passer domesticus</i>	Somerton	?	1	1867
<i>Passer domesticus</i>	St. Arnaud	?	1	1867
<i>Passer domesticus</i>	The Murray	?	1	1867
<i>Passer domesticus</i>	Warrnambool	?	1	1867
<i>Passer domesticus</i>	Winchelsea	?	1	1867
<i>Passer domesticus</i>	Melbourne	100	1	1872
<i>Passer montanus</i>	?	45	1	1863
<i>Passer montanus</i>	?	20	1	1864
<i>Pycnonotus cafer</i>	Melbourne	?	5	1917
<i>Pycnonotus jocosus</i>	?	?	1	?
<i>Pyrrhula pyrrhula</i>	?	?	0	1856
<i>Serinus canaria</i>	Melbourne	18	0	1859
<i>Serinus canaria</i>	Melbourne	?	0	1856
<i>Sturnus vulgaris</i>	?	36	1	1863
<i>Sturnus vulgaris</i>	?	6	1	1864
<i>Sturnus vulgaris</i>	?	15	1	1866
<i>Sturnus vulgaris</i>	?	20	1	1871
<i>Sturnus vulgaris</i>	Melbourne	?	3	1856
<i>Turdus merula</i>	?	6	1	1864
<i>Turdus merula</i>	?	45	1	1864
<i>Turdus merula</i>	?	17	1	1866
<i>Turdus merula</i>	?	22	1	1872
<i>Turdus merula</i>	Melbourne	?	1	<1862
<i>Turdus philomelos</i>	Melbourne	?	1	1857
<i>Turdus philomelos</i>	Melbourne	48	1	1858
<i>Turdus philomelos</i>	Melbourne	37	1	1860
<i>Turdus philomelos</i>	?	4	1	1866
<i>Turdus philomelos</i>	?	6	1	1866
<i>Turdus philomelos</i>	?	12	1	1880

Table 7 continued

Species	Place	Number	Fate	Date
WA				
<i>Aegintha temporalis</i>	Perth	?	1	1958
<i>Alauda arvensis</i>	?	?	0	1912
<i>Carduelis carduelis</i>	Perth	?	0	<1912
<i>Corvus splendens</i>	?	?	0	1967
<i>Leiothrix lutea</i>	?	?	0	<1912
<i>Passer montanus</i>	Perth	?	0	<1966

Key to States; *VIC* Victoria, *ACT* Australian Capital Territory, *NSW* New South Wales, *SA* South Australia, *QLD* Queensland, *TAS* Tasmania, *WA* Western Australia, 'Place' refers to the specific site of the introduction; Number = number of individuals released; Key to Fates; 0 = failed; 1 = successful; 3 = imported but not released?; 4 = initially established but failed later; 5 = exterminated; 6 = natural range extension; v vagrant. Date = date of the introduction

Appendix 2

See Table 8.

Table 8 List of passerines introduced to Australia and surrounding islands by state taken from Jenkins (1977)

Species	Number	Date
VIC		
<i>Passer domesticus</i>	60	1860
<i>Passer domesticus</i>	40	1860
<i>Passer domesticus</i>	25	1860
<i>Passer domesticus</i>	5	1860
<i>Passer domesticus</i>	?	1867
<i>Sturnus vulgaris</i>	6	1860
<i>Sturnus vulgaris</i>	36	1863
<i>Sturnus vulgaris</i>	120	1865
<i>Sturnus vulgaris</i>	6	1866
<i>Alauda arvensis</i>	6	1866
<i>Alauda arvensis</i>	12	1866
<i>Alauda arvensis</i>	6	1866
<i>Alauda arvensis</i>	4	1866
<i>Alauda arvensis</i>	4	1866
<i>Alauda arvensis</i>	4	1866
<i>Alauda arvensis</i>	80	1867
<i>Alauda arvensis</i>	25	1870
<i>Alauda arvensis</i>	?	1880
<i>Turdus philomelos</i>	14	1860
<i>Turdus philomelos</i>	4	1860

