9 Factors Affecting the Release, Establishment and Spread of Introduced Birds in New Zealand

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> *"it was not good work bringing those birds out here; they eat all the potatoes and the oats; they are not good birds to bring out ... were there not plenty of good birds in New Zealand that eat no man's food?"*
> Te Whiti of Parihaka in 1883

9.1 Introduction

Attempts to introduce non-native birds to New Zealand began with the arrival of the first Europeans in 1773, when Captain James Cook liberated geese (*Anser anser*) in Dusky Sound. Not until the mid-1800s, however, did bird introductions begin in earnest with the setting up of acclimatization societies in New Zealand whose major aim was "the introduction, acclimatization and domestication of all animals, birds, fishes, and plants, whether useful or ornamental" (McDowall 1994). The acclimatization societies kept records of the birds they introduced and the outcome of those introductions which, along with information from other sources, was compiled into a book by George Thomson in 1922. Thomson's book, along with other sources, provide a unique record of the history and outcome of bird introductions to New Zealand. Because this record appears reasonably complete and frequently includes details such as the location of individual introductions and the numbers of birds released, these data have been used extensively to address questions about the factors determining whether introductions succeed to establish wild populations (see references in Table 9.1). Given the difficulties of conducting experiments at an appropriate scale to address such questions, these detailed records provide a rare opportunity to gain insight into the mechanisms underlying the successful establishment and spread (i.e. invasion) of species into a novel environment.

Table 9.1 Studies which have used the record of New Zealand bird introductions to quan-titatively address questions concerning factors affecting establishment success or spread following introduction[a]

Reference	Taxonomic group of interest	Species used in analysis (n)
Veltman et al. (1996)	All species	79
Duncan (1997)	Passeriformes	42
Green (1997)	All species	47
Sorci et al. (1998)	All species	79
Duncan et al. (1999)	All established species	34
Legendre et al. (1999)	Passeriformes	31
Sol and Lefebvre (2000)	All species	39
Blackburn et al. (2001)	Established passeriformes	12
Cassey (2001)	All species	118
	All established species	31
Moulton et al. (2001)	Galliformes	20
Duncan and Blackburn (2002)	Galliformes	20
Duncan and Forsyth (2005)	Passeriformes	42

[a]We identified 120 bird species which have been introduced to New Zealand, of which 34 succeeded in establishing. For various reasons, most earlier studies considered only a subset of these species

In this chapter, we review what is known about factors explaining the release, successful establishment and spread of introduced bird species in New Zealand. As a framework for our review, we recognize four stages through which a species must progress in order to successfully invade a new location (Williamson 1996; Kolar and Lodge 2001; Duncan et al. 2003). First, the species must be transported to its new location. Second, the species must be released (or escape) into the environment. Third, the species must establish a self-sustaining wild population. Fourth, to become widespread, that population has to increase in size and spread from its point of establishment. In this chapter, we consider variables likely to explain patterns in the outcome of bird introductions through the last three stages in this invasion process (release, establishment and spread). We do not consider the first stage in the process, and therefore exclude five species transported to New Zealand by acclimatization societies, but which records indicate were not released (*Anas falcata*, *Anser cygnoides*, *Chrysolophus pictus*, *Lagopus mutus*, *Lophura nycthemera*, Thomson 1922), or species which have been transported to New Zealand only to be kept as cage birds. While we will draw extensively on the results of previous studies, most have focused on only a subset of the 120 bird species introduced to New Zealand (Table 9.1).

9.2 Data Sources and Analysis

To identify variables which might explain the patterns of release, establishment and spread, we compiled a list of the 120 bird species which have been recorded as introduced (i.e. transported and released) to New Zealand, based primarily on the information in Thomson (1922), supplemented with data from other sources (Hutton 1871; Buller 1888; Drummond 1907; Williams 1950, 1969; Westerskov 1953; Lamb 1964; Wellwood 1968; Heather and Robertson 1996). Unless historical records stated otherwise, we assumed that all birds introduced for acclimatization purposes were released. Our list of introduced birds differs from previous lists in several ways. First, as far as we can tell, this list is comprehensive and includes more species than have been identified in previous lists (Table 9.1). Second, our list excludes several species which appear in previous lists but for which we could find no evidence of release. For example, Veltman et al. (1996) and Sorci et al. (1998) list the nightingale (*Luscinia megarhynchos*) as having failed to establish following introduction to New Zealand. Thomson (1922) states that all of the nightingales transported to New Zealand died on the journey out, except one which died soon after arriving. We could find no other record confirming the release of this species. We excluded *Pycnonotus cafer*, which established a population in Auckland but which was subsequently eradicated (Turbott 1990).

