Biological Invasions

The Ins and Outs of Acclimatisation: Imports versus Translocations of Skylarks and Starlings in 19th century New Zealand --Manuscript Draft--

Manuscript Number:	BINV-D-18-00423R1		
Full Title:	The Ins and Outs of Acclimatisation: Imports versus Translocations of Skylarks and Starlings in 19th century New Zealand		
Article Type:	Research paper		
Keywords:	acclimatisation, alien, birds, New Zealand,	propagule pressure	
Corresponding Author:	Pavel Pipek, Ph.D. Institute of Botany, Czech Academy of Scie Průhonice, CZECH REPUBLIC	ences	
Corresponding Author Secondary Information:			
Corresponding Author's Institution:	Institute of Botany, Czech Academy of Scie	ences	
Corresponding Author's Secondary Institution:			
First Author:	Pavel Pipek, Ph.D.		
First Author Secondary Information:			
Order of Authors:	Pavel Pipek, Ph.D.		
Tim M. Blackburn			
	Petr Pyšek		
Order of Authors Secondary Information:			
Funding Information:	The Czech Academy of Sciences (RVO67985939)	Prof. Petr Pyšek	
	Hlávka foundation	Dr. Pavel Pipek	
	Rector's Mobility Fund of the Charles University	Dr. Pavel Pipek	
Abstract:	New Zealand is home to around 40 alien bird species, but about 80 more were introduced in the 19th century and failed to establish. As most of these introductions were deliberate and documented in detail by the Acclimatisation Societies responsible for them, New Zealand bird invasions are often used as a model system to unravel what determines the outcome of introduction events, especially the role of propagule pressure. However, the credibility of these data was challenged recently, as different authors have reported different numbers of liberated birds. This discrepancy has several causes. Using introductions of Eurasian skylark (Alauda arvensis) and Common starling (Sturnus vulgaris) as examples, we show that the most important issue is that not all liberated birds were imported from overseas, and so import records underestimate the total propagule pressure for particular regions. There is evidence for the import to New Zealand from overseas of 361 skylarks and 619 starlings, versus at least 1491 and 1678 individuals, respectively, being translocated to other regions within the country. The majority of liberated birds in some regions of New Zealand were translocations from other parts of the country where the species had already previously established. Nelson was the main source of translocated skylarks, while Otago was the main source of translocated starlings. Canterbury, Hawke's Bay and Wellington were the main recipient regions for these translocations. Our findings may have implications for analyses of propagule pressure, as well for studies of population genetics and spread of alien birds in New Zealand.		
Response to Reviewers:	Response to Referee 1. Even so, I believe some relevant variables First, there are contextual details that may		

mapping numbers of the target species finally located in the various locations (other than those arising from imports or translocations)- eg, destruction by farmers and hunters (although the authors make one reference to some discontent amongst farmers (in Otago, unsurprisingly given the focus on grain production there and in Canterbury) it is likely such was widespread given the implementation in 1882 of the Small Birds Nuisance Act), interspecies competition, local climate, food availability, and limitations to natural range.

- The subsequent spread of skylarks is outside the scope of our paper. While the skylarks certainly were later persecuted by farmers, even officially, this process started only after the last translocation in the 1880s. In contrast, starlings were long considered as a beneficial addition to the New Zealand fauna.

Secondly, I note (p7, lines 2-3), that the authors assume that translocations "would have been prefiltered in terms of their ability to survive..." and therefore supply "better quality propagules". This statement appears to suggest a reasonably consistent environment for such species across the country - which is not so - and therefore potentially raises questions around the relative success of translocations over imported birds, and the minimum populations for successful establishment. While it may not disprove the authors' hypotheses, I think this should be specifically mentioned as a limitation or refuted.

- We agree that due to longitudinal orientation of New Zealand, the climatic conditions between particular regions may differ substantially, especially between sub-tropical North and temperate South. With exception of the subtropical part of the North Island, environmental conditions in the other regions would be well within those experienced by the species in its native distribution, which spans a wide range of environmental conditions across Eurasia. In general, climatic conditions in winter in particular are less severe within New Zealand than in the U.K., where skylarks are widespread in summer and winter. Nevertheless, ultimately none of this provides strong support for our statement about pre-filtering, and so we have edited this section, hopefully to make the text less contentious.

Although I would still recommend its publication, I also would like to see limitations identified. It would also be interesting to have avenues for future research. Finally, it may be helpful, at least for those unfamiliar with New Zealand geography or topography, to have the relevant regions and character shown on the maps in figs 1 and 2.

- We updated the figures as indicated. The final paragraph of the manuscript is largely dedicated to suggestions for future studies, albeit that most of this relates to revisiting previous hypotheses. We now state this explicitly.

1 2 3

4 5 6

7

8

9

10

11 12

13

14 15

20 21 22

23

24

25

26

27 28

29

30

31

32

33 34

35

36

37

38 39

40

41

42

43

44 45 46

51 52

53

54

55 56

57

58

59

60 61 62

63 64 65

The Ins and Outs of Acclimatisation: Imports versus Translocations of Skylarks and Starlings in 19th century New Zealand

Pavel Pipek^{1,2,*}, Tim M. Blackburn^{3,4}, Petr Pyšek^{1,2}

¹The Czech Academy of Sciences, Institute of Botany, Department of Invasion Ecology, CZ-252 43 Průhonice, Czech Republic

²Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Prague, Czech Republic

³Centre for Biodiversity and Environment Research, University College London, Gower Street, London WC1E 6BT, United Kingdom

⁴Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK

*ppipek@gmail.com, tel. 00420271015248

Abstract

New Zealand is home to around 40 alien bird species, but about 80 more were introduced in the 19th century and failed to establish. As most of these introductions were deliberate and documented in detail by the Acclimatisation Societies responsible for them, New Zealand bird invasions are often used as a model system to unravel what determines the outcome of introduction events, especially the role of propagule pressure. However, the credibility of these data was challenged recently, as different authors have reported different numbers of liberated birds. This discrepancy has several causes. Using introductions of Eurasian skylark (Alauda arvensis) and Common starling (Sturnus vulgaris) as examples, we show that the most important issue is that not all liberated birds were imported from overseas, and so import records underestimate the total propagule pressure for particular regions. There is evidence for the import to New Zealand from overseas of 361 skylarks and 619 starlings, versus at least 1491 and 1678 individuals, respectively, being translocated to other regions within the country. The majority of liberated birds in some regions of New Zealand were translocations from other parts of the country where the species had already previously established. Nelson was the main source of translocated skylarks, while Otago was the main source of translocated starlings. Canterbury, Hawke's Bay and Wellington were the main recipient regions for these translocations. Our findings may have implications for analyses of propagule pressure, as well for studies of population genetics and spread of alien birds in New Zealand.

Keywords: acclimatisation, alien, birds, New Zealand, propagule pressure

Introduction

Biological invasions by alien species are one of the major facets of anthropogenic environmental change, and pose threats to both biodiversity (Suarez and Tsutsui 2008; Kenis et al. 2009; Winter et al. 2009; Vilà et al. 2011; Ricciardi et al. 2013) and economic activities (Pimentel et al. 2005). To help the search for feasible management or preventive strategies, it is important to understand what it is that makes a species a potential invader. One widely accepted factor that promotes the establishment of alien species is the size of the founding population, generally termed propagule pressure (Lockwood et al. 2005; Blackburn et al. 2009; Simberloff 2009; Cassey et al. 2018). Evidence for a positive effect of propagule pressure on establishment success comes from many taxa and locations (Cassey et al. 2018), but one of the best studied systems in this respect is bird introductions to New Zealand (Blackburn et al. 2011). These introductions were deliberate and in large part organised by dedicated Acclimatisation Societies (Lever 1992), which documented the process in some detail (McDowall 1994). As a result, we have good quality data on the composition of bird shipments brought to New Zealand from overseas, in terms both of the species and the number of individuals imported (e.g. Drummond 1906; Thomson 1922; Long 1981), as well as on the success of the subsequent introductions (Duncan 1997). These data have underpinned several statistical analyses supporting the influence of propagule pressure on establishment success (e.g. Veltman et al. 1996; Green 1997; Duncan 1997; Sol and Lefebvre 2000; Cassey 2001; Duncan and Blackburn 2002; Duncan et al. 2006; Blackburn et al. 2011; Moulton et al. 2011, 2012).

