

Morphological over-dispersion in game birds (Aves: Galliformes) successfully introduced to New Zealand was not caused by interspecific competition

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ABSTRACT

A pattern of significant morphological over-dispersion among successfully introduced bird species has previously been documented on several islands. In a recent paper, Moulton *et al.* also document this pattern for game birds introduced to New Zealand and, in line with previous studies, infer that competition among morphologically similar species played an important role in determining the outcome of these introductions. Here, we show that competition among morphologically similar species could not have been responsible for the failure of most game bird introductions to New Zealand because most species were released at widely separated locations or at different times, did not spread and rapidly became extinct if they failed to establish, and would never have encountered other morphologically similar introduced game birds. Even when morphologically similar species were released in the same district at the same time, historical records suggest that it is unlikely that two species were ever released at precisely the same location and, even if they were, competition is an unlikely cause of introduction failures because most species were present in extremely low numbers. Our results imply that factors other than competition can generate patterns of significant morphological over-dispersion in introduced avifaunas. We show that greater introduction effort expended on more morphologically distinct species could account for over-dispersion in game birds introduced to New Zealand.

Keywords: biological invasions, community assembly, competition, game birds, introductions, morphological over-dispersion.

INTRODUCTION

In a recent paper, Moulton *et al.* (2001) describe patterns in the success of game bird (Galliformes) introductions to the Hawaiian Islands and New Zealand. For New Zealand, there is a highly significant pattern of morphological over-dispersion among the successfully introduced game birds. Although introductions to each of the six Hawaiian Islands do not show significant morphological over-dispersion, when results from the Hawaiian

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Islands and New Zealand are combined there is a consistent tendency towards over-dispersion across all islands. Moulton *et al.* (2001) argue that this pattern of morphological over-dispersion is consistent with the failure of some introductions due to interspecific competition and, therefore, that competition between morphologically similar species played an important role in determining the outcome of game bird introductions to these islands (see also Moulton and Pimm, 1987; Moulton and Lockwood, 1992; Lockwood *et al.*, 1993; Moulton, 1993; Lockwood and Moulton, 1994; Moulton *et al.*, 1996; but see Simberloff and Boecklen, 1991, for an alternative view). Because the pattern is most pronounced in New Zealand, competition presumably played a particularly important role in the outcome of game bird introductions to this country.

The data that Moulton *et al.* (2001) present for game birds introduced to New Zealand show that, with one exception (*Oreortyx pictus*), the failed species fall into three clusters of morphologically similar species, with one additional surviving species in each cluster (Fig. 1). For interspecific competition to have generated this pattern implies that there was strong competition among the morphologically similar species in each cluster, resulting in the failure of all but one species. The 'thinning out' of these clusters is what generates the pattern of morphological over-dispersion among the surviving species.

Game birds introduced to New Zealand, however, were typically released on multiple occasions at different locations. For example, Thomson (1922) records that individuals of *Perdix perdix* were released on 25 separate occasions between 1864 and 1909, with those releases occurring at a minimum of 10 separate locations (Appendix 1). Consequently, the failure of *P. perdix* to establish successfully in New Zealand before 1922 resulted from the failure of at least 25 separate introductions. If interspecific competition played an important role in determining the outcome of game bird introductions to New Zealand, as Moulton *et al.* (2001) argue, then interspecific competition must presumably have played a role in the failure of a large number of these introduction attempts.

Here, we show that, in most cases, interspecific competition between morphologically