We obtained an estimate of introduction effort (the total number of individuals released in New Zealand) for 112 of the 120 introduced species. These data varied in quality – for many species, the number of individuals released was recorded whereas for others, only a qualitative estimate was available for some locations (e.g. a few, several). We used this information to classify species into one of three broad effort categories (a total of ≤20, 21–100 or >100 individuals released). These categories result in a loss of information for some species but have the advantage that, given the data available, we could classify all species into categories. In addition, for all species we obtained the following variables: native latitudinal range (degrees), body mass (g), clutch size, incubation period (days), migratory status (migratory, partially migratory, or sedentary) and plumage dichromatism (monochromatic or dichromatic, the latter if the sexes are recognizable on the basis of plumage differences). Relative brain size (the residual deviation for a species from an interspecific regression of brain mass on body mass) was available for 46 species (Sol and Lefebvre 2000; Sol et al. 2002), and year of first release for 113 species.

Our analyses focus on which of the above variables can explain patterns in the release and establishment of species; variables which account for the pattern of spread of introduced birds in New Zealand have previously been identified (Duncan et al. 1999; Cassey 2001). We used generalized linear models (GLMs), specifying a logit link function and binomial error distribution, to

model establishment success or failure (a binary response variable) as a function of the explanatory variables listed above. Closely related species tend to share traits in common, some of which may affect the probability of establishment. If this is the case, then establishment outcomes may be phylogenetically correlated: closely related species are more likely to share the same outcome than are less closely related species, violating the assumption that each observation represents an independent data point. To control for possible non-independence due to phylogeny, we also modelled establishment success or failure using generalized estimating equations (GEEs), an extension of GLMs, to include situations where errors are likely to be correlated (Diggle et al. 1994). We measured phylogenetic correlation for each species pair as the distance from the last common ancestor to the root of the phylogenetic tree divided by the distance from the root to the tip of the tree (i.e. that proportion of the total evolutionary history of the species pair which is shared in common; Martins and Hansen 1997; Garland and Ives 2000). Distance was measured as the number of nodes separating species on a complete phylogeny of the world's birds. This phylogeny was derived from Sibley and Ahlquist (1990), supplemented with information in Sibley and Monroe (1990). GLMs and GEEs were fitted using PROC GENMOD in SAS (1990), with the matrix of between-species phylogenetic distances included as a user-specified correlation matrix when fitting GEEs.

9.3 Factors Affecting Release

Birds which have been released in new locations around the world are not a random subset of the world's bird species (Lockwood 1999; Lockwood et al. 2000; Blackburn and Duncan 2001b). Rather, there is a strong bias towards species in certain taxonomic groups (reflecting the "types" of birds which humans desired for introduction) and species from certain geographic regions (often reflecting the origin of the settlers who transported birds to new locations). Of the 25 families of birds introduced to New Zealand, two families (Anatidae, ducks; Phasianidae, gamebirds) are significantly over-represented relative to their availability in the global avifauna (Table 9.2). Over one-third of the species introduced are in these two families. Species in these two families are also significantly over-represented in bird introductions globally (Lockwood 1999; Blackburn and Duncan 2001b), reflecting repeated attempts by European settlers to establish waterfowl and gamebird populations for hunting in the areas they colonized.

Over half of the bird species introduced to New Zealand originate from Palaearctic and Australasian geographic regions (Table 9.3). This mirrors the pattern for global bird introductions (Blackburn and Duncan 2001b), where settlers at new locations tended to introduce birds from their home region (in

this case, western Europe) and birds found in nearby regions (in this case, Australasia), places with which trade and transport would have been particularly important and frequent.