Although the Acclimatisation Society data on bird introductions to New Zealand are probably the best available for a non-experimental system, they are nevertheless not without problems. As has already been pointed out (Moulton et al. 2011), studies differ greatly in the exact numbers of individuals of a given species they report as released, especially for Canterbury province (Thomson 1922; Veltman et al. 1996; Duncan 1997; Lever 2005). This has led to the credibility of the Acclimatisation Society data being questioned, and along with it the propagule pressure effect (Moulton et al. 2011, 2012) – although that effect is a general finding from tests from a range of experimental and historical data sources (Cassey et al. 2018).

Pipek et al. (2015a, b) identified two types of error that may be perpetuated in studies (Thomson 1922; Lamb 1964; Veltman et al. 1996; Lever 2005) dealing with the history of acclimatisation in New Zealand, and that can lead to incorrect estimates of propagule pressure. First, some data on introductions may be missing. For example, Thomson (1922) missed a large shipment on the Tintern Abbey in 1875, which had around 800 birds on board. Missing data lead to propagule pressure being underestimated. Second, some data may be mistakes, when some incorrect data have been included in estimates of propagule pressure. One type of mistake is when birds were imported but never actually liberated; for example, a large shipment of birds that arrived to New Zealand in 1880 on the Waimate, included in Lamb (1964), was in fact sent on to Australia. Williams (1969) included information about 300 skylarks liberated in Canterbury province, which in fact concerned only 165 surviving birds. Mistakes can lead to over- or underestimation of propagule pressure, depending on the type of error concerned. Both types of error can be propagated between studies in a process of "Chinese whispers". For example, Williams' (1969) claim that 108 yellowhammers were ordered from England in 1872 and 40 liberated in 1875 seems to have morphed into Lever's (2005) statement that 148 were freed in Canterbury. In reality, out of the 108 ordered, only 34 arrived, and the 40 from 1875 were actually South Canterbury's share of 180 yellowhammers arriving on the Tintern Abbey (Pipek et al. 2015b).

One potentially important source of both of these types of error in Acclimatisation Society data concerns translocations, an issue that was identified by Star (2014), and subsequently – and independently – by Pipek et al. (2015a). We define translocations as referring to birds transferred between acclimatisation regions within New Zealand, to distinguish them from imported birds brought in from overseas. Studies of propagule pressure have typically focused on the latter group, as quantified by Acclimatisation Society records of birds purchased from overseas. However, translocated birds may have contributed substantially to propagule pressures for some species in some regions. For example, significant numbers of birds liberated by the Otago Acclimatisation Society (assumed by Moulton et al. 2014 to be introductions of individuals from overseas) were translocations of

individuals from populations already established in New Zealand (Pipek et al. 2015a). Likewise, the 165 skylarks erroneously recorded as 300 by Williams (1969) were birds translocated from a population already established in Nelson. This may be a problem if translocations have sometimes been included in propagule pressure figures, but other times not. Thus, Veltman et al. (1996) included in their estimates of propagule pressure birds released on Stewart Island which were in fact individuals relocated from Otago, and not imported from overseas (see also Pipek et al. 2015a, b). However, the translocations identified by Moulton et al. (2014) to Otago were not included in Veltman et al.'s data. Recent experience leads us to suspect that translocations happened systematically and on a large scale between New Zealand acclimatisation regions (Pipek et al. 2015a, b).

Given this background, here we use a case study of two bird species introduced by Acclimatisation Societies to New Zealand – Eurasian skylark (*Alauda arvensis*) and Common starling (*Sturnus vulgaris*) – to explore the extent to which translocations may have contributed to propagule pressure. We mined historical archives to obtain answers to three questions: (i) How many individuals were imported from overseas to the New Zealand regions of interest? (ii) Which of these regions then became donors and which acceptors of translocated birds? (iii) What proportion of birds liberated within accepting regions was of New Zealand origin? We focus on introductions of skylarks and starlings because preliminary research (Pipek et al. 2015a, b) showed that these two species were the most frequently translocated passerines in New Zealand. Exploring the origin of released birds is important not only to ensure correct estimates of propagule pressure, but also to improve the robustness of genetic studies on alien populations, and to help trace the spread of specific invasions.

Methods

We followed the methods previously described in Pipek et al (2015a) and browsed all articles available in Paperspast newspaper archive (https://paperspast.natlib.govt.nz/newspapers) that contained the name of the species of concern (starlings, skylarks) between 1860s and 1870s. We located such articles using "skylark", "sky*lark", "lark" and "starling", in singular and plural form, as search terms. Along with the data from newspapers, we extracted information from annual reports, cashbooks, letterbooks and minute books of individual Acclimatisation Societies. Relevant articles are referenced directly in the text with the appropriate link, as the authors are mostly anonymous. The documents of the societies are referenced in a standard way.

Subsequent to the submission of our original manuscript, we were made aware of a paper that used a similar approach to search the newspaper archive for information on skylark introductions and translocations (Star 2014). Star's data are broadly similar to ours, but not as comprehensive, as he did not search Acclimatisation Society documents, and in addition did not search for "lark" or "larks". Our use of these latter search terms introduces the possibility that we may include woodlarks (*Lullula arborea*) in our data, as these were also shipped to New Zealand. However, woodlarks were specifically named in only four, largely unsuccessful shipments, and we are aware of only three surviving individuals (on the Wild Duck to Auckland in 1872). For the sake of clarity, shipments which included birds identified just as "larks" are marked in Table 1. In the case of translocations, there is no doubt that all "larks" are skylarks, as woodlarks never established a viable population that could serve as a source for translocations.

Duncan (1997) separated propagule pressure to New Zealand among four acclimatisation districts: Auckland, Wellington, Canterbury and Otago. However, there were more Acclimatisation Societies active at the time, some of which were organising shipments of birds from overseas. These were ignored by Duncan (1997) because the data were

incomplete or missing altogether. Here, we add data from Hawke's Bay, Wanganui, Taranaki, Nelson, West Coast, Marlborough and Southland districts, which were either actively introducing alien species (Wanganui, Nelson, Hawke's Bay, Southland, Taranaki), or were clearly separate administrative units for the purposes of acclimatisation (Marlborough, West Coast), and Stewart Island, which is separated from the "mainland". We are aware of some problems associated with the additional societies. For example, records for the Hawke's Bay and Nelson societies were lost, meaning that here we have to rely only on the information from newspapers, whereas for other very active regions (Auckland, Canterbury, Otago, Wellington), we can cross-check information in newspapers with Acclimatisation Society records. We included data from further smaller Acclimatisation Societies (e.g. Hawera, Wairarapa, South Canterbury) within the larger districts.

We use the data obtained from the various sources to quantify the numbers of skylarks and starlings imported from overseas to the principal Acclimatisation Society regions, and the numbers of birds of these two species translocated between these regions. From the 1870s, Auckland and Otago Acclimatisation Societies were also redistributing starlings (the latter also skylarks) to their remoter districts to help their spread (e.g. Auckland Acclimatisation Society 1870, 1871, 1872, 1873; Otago Acclimatisation Society 1875, 1878). We ignored these redistributions, however, as they do not result in incorrect estimates of the number of individuals introduced to a region.