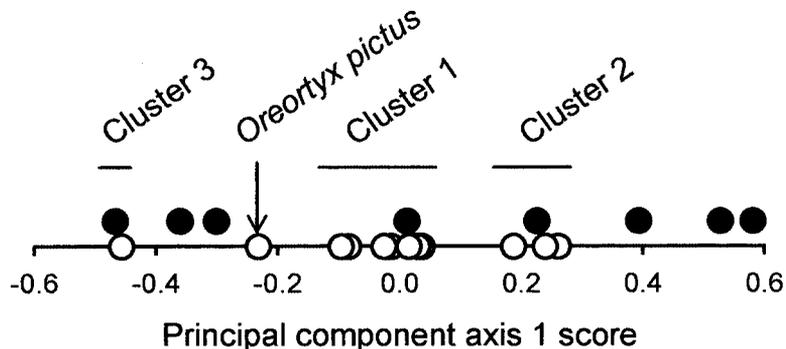


Fig. 1. The morphological relationships of the eight successfully (●) and 12 unsuccessfully (○) introduced game birds in New Zealand (redrawn from Moulton *et al.*, 2001). Species are arrayed along the first principal component axis derived from four morphological measurements made on individuals of each species. Species that are closer together on this axis are more morphologically similar to each other. The three species clusters considered in this study and the failed species *Oreortyx pictus*, which falls outside these clusters, are also shown.

similar species could not have played a role in the failure of game bird introductions to New Zealand because most species were released at widely separated locations or at different times, did not spread and rapidly became extinct if they failed to establish, and would never have encountered other morphologically similar introduced game birds. Even in those cases where morphologically similar species were released in the same district at the same time, competition is an unlikely explanation for introduction failures.

If competition is not the cause of morphological over-dispersion among successfully introduced game birds in New Zealand, what is? One possibility is that over-dispersion arises through biases (conscious or unconscious) in the effort expended in introducing each species (Duncan, 1997). Compared with early introductions, those species introduced later on are likely to be more morphologically similar to species that have already been introduced. The first species introduced had no other introduced game birds that were morphologically similar to it, but progressively later introductions would have been to a fauna more likely to have a similar species previously introduced. Less effort may have gone into introducing species that were similar to previously introduced species because, for game birds at least, similar species may provide essentially the same sporting opportunities for hunters. Since bird species released in lower numbers are less likely to establish successfully (Newsome and Noble, 1986; Pimm, 1991; Veltman *et al.*, 1996; Duncan, 1997; Green, 1997; Duncan *et al.*, 2001), this could lead to later introductions of species that were morphologically similar to species already introduced being more likely to fail. The result would be a tendency towards morphological over-dispersion in the successfully introduced species that was not a result of interspecific competition. We use data on game bird introductions to New Zealand to test several predictions of this non-competitive hypothesis for over-dispersion.

METHODS AND MATERIALS

Evidence for interspecific competition

For New Zealand game birds, the pattern of morphological over-dispersion in the surviving species is generated by the 'thinning out' of morphologically similar species in each of the three clusters shown in Fig. 1. We therefore examined the record of introductions for species in each of these clusters. Cluster 1 comprises *Alectoris gracea*, *A. chukar*, *A. barbara*, *A. rufa*, *Perdix perdix*, *Tympanuchus phasianellus* and *T. cupido*. Cluster 2 comprises *Lophura nycthemera*, *Syrnaticus reevesii*, *Phasianus colchicus* and *Tetrao tetrix*, while cluster 3 comprises *Coturnix pectoralis* and *C. ypsilophora*.

We compiled records of the introductions of these species to New Zealand (see Results for data sources), with an introduction being defined as a separate release of individuals at a particular location or at the same location but in a different year (Appendix 1). For each introduction, we recorded the district (usually defined by the Acclimatization Society that carried out the introduction), the specific location (where given) and the year the introduction took place. We accepted the list of game birds introduced to New Zealand that Moulton *et al.* (2001) used in their analysis (see their Table 1 and Appendix 2).

A significant question in a study of this sort is the quality of the data on which the analyses are based. The robustness of the conclusions drawn depends on the accuracy of the data, which in this case are based on the records of several amateur societies, often dating from more than a century ago. The completeness and accuracy of these records are hard to

guarantee. Nevertheless, records of avian introductions to New Zealand form what is undoubtedly the best and most comprehensive source of information on the introduction process anywhere in the world. Moreover, since we use the same set of sources and species as Moulton *et al.* (2001), both sets of analyses will be equally influenced by any shortcomings of these data.