Nevertheless, only a small proportion of the bird species native to a particular geographic region were transported and released in new locations. The majority of early settlers to New Zealand came from Britain, yet of the 214

Table 9.2 Species introduced and successfully established in New Zealand, by family

Family	Species introduced (*n*)	Species successfully established (*n*)	Species in family[a] (*n*)	*P*[b]
Anatidae	23	4	148	*<0.001*
Phasianidae	21	5	176	*<0.001*
Casuariidae	2		4	0.003
Columbidae	10	3	313	0.005
Odontophoridae	3	1	31	0.007
Pteroclidae	2	–	16	0.016
Passeridae	10	2	388	0.021
Numididae	1	1	6	0.079
Charadriidae	3	–	88	0.094
Fringillidae	17	7	995	0.106
Turnicidae	1		17	0.192
Tytonidae	1	–	17	0.193
Megapodiidae	1	–	19	0.204
Maluridae	1	–	26	0.278
Strigidae	3	1	156	0.297
Alaudidae	2	1	91	0.312
Cracidae	1	–	50	0.471
Halcyonidae	1	1	61	0.530
Paridae	1	–	65	0.556
Sturnidae	2	2	148	0.572
Meliphagidae	2	–	182	0.664
Psittacidae	3	2	360	0.834
Muscicapidae	3	2	452	0.919
Corvidae	4	2	650	0.966
Sylviidae	2	–	560	0.997

[a] Total number of species in each introduced family follows Sibley and Monroe (1990)
[b] The probability of observing as many or more introductions from that family, given the total number of species in the family and the number of species introduced to New Zealand. Italics indicate probabilities which are significantly ($\alpha=0.05$) lower than expected once a sequential Bonferroni correction for multiple tests has been applied. *P* values were calculated by selecting 120 species at random, and without replacement, from the total global avifauna (9,702 species) and summing the number of these randomly chosen species in each family. This simulation process was repeated 4,000 times, and *P* was calculated as the proportion of simulations in which the simulated number of introduced species in the family exceeded the observed number

Table 9.3 Species introduced and successfully established in New Zealand, by biogeographic region of origin

Biogeographic region of origin[a]	Species introduced (*n*)	Species successfully established (*n*)
Palaearctic	41	14
Australasia	30	6
Nearctic	14	3
South-east Asia	12	4
Holarctic	8	2
Afrotropics	6	2
Multi-regional	6	3
Central/South America	2	0
Pacific	1	0

[a] Region definitions follow Blackburn and Duncan (2001b)

breeding bird species in Britain, only 37 were released in New Zealand. These 37 species are a non-random subset of the British birds, being strongly biased towards species which are widespread, abundant and resident in Britain (Blackburn and Duncan 2001b). Hence, British settlers caught, transported and released birds which were common and readily available in their homeland.

Overall, a strong set of historical and cultural factors appear to have influenced the birds released in New Zealand, with European settlers desiring certain types of bird species for introduction. It seems likely that similar patterns in selectivity will hold for other groups of non-native species purposefully introduced to New Zealand.

9.4 Factors Affecting Establishment

In all, 34 of the 120 bird species in our data set successfully established a self-sustaining wild population following release in New Zealand. We consider four categories of variables which might explain why these 34 species succeeded whereas the remainder failed. These are categories which have dominated previous attempts to explain establishment success in many taxa and regions, and not only for New Zealand birds.