Results

Shipments of skylarks and starlings into New Zealand from overseas for which there is a written record are listed in Table 1. Known translocations of birds from one region to another within New Zealand are listed in Table 2 for skylarks and in Table 3 for starlings. The total number of birds shipped in from overseas (361 for skylarks, 619 for starlings) is lower than reported by Thomson (1922), Veltman et al. (1996) or Lever (2005) for both species (Table 4), even though our data are based on more shipments. The higher totals of 391 skylarks and 653 starlings in Thomson (1922) and Veltman et al. (1996) are primarily due to the inclusion of data on translocations of birds within New Zealand, to Wellington and Stewart Island, by Thomson (1922) and subsequently duplicated by Veltman et al. (1996). Lever (2005) also incorporated a further 300 skylarks in his total for this species although this number is incorrect, as noted in Table 4.

Eurasian skylarks

The main source of translocated skylarks was the Nelson region of South Island, although this was not the region where most skylarks were imported (Table 1). Skylarks arrived in Nelson from overseas in at least five separate shipments, four of which (the Napier in 1863, Violet in 1864, Magna Bona in 1865, and Gertrude in 1868) were direct from London, and the fifth (Prince Alfred in 1864) from Australia. In total, 42 skylarks were imported from England, and this number was apparently sufficient to establish a viable population in Nelson. Thomson (1922) reports that other viable populations were established in Canterbury, Otago, Wellington and Auckland.

Between 1871 and 1878, at least 1180 skylarks were translocated from Nelson to other regions within New Zealand, while another 48 were translocated from Otago to Canterbury (Table 2, Figure 1), and 12 from Canterbury and 37 from Otago to Southland. The principal recipient of Nelson's skylarks was Canterbury, where more than 634 birds were sent – an order of magnitude more than were imported to Canterbury from England or Australia (Tables 1, 4). These translocations are the major cause of discrepancy in propagule

pressure estimates between Thomson (1922) and other authors (Duncan 1997, Lever 2005). In Otago, the numbers of imported and translocated skylarks were similar, at 153 and 205 birds, respectively (Table 1, 4).

Common starlings

Starlings were imported from England in much larger numbers than skylarks (Tables 1, 4). Most starlings that were translocated within New Zealand came from one population in Otago, which successfully established from imported birds (Table 3, Figure 2). However, they were also successfully introduced from overseas to Auckland, and subsequently distributed to other regions within the greater Auckland area, and to other regions on the North Island. Starlings also established a population in Canterbury from overseas stock, although they were not further exported from there. Thomson (1922) reports that a viable population was also established in Wellington.

Starlings were imported to Auckland in at least nine shipments (the Lord Ashley, Cashmere in 1862, Aloe 1863, Kaikoura 1867, Water Nymph in 1867, Novelty, Empress and Mataura in 1868, and Maori in 1869), where at least 118 were imported in total (Table 1). From 1869 starlings were being caught and distributed to further districts (Auckland Acclimatisation Society 1870) and from 1871 also to other regions (Auckland Acclimatisation Society 1872), although probably to a lesser extent (Table 2). They were expected to come to Nelson, where they became scarce (Star 18 Nov 1870), in exchange for skylarks (Evening Star 21 Jun 1871), but this transaction was never confirmed by newspapers. The precise number of birds transported is, however, in most cases unknown.

At least 205 starlings were imported to Otago in five separate shipments (the Star of Tasmania in 1864, William Davie in 1867, Warrior Queen in 1868 and 1869, Lady Jocelyn 1873; Table 1) and by 1872 the species was firmly established, especially in the East Taieri region (Otago Acclimatisation Society 1872). The process of translocation within New Zealand started in 1872, but the Otago Acclimatisation Society was most active in this regard in the 1880s. The principal recipients were Wellington (418) and Hawke's Bay (445, including those from Auckland) on the North Island. While Nelson furnished Southland with some starlings in 1874, seven years later starlings were sent from Otago to Nelson (Table 3).

Discussion

Ecological theory tells us that founding population size is a critical factor for the persistence of biological populations. It matters for native species colonising areas naturally, in conservation reintroductions (IUCN/SSC 2013), and for alien species moved by human agency. The importance of propagule pressure as a determinant of alien establishment success is not in doubt (Cassey et al 2018). However, it is important for our understanding of the invasion process, and when designing management or preventive strategies, to understand exactly how variation in propagule pressure translates into establishment success or failure (Lockwood et al. 2005). This requires our data on introductions to be as accurate as possible. Given that New Zealand Acclimatisation Society records are considered to be the gold standard in respect of historical introduction data, the potential presence of errors in them clearly requires investigation. Our analysis shows that there is the potential for such errors because of the different origins of introduced individuals.

We have demonstrated that translocations of alien birds within New Zealand were happening on a much larger scale than previously suspected by the biological community, although a paper by Star (2014) published in the historical literature, independently reached

the same conclusion. Our more comprehensive search of the available historical literature sources, including Acclimatisation Society documents, revealed evidence for the import to New Zealand from overseas of 361 skylarks (out of which 22 were referred to just as "larks") and 619 starlings (Table 1), versus at least 1491 (Table 2) and 1678 (Table 3) individuals, respectively, being translocated to new acclimatisation regions from other parts of New Zealand. Thus, translocations outnumber imports by roughly three or four to one, at least for the two species analysed here. Although we cannot be sure what proportion of imported and translocated birds were actually liberated into the environment in a given region, it is highly likely that most liberated birds derive from translocations. Nelson was the main source of translocated skylarks (Table 2), while Otago was the main source of translocated starlings (Table 3). Canterbury, Hawke's Bay and Wellington were the main recipient regions for these translocations (Table 4). For some regions, the majority of birds released were of New Zealand origin. Our work dismisses the notion that starlings became numerous in Hawke's Bay from only four founders (Thomson 1922; Lever 2005). Not only were they actually imported in larger numbers (Table 1), many starlings were also translocated on a large scale from Otago to Hawke's Bay: as many as several hundred birds went there (Table 3).

The population of skylarks in Nelson was established from 41 birds imported in the period 1863–1868 (although only one bird was imported after 1865; Table 1), and evidently flourished there. Indeed, in 1867 they were already declared as perfectly acclimatised (Nelson Examiner and New Zealand Chronicle 4 May 1867), in the 1870s they were already so numerous that they built nests within the town (West Coast Times 9 Dec 1870), and it was said that Nelson could "stock all New Zealand without missing the birds taken away" (Nelson Examiner and New Zealand Chronicle 17 May 1873). In fact, the skylarks started to be considered a nuisance in agricultural fields by some (Otago Daily Times 30 Nov 1870; Colonist 18 Apr 1873). In less "fortunate" regions of New Zealand, though, skylarks were scarce, if present at all, and their arrival still desired (Canterbury Acclimatisation Society 1871; Press 25 Feb 1871; Otago Witness 12 Apr 1873; Star 21 Nov 1870), in evident ignorance of the problems of which they had been accused elsewhere (Press 31 Oct 1872). Although the Canterbury Acclimatisation Society had already been importing skylarks from Nelson, and it seemed unreasonable to risk expensive import from London (Lyttelton Times 15 Jun 1871), skylarks were nevertheless brought from England in the 1870s: five arrived on the Charlotte Gladstone in 1872 (Star 7 Feb 1872) and about twenty on the same ship the following year (Star 3 Mar 1873) (Table 1).