We determined, for each introduction, if any other introduced game bird in the same cluster (i.e. any other morphologically similar species) could have been present at the same location at the time of release or any time after release and before population extinction (if the introduction failed). Most populations that failed to establish appear to have rapidly become extinct (Thomson, 1922). If there was no record of the length of time that a population persisted following introduction, we assumed the population was extinct within 4 years. It is possible that some failed populations survived undetected and unrecorded for longer. In this case, a few additional populations listed in cluster 1 of Appendix 1 might have overlapped (for example, if the 1875 release of *Perdix perdix* in the Auckland district survived undetected for 6 years, then it could have overlapped with the 1881 release of *Tympanuchus cupido* in the Auckland district). We could extend our arguments to cover these possibilities, but we assume that if a population occurs at such low numbers as to remain undetected for at least 4 years, then it is unlikely to be at sufficient density to competitively exclude other species.

Non-competitive hypothesis for over-dispersion

Dates of first introduction of game bird species to New Zealand were taken from Thomson (1922). From information in Thomson (1922) and Heather and Robertson (1996), we estimated the total number of individuals of each species released and assigned them a rank score as follows: <25 individuals = 1, 26–100 individuals = 2 and >100 individuals = 3. For several species, we could not estimate the total number of individuals released with any great accuracy and we used these rank scores as a measure of introduction effort in our analyses below. We excluded introductions of *Alectoris rufa* that occurred after 1984 because the outcome of these introductions is uncertain. We also excluded *Lophura nycthemera* because there is no evidence that this species was released in the wild (see Results), although our results are qualitatively unchanged if we include it.

The morphological similarity of species was assessed using the scores for the first principal component calculated by Moulton *et al.* (2001) from four variables (mean of unflattened wing chord, culmen from anterior of nares to tip, depth and width of the bill at the anterior margin of the nares). These were used to calculate two indices of morphological difference, MDI and MDA. MDI is the minimum difference between the principal component score for a species and the score for all other game bird species introduced to New Zealand up to the date of introduction of the focal species. MDA is the minimum difference between the principal component score for a species and the score for any other game bird species introduced to New Zealand, and provides a test for morphological over-dispersion. Significant morphological over-dispersion should result in significantly higher MDA scores for successfully introduced species relative to failed species.

If the non-competitive hypothesis for over-dispersion holds, then we predict that: (1) MDI should decrease with introduction date, as later introductions are more likely to have previously introduced species that are morphologically similar, but there is no expectation that this should hold for MDA; (2) species that are more morphologically distinct from

previous introductions (higher MDI) should have greater introduction effort and, consequently, a higher probability of introduction success; and (3) if the greater effort put into the introduction of more morphologically distinct species is the cause of over-dispersion, then introduction effort should be a significant predictor of introduction success having controlled for MDA, but not vice versa. We tested for significant relationships between introduction success, year of introduction, introduction effort, MDI and MDA using logistic regression and Spearman rank correlations.

RESULTS

Evidence for interspecific competition

Cluster 1 (*Alectoris gracea*, *A. chukar*, *A. barbara*, *A. rufa*, *Perdix perdix*, *Tympanuchus phasianellus* and *T. cupido*)

One species in this cluster of morphologically similar species established successfully (*A. chukar*). All introductions of species in this cluster that occurred before 1922 failed (Thomson, 1922). *Alectoris chukar*, however, was first introduced to New Zealand in 1926 (Williams, 1950). Hence, the failure of introductions in this cluster before 1922 could not have been due to competition with the successfully introduced *A. chukar*.

Thomson (1922) lists 40 separate introductions of the failed species in this cluster before 1922 (Appendix 1). Of these, there are nine instances in which two species were present in the same district at the same time (ignoring the release of one individual of *A. rufa* in Canterbury in 1867). Hence, over three-quarters of introductions in this cluster failed in the total absence of a morphologically similar competitor. All six species in this cluster that failed to establish before 1922 had been introduced to at least one location where morphologically similar species were absent at the time (*A. gracea*, Auckland; *A. barbara*, Kapiti Island; *A. rufa*, Canterbury; *P. perdix*, Nelson, Otago, Southland, Taranaki; *T. phasianellus*, Auckland; *T. cupido*, Auckland, Otago).