9.4.1 Introduction Effort

Small populations are particularly vulnerable to extinction due to demographic and environmental stochasticity, with the probability of extinction declining as population size increases (Richter-Dyn and Goel 1972). For introduced species, we would therefore expect that the more individuals liberated during a release event, the lower the chance of stochastic population extinction, and hence the greater the chance of successful population establishment. Likewise, there is a greater chance of at least one population establishing if a species is subject to a greater number of release events of a given size (Crawley 1989). Several studies show that for birds introduced to New Zealand, both the total number of birds released and the number of separate release events can serve as particularly strong predictors of establishment success (Veltman et al. 1996; Duncan 1997; Green 1997; see Table 9.4). Most species introduced to New Zealand were released in low numbers, which is unsurprising considering the large distances the birds had to travel by ship. In many cases, the introduction of species was poorly planned, and it was not unheard of for entire shipments to die during transport (Thomson 1922). Fewer than 20 individuals were released for 62 of the 112 species for which we obtained data on introduction effort, of which only one species established (cirl bunting, *Emberiza cirlus*). Of the 23 species with 21–100 individuals released, seven established, and of the 27 species with more than 100 individuals released, 20 established. This result for New Zealand birds highlights a consistent pattern: introduction effort is a key factor explaining the outcome of historical introductions in many taxa (Newsome and Noble 1986; Pimm 1991; Hopper and Roush 1993; Duncan et al. 2001; Forsyth and Duncan 2001). The consistency of this relationship implies that it is likely to be a general rule for bird introductions, although the effort required to establish a species may vary between taxa and regions.

Given the importance of introduction effort in explaining establishment success, what factors might determine how many individuals of each species were released? At least for those species introduced to New Zealand from Britain, species which were more abundant in Britain were released in New Zealand more often and in greater numbers (Blackburn and Duncan 2001b). These common British birds were also more likely to establish in New Zealand, at least in part because the more common species tended to be released in greater numbers. Again, the reasons for this are likely to be because common British species were familiar and desired for introduction, and were more easily caught and transported in greater numbers.

In addition, however, species may differ in their ability to survive long-distance transport in ships or in their condition upon arrival. Cassey (2001) found that the greater the distance between the source and the location of introduction for birds, the lower the probability of establishment, and suggested that birds with a greater distance to travel may have arrived in worse

condition. For birds introduced to New Zealand, we lack sufficient data on the numbers which died in transit to test the hypothesis that species differed in their ability to tolerate long-distance travel, but differential survival in transport may have systematically biased the number of individuals of each species available for release.

Table 9.4 Variables included to explain establishment success for birds introduced to New Zealand[a]

Variable	Category	n[b]	Across-species[c]		Phylogeny controlled[d]	
			Estimate	P	Estimate	P
Introduction effort						
No. individuals	≤20	112	−5.16	<0.001	−3.31	<0.001
Released	21–100		−1.88	0.003	−1.90	<0.001
	>100		0			
Environmental match						
Latitudinal overlap	No	120	−1.44	0.062	−1.32	0.025
	Yes		0			
Log_{10}latitudinal range		120	2.76	0.010	1.68	<0.001
Life history traits						
Log_{10}body mass		120	−0.03	0.911	NC[e]	
Log_{10}clutch size		120	−0.86	0.320	−2.61	0.118
Log_{10}incubation		120	−1.60	0.220	−2.41	0.254
Plumage	No	120	0.38	0.355	0.02	0.907
Dichromatism	Yes		0			
Migration	Migratory	120	−1.79	0.094	−0.76	0.078
	Partial		0.68	0.124	0.46	0.049
	Sedentary		0		0	
Relative brain size		46	0.01	0.934	0.28	0.503
Time of introduction						
Year of 1st release		113	−0.02	0.152	-0.01	0.014

[a] The response variable is binary (a species established in New Zealand or not)
[b] Number of species included in a model
[c] Results of fitting a generalized linear model, specifying a logit link function and binomial error distribution, with the explanatory variable in the left-hand column
[d] Results of fitting a generalized estimating equation model, with the same link and error functions and a working correlation matrix specifying the degree of phylogenetic relatedness among species, measured as the number of nodes along the longest branch separating species on a phylogenetic tree containing all of the world's bird species. Negative parameter estimates further from zero indicate a lower probability of establishment
[e] Model failed to converge