To the best of our knowledge, translocations have either been overlooked in previous tallies of introduced birds, or if included, misclassified as direct imports (Thomson 1922; Williams 1969; Lever 2005; Santos 2012; Moulton et al. 2014). An important question is how recognition of these translocations affects our understanding of the effect of propagule pressure on alien bird establishment success in New Zealand. There are at least two issues here – the effect of translocations on propagule pressure, and the effect of translocations on propagule quality.

With respect to propagule pressure, for translocations to happen some alien populations must have established from birds imported from overseas. For starlings, for example, the import and introduction of 118 birds to the Auckland acclimatisation region between 1862 and 1869 was sufficient to found a persistent population (Table 1), and one robust enough to contribute birds to other regions. The records show that Auckland received no translocated starlings, but was the source for birds translocated to Hawke's Bay, Taranaki and Wanganui (Table 3). Here, there is no doubt that the maximum propagule pressure needed to found a population of starlings in the Auckland region was 118 birds, and that all these birds were directly imported from overseas. In contrast, 53 starlings were imported to Hawke's Bay in 1873 and 1876 (Table 1). This number was supplemented by 439 birds from

61 62

63 64 65

Otago between 1877 and 1881, and further six from Canterbury in 1885, with an unknown additional number coming from Auckland in 1871 and 1876, thus bracketing the 1873-76 introduction dates for imported birds (Table 3). While the population could have been founded from just the 53 birds imported, it is more likely that the 445+ translocated birds would also have contributed. While Thomson's (1922) estimates of propagule pressure for skylark and starling are relatively close to the true numbers imported in total from overseas, and even within some regions, these propagules were added to by around three times as many birds translocated between acclimatisation districts within New Zealand (Table 4). While not all districts received translocated individuals, previous estimates of propagule pressure for some districts are therefore likely to have been underestimated, often significantly so.

With respect to propagule quality, the question is whether translocated and imported birds are equivalent. It seems most likely that they are not. The great majority of imported birds would have had to endure a trans-equatorial sea voyage lasting several weeks, where mortality rates were often high (Pipek, Blackburn, Cassey, Delean, Sekercioğlu & Pyšek, unpublished ms.), although mortality could be high even in short-distance translocations: 45% of skylarks transported from Nelson to South Canterbury in 1875 died on the way (Timaru Herald 12 Nov 1875). As a result, translocation seems likely to supply propagules in better condition for founding new populations within New Zealand. The proximity of source and destination locations also means that larger numbers of birds can more easily be moved (cf. the last two columns in Table 4). This suggests the hypotheses that alien populations would be more likely to establish from a given number of translocated birds than from the same number of imported birds, for reasons of quality, and that propagule pressures would be on average higher for translocated birds. Our data support the second of these two hypotheses for skylarks and starlings, but for that reason make the first hypothesis untestable. Nevertheless, both sources of birds (importation and translocation) add to the size of founding populations, and so increase the likelihood of establishment. There is a strong case for revisiting analyses of the effect of propagule pressure on establishment success in New Zealand birds in the light of this.

Although we have primarily considered the issue of translocation of alien birds within New Zealand in terms of its potential effect on the relationship between propagule pressure and establishment success, it is also of relevance to other questions concerning these invasions. For example, Briskie & Mackintosh (2004) used propagule pressure data to assess the effect of population bottlenecks on egg failure rates in alien passerines in New Zealand. Their measure of bottleneck size was propagule pressure, from data in Long (1981) and Thomson (1922). Clearly, those numbers may be affected by confusion between imported and translocated birds. Studies on topics such as changes in genetic variability after establishment (Merilä et al. 1996), the development of geographic structure in alien ranges (Ross 1983), or patterns of spread following introduction (Duncan et al. 1999), will all also be affected by a failure to recognise translocations, or a failure to distinguish translocations from imports. Revisiting these hypotheses in the future with our revised and better understanding on the naturalisation process represents a clear opportunity for future research. While translocation clearly may affect the conclusions of previous studies of the invasion process from New Zealand, the quality of information available from there, through Acclimatisation Society records and digitised newspaper archives, means that data from this country are likely once again to be the gold standard for studies of this feature of the invasion process.

Acknowledgements

Pavel Pipek and Petr Pyšek were supported by long-term research development project RVO 67985939 (The Czech Academy of Sciences). We also thank Hlávka foundation, the Rector's Mobility Fund of the Charles University for financial support, CBER, University College London and BioProtection Centre, Lincoln for facilities. We thank the staff of National Library in Wellington, Hocken Archive in Otago, Archives New Zealand in Christchurch, Central City library in Auckland and Research Library of Te Papa museum for their assistance. We also thank Richard Duncan and one anonymous reviewer for useful comments, and Paul Star for drawing our attention to his related article.

References

- Auckland Acclimatisation Society (1868) Report of the Auckland Acclimatisation Society for 1867-1868. Daily Southern Cross, Auckland
- Auckland Acclimatisation Society (1869) Report of the Auckland Acclimatisation Society for 1868-1869. C. Williamson, Auckland
- Auckland Acclimatisation Society (1870) Report of the Auckland Acclimatisation Society for 1869-1870. William Atkin, Book and general printer, Auckland
- Auckland Acclimatisation Society (1871) Report of the Auckland Acclimatisation Society for the year ending February 28, 1871. New Zealand Herald, Auckland
- Auckland Acclimatisation Society (1872) Report and Financial statement of the Auckland Acclimatisation Society for the year ending February 29, 1872. C. Williamson, Auckland
- Auckland Acclimatisation Society (1873) Report and Financial statement of the Auckland Acclimatisation Society for the year ending February 28,1873. William Atkin, Book and general printer, Auckland
- Auckland Acclimatisation Society (1877) Report and Financial statement of the Auckland Acclimatisation Society for 1876-1877. William Atkin, Book and general printer, Auckland
- Auckland Acclimatisation Society (1878) Report and Financial statement of the Auckland Acclimatisation Society for 1877-1878. William Atkin, Book and general printer, Auckland
- Blackburn TM, Lockwood JL, Cassey P (2009) Avian invasions: the ecology and evolution of exotic birds. Oxford University Press, Oxford
- Blackburn TM, Prowse TAA, Lockwood JL, Cassey P (2011) Passerine introductions to New Zealand support a positive effect of propagule pressure on establishment success. Biodivers Conserv 20:2189–2199. doi: 10.1007/s10531-011-0081-5
- Canterbury Acclimatisation Society (1871) Seventh annual report of the Canterbury Acclimatisation Society. Daniel Hagett, Christchurch
- Canterbury Acclimatisation Society (1873) Ninth Annual report of Otago Acclimatisation Society. Christchurch
- Cassey P (2001) Determining variation in the success of New Zealand land birds. Glob Ecol Biogeogr 10:161–172
- Cassey P, Delean S, Lockwood JL, et al (2018) Dissecting the null model for biological invasions: A meta-analysis of the propagule pressure effect. PLOS Biol 16:e2005987. doi: 10.1371/journal.pbio.2005987

Drummond J (1906) On Introduced Birds. Trans New Zeal Inst

Duncan RP (1997) The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. Am Nat 149:903–915. doi: 10.1086/286029