Even in the nine instances where two species were present in the same district at the same time, there is no evidence that species ever came into contact. For this to have happened would have required a fortuitous set of circumstances in each case. For example, in 1879, the Canterbury Acclimatization Society released 17 individuals of *Tympanuchus cupido* near Mt Thomas in North Canterbury. These birds did not spread far because the last recorded sighting was within 10 km of the release site, at North Loburn, in 1885. In the same year, 'a few' *Perdix perdix* were released at Hororata, about 50 km from the *T. cupido* liberation near Mt Thomas. Given that there is no further record of this population, it presumably failed to establish and spread. A further release of 19 *P. perdix* occurred in Canterbury in 1880, but the precise location of release is not recorded by Thomson (1922). These two species could have come into contact only if the 1880 release of *P. perdix* was to precisely the same location as the *T. cupido* release of 1879. Although this is possible, it appears unlikely because, where documented, different species were never recorded as being released at the same location (Appendix 1). Even if they had been, interspecific competition is an unlikely cause of extinction given the extremely small population sizes and the large areas of habitat that would have been unoccupied by either competitor. Similar circumstances apply to the remaining eight instances where species in this cluster were introduced to the same district at about the same time, before 1922.

Between 1959 and 1970, 28,000 individuals of *P. perdix* were liberated in both North and South Island without success (Heather and Robertson, 1996). The widespread failure of *P. perdix* releases cannot be attributed to competition with *A. chukar*. *Alectoris chukar* has a restricted distribution in New Zealand, particularly in North Island. It was absent in North Island before at least 1950, earlier liberations having failed (Williams, 1950, 1951; note that these failures occurred in the absence of any morphologically similar competitors), and at present only a few birds persist from recent liberations near Tauranga and in Hawke's Bay (Heather and Robertson, 1996). Yet *P. perdix* was released throughout North and South Island and failed at all locations regardless of whether *A. chukar* was present or absent.

Attempts have been made to introduce *A. rufa* to both North and South Island since 1984. Although most releases appear to have failed, it is too early to determine the outcome in some districts (Heather and Robertson, 1996). Notably, however, releases appear to have failed regardless of whether they were to sites within (Nelson, Marlborough, Canterbury, Hawke's Bay) or outside (Kaipara, Taumarunui, Gisborne) the current range of *A. chukar*.

Cluster 2 (*Lophura nycthemera*, *Syrmaticus reevesii*, *Phasianus colchicus* and *Tetrao tetrix*)

Of the four species in this cluster, only *P. colchicus* established successfully following wide-spread liberation.

Thomson (1922) states that *L. nycthemera* 'has only been treated as a bird for the aviary, and there is no record of their liberation'. Nevertheless, Taylor (1868) states that 'The Honorable Henry Walton, of Whangarei, brought the silver pheasant, which is to be found near that place', a statement that could be interpreted as a possible liberation of *L. nycthemera* at Whangarei. Thomson was aware of Taylor's statement, which implies that Thomson did not consider it evidence for a release. This is supported by Hutton (1871), who listed *L. nycthemera* among those species that 'have been bred in the Colony, but are not yet turned out'. Hence, the most likely explanation for the failure of *L. nycthemera* to establish is that it was never liberated in the first place. Even if we accept a liberation of *L. nycthemera* at Whangarei, it is not possible for the three failed species in this cluster to have encountered each other because they were released at locations separated by many hundreds of kilometres, with no record of their spread from those locations. *Tetrao tetrix* was released only in Otago (lower part of South Island), *S. reevesii* was released at Wellington and Wanganui (lower part of North Island), and the one possible release of *L. nycthemera* was at Whangarei (upper part of North Island). The only circumstances in which interspecific competition might have played a role in the failure of species in this cluster to establish would be if introductions of *S. reevesii* and *T. tetrix* had failed due to competition with *Phasianus colchicus*.