9.4.2 Environmental Match

We would predict that species introduced to a new environment which closely matches that in their natural range should have a greater probability of establishing than species introduced into a very different environment (Mack 1996; Williamson and Fitter 1996). When environmental features such as climate and habitat are closely matched, introduced species are more likely to posses the necessary pre-adaptations for survival and reproduction in the new environment (Daehler and Strong 1993). This hypothesis is not easy to test because it is difficult to quantify both a species' environmental niche and its match to the location of introduction, although the few attempts to do so suggest this is an important factor. For bird species introduced to Australia, those with a closer match between the climate in their natural range and the climate in Australia were significantly more likely to establish (Duncan et al. 2001). For global bird introductions, species introduced to latitudes closer to the midpoint of their natural range and species introduced to locations in their native biogeographic region were also more likely to establish (Blackburn and Duncan 2001a), perhaps because locations at similar latitudes within the same biogeographic region are more likely to share similar climate and habitat than locations elsewhere.

For birds introduced to New Zealand, we assessed whether the natural latitudinal range of each species included the latitudinal range of the three main islands of New Zealand (North, South and Stewart islands; 34–47°S), without reference to hemisphere. Species whose natural range includes latitudes between 34 and 47°S were significantly more likely to establish following introduction to New Zealand than species whose natural range falls outside these latitudes, although the relationship is weak (Table 9.4). Assuming that latitude acts as a surrogate for some broad features of climate, this provides limited support for the hypothesis that a closer environmental match increases the chance of establishment (see also Green 1997).

In a variety of taxa, species with larger geographic ranges are consistently found to have a greater probability of establishing following introduction (Moulton and Pimm 1986; Rejmánek 1996; Reichard and Hamilton 1997; Blackburn and Duncan 2001a). Species with larger geographic ranges have more chance of being captured and transported in greater numbers, which could account, at least in part, for their higher probability of establishment (Forcella and Wood 1984; Forcella et al. 1986; Goodwin et al. 1999; see above). In addition, however, species occupying larger geographic ranges are more likely to be pre-adapted to a wider range of environments (Stevens 1989), and are therefore more likely to encounter suitable conditions when released at a new location than species occupying smaller ranges. For example, Cassey (2002) found that the probability of successful establishment was greater for

species which occupied a greater number of habitat types. For bird species introduced to New Zealand, natural latitudinal range is a highly significant predictor of establishment success (Table 9.4).

9.4.3 Life History Traits

Species differ in many characteristics which could influence their probability of establishing a population following release in a novel environment. For example, characteristics which reduce vulnerability to extinction due to demographic and environmental stochasticity may increase establishment success (Pimm 1991). Thus, species with rapid rates of population increase, or long-lived species which are relatively unaffected by environmental fluctuations, may have a greater probability of establishing.

   Results from studies which have examined life history traits among introduced birds suggest that species are more likely to establish if they are sedentary (Veltman et al. 1996; Sol and Lefebvre 2000; Cassey 2002), have larger body masses (Green 1997; Duncan et al. 2001), larger clutch sizes (Green 1997), larger relative brain size (Sol and Lefebvre 2000; Sol et al. 2002, 2005) and are habitat generalists (Cassey et al. 2004). Sexually dichromatic species are less likely than monochromatic species to have established (McLain et al. 1995, 1999; Green 1997; Cassey 2002), even when the number of individuals introduced is statistically controlled (Sorci et al. 1998; but see Cassey et al. 2004). Legendre et al. (1999) found that monogamous mating led to a higher extinction risk, and that demographic uncertainty imposed a greater probability of introduction failure on populations of short-lived species.

   Of the traits we examined, only migratory tendency explained significant variation in establishment success for birds introduced to New Zealand (Table 9.4). A number of additional traits, which have been shown in previous studies to significantly predict establishment success in birds introduced to New Zealand, were not significant predictors in this study. The most likely reason for this inconsistency is that the lists of species used in previous studies were incomplete (see Table 9.1). Overall, life history and demographic traits were weak predictors of establishment success. It appears that, in New Zealand, these characteristics have had much less effect on establishment probability than introduction effort and the degree to which the new environment is suitable for the introduced species. Indeed, when we fitted a multivariate model and eliminated non-significant predictor variables by backward selection, only introduction effort and latitudinal range were retained in the model as significant predictors of establishment.