- Duncan RP, Blackburn TM (2002) Morphological over-dispersion in game birds (Aves: Galliformes) successfully introduced to New Zealand was not caused by interspecific competition. Evol Ecol Res 4:551–561
- Duncan RP, Blackburn TM, Cassey P (2006) Factors Affecting the Release, Establishment and Spread of Introduced Birds in New Zealand. In: Allen RB, Lee WG (eds) Biological Invasions in New Zealand. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 137–154
- Green R (1997) The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. J Anim Ecol 66:25–35
- IUCN/SSC (2013) Guidelines for Reintroductions and Other Conservation Translocations.
- Kenis M, Auger-Rozenberg M-A, Roques A, et al (2009) Ecological effects of invasive alien insects. Biol Invasions 11:21–45. doi: 10.1007/s10530-008-9318-y
- Lamb RC (1964) Birds, beasts and fishes: the first hundred years of the North Canterbury Acclimatisation Society. Caxton, Christchurch
- Lever C (1992) They Dined on Eland: The Story of the Acclimatization Societies, 1st edn. Quiller Pr
- Lever C (2005) Naturalised birds of the world. T & A D Poyser, London
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol. Evol. 20:223–228
- Long JL (1981) Introduced birds of the world. David & Charles, Newton Abbot
- McDowall RM (1994) Gamekeepers for the Nation: The story of New Zealand's acclimatisation societies, 1861-1990. Canterbury University Press, Christchurch
- Merilä J, Björklund M, Baker AJ (1996) The successful founder: genetics of introduced Carduelis chloris (greenfinch) populations in New Zealand. Heredity (Edinb) 77:410–422. doi: 10.1038/hdy.1996.161
- Moulton MP, Cropper WP, Avery ML (2011) A reassessment of the role of propagule pressure in influencing fates of passerine introductions to New Zealand. Biodivers Conserv 20:607–623. doi: 10.1007/s10531-010-9969-8
- Moulton MP, Cropper WPJ, Avery ML (2012) Historical records of passerine introductions to New Zealand fail to support the propagule pressure hypothesis. Biodivers Conserv 21:297–307. doi: 10.1007/s10531-011-0165-2
- Moulton MP, Santos ESA, Cropper WPJ, Lim JN (2014) New records for passerine introductions to the Otago Acclimatisation Region in New Zealand. Notornis 61:219–222
- Otago Acclimatisation Society (1867) Third Annual Report of the Otago Acclimatisation Society. Henry Wise, Printer, Dunedin
- Otago Acclimatisation Society (1871) Seventh Annual Report of the Otago Acclimatisation Society. Dunedin
- Otago Acclimatisation Society (1872) Eighth Annual report of Otago Acclimatisation Society. Dunedin
- Otago Acclimatisation Society (1875) Tenth Annual report of Otago Acclimatisation Society
- Otago Acclimatisation Society (1878) Eleventh and Twelth Annual Report of the Otago Acclimatisation Society. Dunedin
- Otago Acclimatisation Society (1880) Fourteenth Annual Report of the Otago Acclimatisation Society. Dunedin
- Otago Acclimatisation Society (1882) Sixteenth Annual Report of the Otago Acclimatisation Society.

Dunedin

- Otago Acclimatisation Society (1883) Seventeenth Annual Report of the Otago Acclimatisation Society. J.Wilkie & Co, Booksellers, Dunedin
- Otago Acclimatisation Society (1886) Twentieth Annual Report of the Otago Acclimatisation Society. Dunedin
- Otago Acclimatisation Society (1891) Twenty-fifth Annual Report of the Otago Acclimatisation Society. Dunedin
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288. doi: 10.1016/j.ecolecon.2004.10.002
- Pipek P, Pyšek P, Blackburn T (2015a) A clarification of the origins of birds released by the Otago Acclimatisation Society from 1876 to 1882. Notornis 62:105–112
- Pipek P, Pyšek P, Blackburn TM (2015b) How the Yellowhammer became a Kiwi: the history of an alien bird invasion revealed. NeoBiota 24:1–31. doi: 10.3897/neobiota.24.8611
- Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr 83:263–282. doi: 10.1890/13-0183.1
- Santos E (2012) Discovery of previously unknown historical records on the introduction of dunnocks (Prunella modularis) into Otago in the 19th century. Notornis 59:79–81
- Simberloff D (2009) The Role of Propagule Pressure in Biological Invasions. Annu. Rev. Ecol. Evol. Syst. 40:81–102
- Sol D, Lefebvre L (2000) Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos 90:599–605. doi: 10.1034/j.1600-0706.2000.900317.x
- Star P (2014) Human Agency and exotic birds in New Zealand. Environment and History 20: 275-299. doi: 10.3197/096734014X13941952681070
- Suarez A V., Tsutsui ND (2008) The evolutionary consequences of biological invasions. Mol Ecol 17:351–360. doi: 10.1111/j.1365-294X.2007.03456.x
- Thomson G (1922) The naturalisation of plants and animals in New Zealand. Cambridge University Press, Cambridge
- Veltman CJ, Nee S, Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. Am Nat 147:542–557
- Vilà M, Espinar JL, Hejda M, et al (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702–708. doi: 10.1111/j.1461-0248.2011.01628.x
- Wanganui Acclimatisation Society (1870) Report. Wanganui
- Williams GR (1969) Introduced birds. In: Knox GA (ed) The Natural History of Canterbury. Reed, Wellington, pp 435–451
- Winter M, Schweiger O, Klotz S, et al (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. Proc Natl Acad Sci U S A 106:21721–5. doi: 10.1073/pnas.0907088106

Figure 1: Propagule pressures of skylarks (*Alauda arvensis*) in different Acclimatisation Society regions. The size of the circle relates to the magnitude of propCaagule pressure (the number indicated within the circle), with the divisions of the circles relating to the proportions of birds deriving from translocation (yellow) and import (red). Lines indicate the translocation of birds between acclimatisation regions, with the direction of movement towards



Figure ² Figure 2: Propagule pressures of starlings (*Sturnus vulgaris*) in different Acclimatisation Society regions. The size of the circle relates to the magnitude of propagule pressure (the number indicated within the circle), with the divisions of the circles relating to the proportions of birds deriving from translocation (yellow) and import (red). Lines indicate the translocation of



Table 1: List of shipments bringing starlings and skylarks from overseas. The species columns list the numbers of birds on each ship that reached the final destination and the numbers originally loaded in the shipments (in parentheses). Shipments which refer to "larks" and not specifically to "skylarks" are in italics.

Year	Ship	Source region	Target region	Skylarks (loaded)	Starlings (loaded)	Reference	Note
1860	Thames city	London	Auckland	3 (60)	0 (36)	Nelson Examiner and New Zealand Chronicle 1 Dec 1860	it was before establishment of the accl. Society, fate is unknown.
1860	Jura	London	Auckland	0	-	Daily Southern Cross 17 Jan 1860	
1862	Cashmere	London	Auckland	10 (12)	12 (12)	Daily Southern Cross 8 Apr 1862, Daily Southern Cross 9 May 1862	
1863	Aloe	London	Auckland	1 (11)	2 (9)	Daily Southern Cross 9 Jun 1863	
1865	Lord Ashley	Australi a	Auckland	-	5	Daily Southern Cross 22 Nov 1862	
1867	Kaikoura	London (via Panama)	Auckland	-	2	Daily Southern Cross 4 Jan 1867	
1867 - 1868ª	Ruahine	London (via Panama)	Auckland	3	-	New Zealand Herald 3 Oct 1867, (Auckland Acclimatisation Society 1868)	Received 2, one later died
	Ida Ziegler	London	Auckland	0	-	Wellington Independent 24 Oct 1867, (Auckland Acclimatisation Society 1868)	Some arrived but likely died
	Water nymph	London	Auckland	3 (150)	11 (200)	Daily Southern Cross 28 Oct 1867, Wellington Independent 5 Dec 1867, (Auckland Acclimatisation Society 1868)	
	Novelty	London	Auckland	4	4	<u>New Zealand Herald 11 Feb 1868, (Auckland</u> Acclimatisation Society 1868)	
1868 - 1869	Empress	London	Auckland	33	19	Daily Southern Cross 14 Mar 1868, Numbers deduced from annual report, 52 skylarks and 82 starling were imported in season 1868/1869, (Auckland Acclimatisation Society 1869)	
	Mataura	UK (via Panama)	Auckland	16 (24)	22 (24)	Wellington Independent 28 Mar 1868	