For *S. reevesii*, Thomson (1922) records that nine birds were introduced by the Wellington Acclimatization Society in 1897, with no further record, and that 'several' birds were released in Wanganui in 1899 and were never seen again. Competition with *P. colchicus* is an unlikely explanation for the failure of these introductions. Although *P. colchicus* were present in the Wellington and Wanganui districts at this time, they had all but disappeared, having previously been abundant. Thomson (1922) quotes the Wellington Acclimatization Society's report for 1885: 'The number of these birds in this district has decreased of late years', and that pheasants were nearly extinct in the adjacent Wairarapa district. Thomson goes on to state that in the lower North Island, pheasants were 'all but exterminated' at the

time *S. reevesii* was introduced to Wellington and Wanganui. It is most unlikely that competition with *P. colchicus* would have caused the extinction of the *S. reevesii* population when *P. colchicus* was present in such low numbers as to have all but disappeared. Instead of competition with other game birds, more likely explanations for the failure of game bird populations to establish at this time (including populations of *S. reevesii*) are the factors highlighted by Thomson as contributing to the marked decline of *P. colchicus* in many parts of the country: the introduction of stoats, weasels and ferrets, consumption of rabbit poison, poaching, wet weather during the nesting season and the failure of food due to decimation by the large populations of introduced sparrows and starlings. Coupled with these factors is the small number of game birds released at many introduction sites (Appendix 1).

The Otago Acclimatization Society liberated 10 *T. tetrax* in 1879, of which three were subsequently seen in 1882, and they liberated a further three birds in 1900. Thomson (1922), citing the Otago Society report, states that in 1881 *P. colchicus* were plentiful but scattered in Otago, so that it is possible that the *T. tetrax* liberated in 1879 could have encountered *P. colchicus*. However, given that populations of *P. colchicus* were scattered throughout the district, contact is contingent on *T. tetrax* being liberated at a location where *P. colchicus* was present; this is possible but by no means certain. By 1892, *P. colchicus* in Otago were 'few and far between, it is very rare to see one', with the decline attributed to predation by stoats and weasels and to consumption of poison intended for rabbits (Thomson, 1922). With this decline, it requires an even more unlikely set of circumstances to argue that *P. colchicus* had any impact on the failure of the 1900 liberation of *T. tetrax*.

Cluster 3 (*Coturnix pectoralis* and *C. ypsilophora*)

Hutton (1871) lists *C. pectoralis* as introduced to Auckland and Canterbury some time before 1871, where it failed, while Thomson (1922) cites Robert Kemp as stating that *C. pectoralis* was introduced to the Hokianga in the 1870s but failed to establish.

Coturnix ypsilophora was also introduced to Auckland and Canterbury before 1871 (Thomson, 1922), so it is possible that the two species in this cluster came into contact. Like *C. pectoralis*, *C. ypsilophora* failed to establish in Canterbury and at other introduction sites throughout the South Island. Hence, contact between these two species, in Canterbury at least, is contingent on both species being released at precisely the same location at the same time, as both failed to establish and spread from introduction sites. Again, to argue that competition was important in the failure of one or both of these species relies on a particular (and rather unlikely) set of circumstances. Furthermore, *C. ypsilophora* failed to establish at three locations (Otago, Southland and Stewart Island) where *C. pectoralis* was never introduced.

Test of the non-competitive hypothesis for over-dispersion

MDI decreases significantly through time (Spearman $r = -0.76$, $n = 18$, $P < 0.001$), showing that species introduced to New Zealand later were more likely to find morphologically similar species already introduced. MDA is not significantly related to introduction date (Spearman $r = -0.12$, $n = 19$, $P = 0.61$). There is a positive relationship between MDI and introduction effort (Spearman $r = 0.53$, $n = 18$, $P = 0.022$), showing that greater effort was made to introduce game bird species more dissimilar to those already introduced.