9.4.4 Competition

Several studies have suggested that interspecific competition is an important determinant of establishment success for birds introduced to islands (e.g. Moulton and Pimm 1983, 1986, 1987; Moulton 1993; Lockwood and Moulton 1994; Brooke et al. 1995; Moulton et al. 1996). Two patterns in introduction data have been used to infer the importance of competition. First, bird species introduced later tend to have a lower rate of establishment because later introductions face a higher level of competition from already established species. Second, interspecific competition should be greater between morphologically similar species, and hence establishment success should be higher for species introduced to islands where no morphologically similar species are present.

For passerine birds introduced to New Zealand, there is a significant order of introduction effect: later introductions are significantly less likely to establish (Duncan 1997). This pattern holds for all bird species introduced to New Zealand, but is much weaker and significant only after controlling for phylogeny (Table 9.4). For passerine birds, this order of introduction effect is confounded with introduction effort because less effort was expended in later introductions (Duncan 1997; this is true also for the entire data set). The median year of introduction for releases involving ≤ 20 individuals is 1871, for 21–100 individuals it is 1868, and for >100 individuals it is 1864 (Kruskal-Wallis $\chi^2=15.0$, $P<0.001$). Hence, the lower establishment rate of later introductions could be due to the diminished effort put into introducing these species. For passerine birds, however, variation in introduction effort fails to explain all of the order of introduction effect, because introduction effort remains a significant predictor of establishment success once effort is controlled for (Duncan 1997). Nevertheless, this residual effect could be due to factors other than competition which vary throughout the period of introductions. In particular, establishment success may be influenced by level of predation (e.g. Lovegrove 1996), which almost certainly increased during the period of bird introductions to New Zealand as introduced predators established and spread throughout the country (King 1990; Holdaway 1999).

For a subset of the gamebirds introduced to New Zealand, there is a significant pattern of morphological overdispersion: successfully established species are less similar to each other than would be expected if introductions had succeeded or failed at random (Moulton et al. 2001). Moulton et al. (2001) attributed this pattern to competition between introduced gamebird species. However, a subsequent reassessment of the data on gamebird introductions showed that the observed pattern of morphological overdispersion could not be due to interspecific competition because gamebird species were rarely introduced to the same location at the same time (Duncan and Blackburn 2002). This implies that factors other than competition can generate a pattern

of morphological overdispersion among successfully introduced birds (see also Simberloff and Boecklen 1991).

To untangle the importance of competition from that of other confounding factors, Duncan and Forsyth (2005) investigated how three factors (viz. introduction effort, the abundance of a competitor, and the strength of competition) interact to determine the probability that an introduced species will establish in the presence of a competitor, using a simple mathematical model. They showed that these factors interact such that the importance of competition varies depending on the relative abundances of the introduced and competitor species, and on introduction effort. Competition should be of much less importance in affecting establishment when a species is introduced in small numbers (because stochastic processes dominate) or when the resident competitor occurs at low abundance. The effects of competition should be most apparent when both the introduced and competitor species occur at high abundance. These model predictions were strongly supported by the data for passerine introductions to New Zealand, implying that competition was an important factor structuring this assemblage, having accounted for the timing and effort put into introductions (Duncan and Forsyth 2005).

9.5 Factors Affecting Spread

Once a species has established a viable population in a new environment, that population may persist only around the site of release, or it may expand and spread more widely. Characteristics which have been suggested to influence the spread of introduced species include the time available for population expansion to occur, the population growth rate, the extent of suitable environment, and dispersal tendency or ability (Duncan et al. 1999).

Time since introduction is not a significant predictor of range size in birds successfully introduced to New Zealand (Duncan et al. 1999). Birds have the potential to disperse rapidly and over large distances. Indeed, following introduction, the spread of most introduced birds in New Zealand appears to have been rapid, such that by the early 1900s most species were occupying close to their present range sizes (Thomson 1926; Heather and Robertson 1996). The same may not be true for other taxa whose dispersal capabilities are lower. Among the birds established in New Zealand, species which are partially migratory in their native range tend to have larger range sizes in New Zealand, which may reflect higher rates of dispersal among partial migrants (Duncan et al. 1999).