Table 1

	Maori	London	Auckland	1 (182)	41 (400)	Daily Southern Cross 5 Jan 1869, New Zealand	
						Herald 19 Feb 1869	
	Queen bee	London	Auckland	2	-	New Zealand Herald 19 Jan 1869	
1873	Durham	London	Auckland	?	-	Waikato Times 3 Apr 1873	purchased by the society and liberated in Auckland (the Pah, T.Russells farm)
1874	Waikato	London	Auckland	?	-	Daily Southern Cross 4 Sep 1874	not by the society, for sale
			TOTAL	min 76 (1)	118		both species established
1851	Travancore	London	Canterbury	-	0	Lyttelton Times 10 May 1851	one escaped on the way
1859	Clontarf	London	Canterbury	?	?	<u>Nelson Examiner and New Zealand Chronicle 12 Feb</u> <u>1859</u>	the shipment was very unsuccessful. Only 22 individuals (across species) survived, and later more died.
1861	Gananoque	London	Canterbury	0	-	<u>Press 17 Aug 1861</u>	
1863	Sebastopol	London	Canterbury	6	-	Lyttelton Times 23 May 1863, Lyttelton Times 6 Jun 1863	agrees with (Lamb 1964)
1864	British Empire	London	Canterbury	2 (66)	1 (8)	Lyttelton Times 10 Sep 1864	
1865	Indian Empire	London	Canterbury	2	-	Nelson Examiner and New Zealand Chronicle 1 Aug 1865	
1865	Mermaid	London	Canterbury	4	?	Press 23 Jan 1865, Lyttelton Times 31 Jan 1865	the society likely did not buy any
1867	Matoaka	London	Canterbury	13 (96)	18 (50)	Press 27 Dec 1866, Lyttelton Times 26 Jan 1867	Agrees with (Lamb 1964) – 20 arrived, only 2 starlings destined to liberation in

							Cheviot Hills escaped in Wellington
May 1867 – April 1868	Mermaid	London	Canterbury	?	-	Daily Southern Cross 16 Mar 1868	Great mortality, likely none survived
May 1868 – Dec 1868	Blue Jacket	London	Canterbury	2	0	<u>Press 14 Nov 1868</u>	
1869	Mermaid	London	Canterbury	6	-	<u>Star 13 Feb 1869</u>	
	Zealandia	London	Canterbury	1	-	Press 27 Nov 1869	
1871	Tararua	Australi a	Canterbury	6	13	Nelson Examiner and New Zealand Chronicle 21 Apr 1871	
1871	Robert Henderson	London	Canterbury	-	0 (19)	New Zealand Herald 29 Dec 1871	
1871	Zealandia	London	Canterbury	?	-	Lyttelton Times 12 Dec 1871	12 died during the trip, maybe all.
1872	Charlotte Gladstone	London	Canterbury	5	32 (72)	<u>Star 3 Feb 1872, Star 7 Feb 1872</u> , Otago Acclimatisation Society Letter Book 1867-1878 (17 Feb 1872)	Agress with (Lamb 1964)
1873	Charlotte Gladstone	London (via Otago)	Canterbury	15	40	<u>Star 3 Mar 1873</u>	Agress with (Lamb 1964)
1875	Tintern Abbey	London	Canterbury	-	33 (100)	Press 5 May 1875	Agress with (Lamb 1964)
1879	Waipa	London	Canterbury	?		<u>Otago Daily Times 8 Nov 1879</u>	for sale, along with canaries, etc.
			TOTAL	62 (5)	137		
1055	-	.					
1873	Forfarshire	London	Hawke's Bay	7	23	Wanganui Herald 19 Mar 1873	
1874	Queen bee	London	Hawke's Bay	18	-	Nelson Evening Mail 13 Jan 1875	

1876	Pym	London	Hawke's Bay	-	30	Evening Post 8 Jul 1876, Otago Witness 15 Jul 1876	
			TOTAL	25	53		
1863	Napier	London	Nelson	23 (51)	9 (18)	Colonist 11 Dec 1863	
1863	Prince Alfred	Australi a	Nelson	-	4	Nelson Examiner and New Zealand Chronicle 3 Dec 1863	
1863	Prince Alfred	Australi a	Nelson	2	-	Colonist 3 Nov 1863, Nelson Examiner and New Zealand Chronicle 12 Dec 1863	
1864	Violet	London	Nelson	1	8 or 12 (42)	Colonist 12 Jul 1864, Nelson Examiner and New Zealand Chronicle 7 Jul 1864	All larks for the government (24) died
1865	Magna Bona	London	Nelson	15	-	Nelson Examiner and New Zealand Chronicle 25 Mar 1865, number deduced from annual report (Nelson Evening Mail 3 Apr 1866)	
1868	Gertrude	London	Nelson	1 (120)	6 (40)	Marlborough Express 27 Jun 1868	
			TOTAL	42	min 27		
1864	Lady Milton	London	Otago	?	-	Lyttelton Times 27 Feb 1864	Before the society was established
1864	Star of Tasmania	London	Otago	-	?	Otago Witness 22 Oct 1864	
1866	Warrior Queen?	London	Otago	min 4	-	Otago Witness 3 Feb 1866, Otago Acclimatisation Society 1867	
1867- Mar	William Davie	Glasgow	Otago	6	3	Otago Daily Times 1 Nov 1867	1 skylark died
1868	Warrior Queen	London	Otago	37 (214)	107 (228)	North Otago Times 31 Dec 1867, Otago Acclimatisation Society Minute Book (1871-1891)	at least 23 starlings died later
	Lochiel	London	Otago	?	-	Otago Daily Times 27 Feb 1868	just for sale – not with acc.soc.
April 1868-	Tararua	Australi a	Otago	?	-	Otago Daily Times 18 Apr 1868	just for sale – not with acc.soc.
June 1869	William Davie	London	Otago	?	-	Otago Daily Times 2 Nov 1868	not for the society, but for the museum – Mr. Purdie was

							rearing birds!
1869- 70	Warrior Queen	London	Otago	35 (60)	94 (95)	Letter from 26 Mar 1870	6 skylarks, 10 starlings sent to Oamaru
1870- 71	Warrior Queen	London	Otago	56 (60)	-	Otago Acclimatisation Society 1871	
1873	Lady Jocelyn	Glasgow	Otago	4	1	Evening Star 13 Nov 1873	
1876	Maulesdeen	London	Otago	11	-	Otago Daily Times 17 Mar 1876	
			TOTAL	min 153 (15)	min 205		
1869	Wild Duck	London (via Wellingt on)	Wanganui	-	31	Wellington Independent 14 Jan 1869, Wanganui Acclimatisation Society 1870	Only 15 for the acclimatisation society (13 liberated), 16 for Mr. Harrison
			TOTAL	-	31		
1864	West Australian	London	Wellington	1	0	Otago Daily Times 8 Jul 1864	
1865	Berar	London	Wellington (Wairarapa)	0 (6)	-	Press 19 May 1865	
1866	Electra	London	Wellington	?	-	Wellington Independent 27 Oct 1866	just for sale, unknown, but low number
1866	James Lester	London	Wellington (Wairarapa)	? (12)	? (14)	Wellington Independent 10 Oct 1865	no information about its arrival
1867	Matoaka	London (via Canterb ury)	Wellington	-	2	Lyttelton Times 21 Mar 1867	Escaped, others returned to Lyttelton, originally meant for Mr. Robinson in Cheviot Hills (North Canterbury)

1869	Wild duck	London	Wellington	2 (84)	34	Hawke's Bay Herald 12 Jan 1869, Wellington	Starlings bought by
			_			Independent 14 Jan 1869	people from the
							Hutt, surviving
							skylark given to
							Mr. Borlase who
							had a female
							skylark.
1873	Charlotte	London	Wellington	-	12	Evening Post 15 Mar 1873	to Wairarapa
	Gladstone	(via					
		Otago)					
			TOTAL	3 (1)	48		
			Overall	361	619		
			TOTAL				

^aWhenever possible we merged the shipments from period between two successive annual reports to make the comparison with data from annual reports more convenient.