Table 8 continued

Species	Number	Date
<i>Turdus philomelos</i>	24	1866
<i>Turdus philomelos</i>	4	1866
<i>Turdus philomelos</i>	6	1866
<i>Turdus philomelos</i>	9	1866
<i>Turdus philomelos</i>	2	1866
<i>Turdus philomelos</i>	4	1866
<i>Turdus merula</i>	?	1860
<i>Turdus merula</i>	?	1860
<i>Turdus merula</i>	18	1866
<i>Turdus merula</i>	4	1866
<i>Turdus merula</i>	10	1866
<i>Turdus merula</i>	6	1866
<i>Turdus merula</i>	12	1880
<i>Passer montanus?</i>	20	1860
<i>Passer montanus?</i>	30–40	1863
<i>Fringilla coelebs</i>	40	1866
<i>Carduelis carduelis</i>	12	1863
<i>Carduelis cannabina</i>	19	1865
<i>Carduelis chloris</i>	20	1863
<i>Emberiza citrinella</i>	15	1863
<i>Acridotheres tristis</i>	100	1862
<i>Acridotheres tristis</i>	50	1866
<i>Acridotheres tristis</i>	?	1865
<i>Acridotheres tristis</i>	20	1865
<i>Carduelis spinus</i>	20	1866
<i>Lonchura oryzivora</i>	35	1863
<i>Lonchura oryzivora</i>	200	1863
<i>Lonchura oryzivora</i>	20	1863
<i>Erithacus rubecula</i>	16	1863
<i>Erithacus rubecula</i>	4	1866
<i>Erithacus rubecula</i>	10	1866
<i>Erithacus rubecula</i>	17	1870
<i>Serinus canaria</i>	18	1859
<i>Corvus frugilegus</i>	3	?
<i>Cardinalis cardinalis</i>	?	?
SA		
<i>Acridotheres tristis</i>	?	1957
<i>Alauda arvensis</i>	?	1862
<i>Alauda arvensis</i>	18	1879
<i>Alauda arvensis</i>	44	1879
<i>Alauda arvensis</i>	18	1879
<i>Alauda arvensis</i>	147	1879
<i>Alauda arvensis</i>	36	1881

Table 8 continued

Species	Number	Date
<i>Alauda arvensis</i>	2	1879
<i>Carduelis carduelis</i>	?	1862
<i>Carduelis carduelis</i>	5	1879
<i>Carduelis carduelis</i>	43	1879
<i>Carduelis carduelis</i>	30	1881
<i>Carduelis carduelis</i>	50	1881
<i>Carduelis carduelis</i>	30	1881
<i>Carduelis chloris</i>	4	1879
<i>Carduelis chloris</i>	10	1879
<i>Euplectes orix</i>	?	1926
<i>Fringilla coelebs</i>	3	1879
<i>Fringilla montifringilla</i>	78	1879
<i>Passer domesticus</i>	?	1863
<i>Pyrrhula pyrrhula</i>	11	1879
<i>Pyrrhula pyrrhula</i>	3	1879
<i>Sturnus vulgaris</i>	?	1860s
<i>Sturnus vulgaris</i>	44	1881
<i>Sturnus vulgaris</i>	45	1881
<i>Sturnus vulgaris</i>	?	1860s
<i>Turdus merula</i>	2	1879
<i>Turdus merula</i>	2	1879
<i>Turdus merula</i>	15	1879
<i>Turdus merula</i>	30	1879
<i>Turdus merula</i>	?	<1878
<i>Turdus philomelos</i>	4	1879
<i>Turdus philomelos</i>	1	1879
<i>Turdus philomelos</i>	20	1879
<i>Turdus philomelos</i>	1	1879
<i>Turdus philomelos</i>	2	1879
WA		
<i>Carduelis carduelis</i>	200	1899
<i>Leiothrix lutea</i>	100	1899
<i>Alauda arvensis</i>	100	1899
<i>Passer domesticus</i>	?	?
<i>Sturnus vulgaris</i>	?	?
Tas		
<i>Alauda arvensis</i>	?	?
<i>Alauda arvensis</i>	36	1899
<i>Passer domesticus</i>	?	?
<i>Passer domesticus</i>	?	1870
<i>Carduelis carduelis</i>	?	?
<i>Sturnus vulgaris</i>	?	?
<i>Sturnus vulgaris</i>	?	1800

Table 8 continued

Species	Number	Date
<i>Acridotheres tristis</i>	?	?
<i>Carduelis cannabina</i>	<12	1907
<i>Turdus merula</i>	?	?
<i>Carduelis chloris</i>	?	1945
NSW		
<i>Emberiza citrinella</i>	15–20	1880
<i>Sturnus vulgaris</i>	?	1880
<i>Alauda arvensis</i>	70	1880
<i>Alauda arvensis</i>	70	1880
<i>Alauda arvensis</i>	70	1880
<i>Carduelis carduelis</i>	32	1880
<i>Carduelis chloris</i>	15–20	1880
<i>Carduelis chloris</i>	15–20	1880
<i>Pycnonotus jocosus</i>	?	1880
<i>Lonchura punctulata</i>	?	1950
QLD		
<i>Prunella modularis</i>	?	
<i>Alauda arvensis</i>	?	
<i>Alauda arvensis</i>	?	1869
<i>Turdus merula</i>	?	
<i>Turdus merula</i>	?	1869
<i>Sturnus vulgaris</i>	?	
<i>Sturnus vulgaris</i>	?	1869
<i>Acridotheres tristis</i>	?	<1919
<i>Corvus frugilegus</i>	?	1869
<i>Turdus philomelos</i>	?	1869
<i>Passer domesticus</i>	?	1869
<i>Lonchura punctulata</i>	?	1940s

Key to States and column headings as in Appendix 1

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