There is also some evidence that the geographic range size of introduced species in New Zealand is greater when the species uses habitats which are themselves more widespread (Duncan et al. 1999). More specifically, species which readily use extensive human-modified habitats, predominantly farm-

land, attain the highest range sizes in New Zealand. In addition, the proportion of non-native bird species in a habitat may increase with increasing habitat modification (McLay 1974; Diamond and Veitch 1981; Case 1996). Cassey (2001) found that of the ten species with the greatest geographic distributions across mainland New Zealand, only two, *Gerygone igata* and *Rhipidura fuliginosa*, were native before the arrival of humans. Two other widespread native species, *Zosterops lateralis* and *Circus approximans*, naturally colonized New Zealand from Australia only after the widespread loss of forest cover and habitat modification which accompanied human arrival. The remaining six widespread species were all introduced during European settlement.

Both Duncan et al. (1999) and Cassey (2001) reported that the introduced species which have established and maintained larger geographic ranges in New Zealand are those which possess life history traits associated with high population growth rates. These are characteristically small-bodied, rapidly maturing species, with high fecundity. The same is also true for bird species introduced to Australia (Duncan et al. 2001). For British birds introduced to New Zealand, these are also characteristics associated with larger native geographic ranges (Blackburn et al. 1996; Duncan et al. 1999).

One unexpected finding is that the range size of introduced bird species in New Zealand is positively related to the number of individuals introduced (Duncan et al. 1999). One explanation for this finding is that species with large founding populations initially captured a greater proportion of any shared resources from species with smaller founding populations. This initial advantage could have been reinforced – those species initially able to capture a greater share of resources would have had a faster population growth and rate of spread, allowing them to dominate resource utilization at newly colonized sites as their ranges expanded. In addition, the species with larger founding populations were released at more sites throughout the country (Veltman et al. 1996; Duncan 1997), giving them a further head-start in range expansion and "first come, first served" resource utilization. This effect should be most pronounced between closely related species because these are more likely to compete for similar resources, which is indeed the case (Duncan et al. 1999). This explanation implies that competition plays a role in limiting range sizes, along with affecting establishment success (Duncan and Forsyth 2005). Indeed, we might expect competitive interactions to be more apparent among established populations which have reached sufficiently high density (Forsyth and Hickling 1998). Nevertheless, other explanations may underlie the relationship between range size and introduction effort; this relationship is not evident among introduced birds in Australia (Duncan et al. 2001).

9.6 Conclusions

The record of bird introductions into New Zealand is remarkably complete and detailed, and thus provides a unique opportunity to identify factors responsible for success at different stages in the invasion process. Analysis of this record shows that historical and cultural factors dominate in determining the probability that a bird species was released and the probability that it established a wild population in New Zealand. Species from certain families were preferentially selected for release (reflecting the types of birds most desired for introduction); these species tended to originate in the Palaearctic (where most settlers to New Zealand in the 19th century originated) or in nearby Australasia, and to be widespread, abundant species at their source locations. People put more effort into introducing these widespread, abundant species and consequently they had a higher rate of successful establishment and, at least in New Zealand, became more widespread. Species also appeared more likely to succeed in establishing and spreading if they had a large natural geographic range size, and if the environment in their native range matched that in New Zealand. Overall, life history and demographic traits were relatively unimportant in explaining patterns of release and establishment, although the widespread introduced bird species tend to be those with small body mass and high reproductive potential.

The establishment of exotic bird species may currently pose less of an ecological and economic threat to New Zealand than the establishment of species in other groups, particularly plants and invertebrates. This does not imply, however, that understanding the outcome of bird introductions is less of a priority than unravelling the factors underlying invasion success in other taxa. The advantage with birds is that the record of introductions allows us to answer key questions which we presently cannot address for other taxa. Moreover, there is evidence that the general factors identified as affecting invasion success in birds are similar to those which influence invasion success in other taxa (see Kolar and Lodge 2001), making bird introductions to New Zealand a particularly useful model system.

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