Table 2	
---------	--

Year	Source region	Target region	Number	Reference	Note
1871	Nelson	Auckland	4	New Zealand Herald 6 Jun 1871	
1871	Nelson	Auckland	12	Colonist 20 Jun 1871, New Zealand Herald 4 Jul 1871	Dtto, should be exchanged for starlings and rooks,
1873	?	Auckland	25	New Zealand Herald 8 Apr 1873, New Zealand Herald 9 Apr 1873	likely already acclimatised in by 1872 (Auckland Acclimatisation Society 1872), these might have served for re-distribution within Auckland
1873	Nelson	Auckland	20	Auckland Star 13 May 1873, Daily Southern Cross 13 May 1873	in 1873 they declared acclimatised (<u>Hawke's</u> <u>Bay Times 21 Nov 1873</u>)
		TOTAL	61		
1871	Nelson	Canterbury	9	Evening Post 4 Jun 1871	listed among birds desirable for importation (Canterbury Acclimatisation Society 1871)
1871	Nelson	Canterbury	36	Nelson Examiner and New Zealand Chronicle 3 Jun 1871, Lyttelton Times 15 Jun 1871	
1872	Nelson	Canterbury	9	Daily Southern Cross 22 Feb 1872, Westport Times 20 Feb 1872	In 1872 still not acclimatised (Canterbury Acclimatisation Society 1873)
1872	Nelson	Canterbury	6	Lyttelton Times 1 Apr 1872	•
1873	Nelson	Canterbury	14	Grey River Argus 29 Jan 1873	
1873	Nelson	Canterbury	120	Wellington Independent 10 Apr 1873	liberated
1875	?	Canterbury	107	<u>Star 30 Jun 1875</u>	All liberated, another ten were meant for Tasmania
1875	Nelson (Ball)	Canterbury - Timaru	165	Timaru Herald 12 Nov 1875	All liberated immediately
1876	Nelson	Canterbury - Timaru	120	Timaru Herald 20 May 1876	
1877	Otago	Canterbury - Timaru	48	Otago reports	

Table 2: Translocation events until 1890 that included skylarks

		TOTAL	634		
1872	Nelson	Otago	?	Otago Witness 6 Apr 1872	Liberated near Blueskin
1873	Nelson	Otago	100	Bruce Herald 11 Apr 1873, Southland Times 15 Apr 1873, Otago Witness 12 Apr 1873	Already in 1872 they were seen in Green Island and North Taieri (Otago report 1872), Bills (maybe Richard)
1873	Nelson	Otago	52	Otago Daily Times 7 Aug 1873	
1875	Nelson	Otago	50	Otago Daily Times 6 Apr 1875, Otago reports	
		TOTAL	202		established in 1874 (Otago report 1874)
1873	Nelson	Southland	84	Southland Times 16 May 1873	
1877	Otago	Southland	37	Otago Acclimatisation Society Minute Book (1871-1891)	To Wyndham, Edendale
1878	Canterbury	Southland	12	Star 27 Mar 1878	
		TOTAL	133		
1879	Otago	Stewart Island	70	Otago Acclimatisation Society 1880	Agrees with Thomson (1922)
		TOTAL	70		
1871	Auckland	Taranaki	?	Auckland reports	
1871	Nelson	Taranaki	12	<u>Taranaki Herald 1 Feb 1871, Taranaki Herald</u> <u>4 Feb 1871, Wanganui Herald 23 Feb 1871,</u> <u>Nelson Evening Mail 21 Mar 1871</u>	

Before 1880	Wanganui	Taranaki- Hawera	6	Hawera & Normanby Star 25 Apr 1887	
		TOTAL	min 18		In 1873, they were rapidly increasing (<u>Otago</u> <u>Witness 11 Oct 1873</u>)
1873	Nelson	Wanganui	17	Evening Post 12 Mar 1873	
1873	Nelson	Wanganui	30	Wanganui Herald 10 Apr 1873, Evening Post 15 Apr 1873, West Coast Times 29 Apr 1873	
1875	Nelson	Wanganui	100	Wanganui Herald 22 Jan 1875	
1875	Nelson	Wanganui	44	Wanganui Chronicle 7 May 1875	
		TOTAL	191		
1871	Nelson	Wellington	Some	Colonist 24 Feb 1871, Nelson Evening Mail 21 Mar 1871	4 remained, the society was formed after this transport (in May) – these birds were for Mr. Ludlam
1871	Nelson	Wellington	20	Colonist 15 Aug 1871	20 were imported in total during this year. This fits.
1873	Nelson	Wellington	?	Nelson Evening Mail 26 Aug 1873	3 cases
1874	Nelson (Ball)	Wellington	12	Wellington Acclimatisation Society Cashbook (1872-1884), <u>New Zealand Times 17 Jul</u> <u>1875</u>)	
1874	Nelson (Ball)	Wellington	40	Wellington Acclimatisation Society Cashbook (1872-1884), pp 13, <u>New Zealand Times 17</u> Jul 1875	
1875	? (Barlow)	Wellington	16	Wellington Acclimatisation Society Cashbook (1872-1884)	
1875	Nelson (Ball)	Wellington	?	Wellington Acclimatisation Society Cashbook (1872-1884)	Wellington introduced 68 that season, which fits – maybe this was just additional payment
1875- 6	Nelson	Wellington	40	Wellington Acclimatisation Society Cashbook (1872-1884), pp 15, Wellington Reports	

		TOTAL	128		
1871	Nelson	West coast	3	Colonist 1 Sep 1871, Colonist 15 Aug 1871	
1871	Nelson	West coast	6	Colonist 15 Aug 1871, West Coast Times 19	
				Aug 1871, Grey River Argus 21 Aug 1871	
1873	Nelson	West coast	21	Grey River Argus 21 Apr 1873	
1876	Nelson	West coast	24	Grey River Argus 30 Oct 1876	
		TOTAL	min 54		
		Overall	1491		
		TOTAL			

	Thomson 1922	Lamb 1964	Williams 1969	Veltman 1996	Duncan 1997	Lever 2005	Imported	Translocated
SKYLARK								
Auckland	62	-		-	62		76	61
Canterbury	31	28	$+300^{d}$	-	434 ^e		62	634
Hawke's Bay	-	-					25	
Nelson	20	-		-	-		42	-
Otago	100 ^a	-		-	100		153	202
Southland	-	-	-	-	-	-	-	133
Taranaki	-	-	-	-	-	-	-	18
Wanganui	-	-	-	-	-	-	-	191
West coast	-	-	-	-	-	-	-	53
Wellington	108^{b}	-		-	108		3	128
Stewart Island	70^{c}	-	-	-	-	-	-	70
TOTAL	391	-		391	704	691 ^f	361	1491
STARLING								
Auckland	109	-		-	109		118	-
Canterbury	60	125		-	125		137	-
Hawke's Bay	-	-					53	445
Marlborough	-	-		-	-	-	-	50
Nelson	17	-		-	-		27	152
Otago	169	-		-	169		205	-
Southland	-	-	-	-	-	-	-	83
Stewart Island	_ ^c	-	-	-	-			22
Taranaki								343
Wanganui							31	105
Wellington	298 ^b	-		-	298		48	418^{h}
West coast	-	-	-	-	-	-	-	60
TOTAL	653	-		653	701	653	619	1678
						+350 by private individuals ^g		

Table 4: Comparison of propagule pressure estimates for skylarks and starlings in different regions from previous studies, and the numbers imported from overseas and translocated from other parts of New Zealand as quantified here.