Game bird introductions to New Zealand were more likely to succeed if more individuals were introduced ($\chi^2 = 8.83$, $n = 19$, $P = 0.003$), and if the species was more morphologically distinct from previous introductions (higher MDI: $\chi^2 = 6.05$, $n = 19$, $P = 0.014$). Game bird introductions were also more likely to succeed if they were more morphologically distinct from species introduced at any time (higher MDA: $\chi^2 = 4.62$, $n = 19$, $P = 0.032$), demonstrating significant morphological over-dispersion among the successfully introduced species. Nevertheless, multiple logistic regression shows that number of individuals introduced explains significant variation in introduction success independently of MDA ($\chi^2 = 7.69$, $n = 19$, $P = 0.006$), but not vice versa ($\chi^2 = 3.48$, $P = 0.062$).

DISCUSSION

Several lines of evidence refute the claim that interspecific competition was an important factor in the failure of game bird introductions to New Zealand. First and foremost, most introduction failures occurred in the absence of any morphologically similar competitors. Of 60 introductions of game birds in the three clusters before 1922, in only 23 cases could two morphologically similar species possibly have come into contact. Seven of the 11 species in these clusters failed to establish at one or more locations in the total absence of morphologically similar species. Hence, factors other than interspecific competition must have caused most introduction failures.

Second, even when two species were introduced to the same district at the same time, they were invariably released in very low numbers. Given that most introductions failed to establish and spread, contact between species was therefore contingent on the release of one species at precisely the location where the second species occurred. Where introduction locations are documented, the historical record shows that this rarely, if ever, occurred (Appendix 1; Thomson, 1922). Even if we accept that individuals of one species were released at a site occupied by a second species, competition must be regarded as an unlikely cause of population extinction given the small population sizes (more than half of the releases in Appendix 1 involved 20 or fewer individuals that failed to establish) and the large areas of unoccupied habitat that must have been available for colonization by either species.

Third, the widespread release of two species (*Alectoris rufa* and *Perdix perdix*) after 1922 failed regardless of whether introductions occurred to areas with or without a morphologically similar competitor. Finally, observers at the time cited a range of factors they considered responsible for introduction failures or population declines in game birds, principally predation, poisoning, hunting and lack of suitable habitat (Thomson, 1922; Williams, 1950). Competition among game birds is never mentioned as a possible cause, despite the fact that observers were alert to the importance of competition; they highlighted large numbers of starlings (*Sturnus vulgaris*) as a possible cause of population declines in *Phasianus colchicus* through competition for food (Thomson, 1922). Overall, we have to conclude that competition among morphologically similar species was not an important factor in the failure of game bird introductions to New Zealand.

Moulton *et al.* (2001) also tested for a pattern of morphological over-dispersion in game bird introductions to six Hawaiian islands. While successful introductions to each of these islands are not significantly over-dispersed, when results from the Hawaiian islands and New Zealand are combined there is a significant tendency towards over-dispersion across all islands. However, this significant result relies on including the outcome for New Zealand. If we exclude New Zealand, on the basis that interspecific competition could not have

caused the observed pattern of morphological over-dispersion, then there is no significant tendency towards over-dispersion across the remaining six Hawaiian islands (using the maximum likelihood test described by Moulton *et al.*: $\chi^2_{12} = 19.33$, $P = 0.081$), collapsing the argument that interspecific competition was an important factor in the outcome of these game bird introductions.

Our results imply that the significant pattern of morphological over-dispersion documented by Moulton *et al.* (2001) in successfully introduced New Zealand game birds arises through a process other than interspecific competition. Our findings are consistent with the hypothesis that over-dispersion arises through non-randomness in introduction effort. Introduction success for game birds increased with the number of individuals introduced, and more individuals were introduced of species that were morphologically distinct from previously introduced species in this assemblage. Hence, progressive introductions favoured the success of more morphologically distinct species as measured by MDI, which translated into significant over-dispersion as measured by MDA. These outcomes could arise through human efforts to establish a greater diversity of game species, resulting in a pattern of introduction successes that mimics the expected outcome of interspecific competition.