^a Thomson also mentions that some were brought by private dealers.

^bThomson combined direct import from overseas with translocations from other regions in New Zealand.

^cAll birds that were liberated in Stewart Island in 1879 (including skylarks) were caught in Otago, not imported from Overseas. While skylarks liberated on Stewart Island were noted by Thomson, starlings were not.

^dThis information is a supplement to information otherwise stored in Annual reports. However, it is wrong. 300 were ordered from Nelson, but in the end only 165 arrived (the rest died on the way). Later, batch of another 120 arrived.

^eThe references leading to this number got lost, unfortunately, and therefore cannot be checked (Duncan pers. comm. 2018). The re-locations of skylarks from Nelson to Canterbury are however likely included too.

^fEvidently, Lever merged data from Thomson (1922) with those of Williams (1969), even though he refers only to Thomson.

⁸There is no reference and the author does not remember where this information came from (Lever 2017 pers. comm.). Private efforts on such a large scale would probably be reflected in newspapers, but they are not. That said, the Wellington Acclimatisation Society claims in its report from 1886 that plenty were introduced by private enterprise.

^h Includes translocation of 120 birds to Wairarapa.

Year	Source region	Target region	Number	Reference	Note
1871- 1872	Auckland	Hawke's Bay	min 20	Auckland Acclimatisation Society 1872, <u>New Zealand</u> Herald 10 Jan 1872	
1876- 1877	Auckland	Hawke's Bay	?	Auckland Acclimatisation Society 1877	
1877- 1878	Auckland	Hawke's Bay	?	Auckland Acclimatisation Society 1878	
1877	Otago	Hawke's Bay	36	Otago Acclimatisation Society Minute Book (1871- 1891)	
1880	Otago	Hawke's Bay	307	Hawke's Bay Herald 15 Mar 1880, Otago Daily Times 18 Oct 1880, Otago Acclimatisation Society Cashbook Proper 1864-1900	
1881	Otago	Hawke's Bay	96	Hawke's Bay Herald 7 Feb 1881, Otago Acclimatisation Society Cashbook Proper 1864-1900, Otago Acclimatisation Society 1882	
1885	Canterbur y	Hawke's Bay	6	Daily Telegraph 20 Apr 1885	
		TOTAL	min 445		
1882	Otago	Marlborough	50	Marlborough Express 24 Apr 1882, Otago Acclimatisation Society 1883	
1883	Otago	Marlborough		Otago Acclimatisation Society Cashbook Proper 1864- 1900, <u>Marlborough Express 29 May 1890</u>	Established, maybe 50
		TOTAL	min 50		
1881	Otago	Nelson	100	Otago Acclimatisation Society 1882, Otago Acclimatisation Society Cashbook Proper 1864-1900	
1882	Otago	Nelson TOTAL	52 min 152	Otago Acclimatisation Society 1883	
1872	Otago	Southland	min 11	Otago Acclimatisation Society Cashbook Proper 1864-	

Table 3: Translocation events until 1890 that included starlings

				1900, Southland Times 13 Sep 1872	
1874 Otago		Southland	?	Evening Star 8 Aug 1874, Otago Daily Times 8 Aug	
				<u>1874</u>	
1874	Nelson	Southland		Southland Times 18 Sep 1874, Colonist 29 Sep 1874	5 died on the way
1877 Otago		Southland	72	Otago Acclimatisation Society Minute Book (1871-	
				1891), Otago Daily Times 10 Aug 1877	
		TOTAL	min 83		
		~ ~			
1879 Otago	Otago	Stewart Island	22	Otago Acclimatisation Society 1880	Thomson (1922) surprisingly does not mention this.
		TOTAL	22		
1871-72	Auckland	Taranaki	?	Auckland Acclimatisation Society 1872	
1876-	Auckland	Taranaki	?	Auckland Acclimatisation Society 1872	
1877	Auckland	1 ar anaki	-	Adexiand Accimiatisation Society 1077	
1883	Auckland	Taranaki -	34	Hawera & Normanby Star 5 Feb 1883	
		Hawera/Patea			
1885	Otago	Taranaki -	30	Patea Mail 30 Mar 1885	
		Hawera/Patea			
1887	Nelson	Taranaki	24	Taranaki Herald 29 Mar 1887	20 survived
1887	Otago	Taranaki-	140	Hawera & Normanby Star 23 Mar 1887, Hawera &	Likely Ch.Bills own business – not
		Hawera		Normanby Star 25 Apr 1887, Patea Mail 27 Apr 1887	in the Cashbook of Otago
1000		T 1'	117		Acclimatisation society.
1890	Otago	Taranaki - Hawera	115	Otago Acclimatisation Society 1891, Otago Acclimatisation Society Cashbook Proper 1864-1900	
		TOTAL	min 343	Acclimatisation Society Cashoook Proper 1804-1900	
			11111 343		
1874	Auckland	Wanganui	?	Wanganui Herald 12 Mar 1874	
1887	?	Wanganui	105	Wanganui Herald 10 May 1888, Wanganui Chronicle 10	Bought for 10 pounds, that would
				<u>May 1888</u>	not be possible, was it an overseas
					transport. Not from Otago
		TOTAL	min 105		
1877	Otago	Wellington	48	Otago Acclimatisation Society	According to Wellington report
10//	Otago	weinington	40	Otago Accimiansation Society	According to wennigton report

		TOTAL Overall	60 1678		
1881	Otago	West coast	60	Grey River Argus 14 Dec 1886, Otago Acclimatisation Society 1882, Otago Acclimatisation Society Cashbook Proper 1864-1900	5 years later abundant
		TOTAL	min 418		
1883	Otago	Wairarapa	120	Otago Acclimatisation Society Minute Book (1871- 1891), Otago Acclimatisation Society 1886, Otago Acclimatisation Society Cashbook Proper 1864-1900	According to Otago reports, 128 were transported (some died, likely)
1883	Otago	Wairarapa	48	Wellington Acclimatisation Society Cashbook (1872- 1884)	
1883	? (Briggs)	Wellington	34	Wellington Acclimatisation Society Cashbook (1872- 1884)	
1882	Otago	Wellington	100	Otago Acclimatisation Society 1883, Otago Acclimatisation Society Cashbook Proper 1864-1900, Wellington Acclimatisation Society Cashbook (1872- 1884)	Thomson mentions this
1881	Otago	Wellington	14	Otago Acclimatisation Society 1882, Otago Acclimatisation Society Cashbook Proper 1864-1900, Wellington Acclimatisation Society Cashbook (1872- 1884)	Thomson mentions this
1878	Otago	Wellington	54	Wellington Acclimatisation Society Cashbook (1872- 1884), Otago Acclimatisation Society Minute Book (1871-1891), Otago Acclimatisation Society Cashbook Proper 1864-1900	According to Wellington report from 1886, 90 were liberated. It costed 9 pounds, which would equal cc. 70 individuals
				Minute Book (1871-1891), Wellington Acclimatisation Society Cashbook (1872-1884)	from 1886, 60 were liberated