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APPENDIX 1

List of the game bird species in each of the three clusters shown in Fig. 1

Species	Year	District	Location	Number released	Potential competitors
Cluster 1					
<i>Alectoris chukar</i>	1926 on	Widespread	introductions		
<i>A. gracea</i>	1897	Wellington			<i>A. rufa</i> , <i>P. perdix</i>
	1898	Hawera		6	
	1912	Auckland	Kaipara	15	
	1912	Auckland	Waikato	4	
<i>A. barbara</i>	1868	Auckland		2	<i>P. perdix</i>
	1892	Wellington	Kapiti Is.	13	
<i>A. rufa</i>	<1897	Wellington	Rangitikei		<i>A. gracea</i>
	1867	Canterbury		1	
	1897	Canterbury		50	
	1899	Stewart Is.		18	<i>P. perdix</i>
	1984 on	Widespread	introductions		<i>A. chukar</i>
<i>Perdix perdix</i>	1864	Nelson		8	
	1867	Auckland		17	
	1868	Auckland	Howick	20	<i>A. barbara</i>
	1871	Auckland		9	
	1875	Auckland	Takapuna	40	
	1867	Canterbury		10	
	1868	Canterbury		1	
	1871	Canterbury		64	
	1875	Canterbury		a number	
	1879	Canterbury	Hororata	a few	
	1880	Canterbury		19	<i>T. cupido</i>
	1869	Otago		31	
	1871	Otago		130	
	1896	Otago		20	

	1897	Otago		23	
	1900	Otago		44	
	1909	Otago	Milton	several	
	1899	Stewart Is.		48	<i>A. rufa</i>
	1879	Southland	Winton	19	
	1889	Wellington			
	1890	Wellington		3	
	1891	Wellington	Upper Hutt	7	
	1897	Wellington	Masterton	32	<i>A. gracea</i>
	1897	Wellington		16	<i>A. rufa</i> , <i>A. gracea</i>
	1894	Taranaki		8	
	1959–70	Widespread introductions			<i>A. chukar</i>
<i>Tympanuchus phasinellus</i>	1876	Auckland	Piako	22	
<i>T. cupido</i>	1879	Canterbury	Mt Thomas	17	<i>P. peridix</i>
	1881	Auckland		20	
	1882	Auckland		20	
	1882	Otago		20	
Cluster 2					
<i>Phasianus colchicus</i>	1842 on	Widespread introductions			
<i>Lophura nycthemera</i>	1868*	Northland	Whangarei		
<i>Syrmaicus reevesii</i>	1897	Wellington		9	<i>P. colchicus</i>
	1899	Wanganui		several	<i>P. colchicus</i>
<i>Tetrao tetrix</i>	1879	Otago		10	<i>P. colchicus</i>
	1900	Otago		3	<i>P. colchicus</i>
Cluster 3					
<i>Coturnix pectoralis</i>	< 1871	Auckland			<i>C. ypsilophora</i>
	1870s	Auckland	Hokianga		<i>C. ypsilophora</i>
	< 1871	Canterbury			<i>C. ypsilophora</i>
<i>C. ypsilophora</i>	1866	Canterbury		2	<i>C. pectoralis</i>
	1868	Canterbury		5	<i>C. pectoralis</i>
	1871	Canterbury		a number	<i>C. pectoralis</i>
	1867	Auckland		4	<i>C. pectoralis</i>
	1869	Auckland		a few	<i>C. pectoralis</i>
	1871	Auckland		510	<i>C. pectoralis</i>
	1868	Otago	Green Is.	3	
	1870	Otago	Green Is.	9	
	1872	Southland	Wallacetown	4	
	1911	Southland	Awarua	25	
	1912	Stewart Is.			
	1875	Wellington		5	
	1876	Wellington		39	

Note: The known introductions for each species are listed with the year, acclimatization district, location, number of individuals released and a list of the potential competitors (species in the same cluster) that could have been present at the same time in the same district or location. When species were introduced on many occasions at many different locations, they are listed as widespread introductions. We included Stewart Island as a 'district' separate from Southland given its large size and geographical separation. Blank spaces indicate missing data; *indicates no evidence of release into the wild.

