

# Propagule Size and the Relative Success of Exotic Ungulate and Bird Introductions to New Zealand

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**ABSTRACT:** We investigated factors affecting the success of 14 species of ungulates introduced to New Zealand around 1851–1926. The 11 successful species had a shorter maximum life span and were introduced in greater numbers than the three unsuccessful species. Because introduction effort was confounded with other life-history traits, we examined whether independent introductions of the same species were more likely to succeed when a greater number of individuals were introduced. For the six species with introductions that both succeeded and failed, successful introductions always involved an equal or greater number of individuals than unsuccessful introductions of the same species. For all independent introductions, there was a highly significant relationship between the number of individuals introduced and introduction success. When data for ungulate and bird introductions to New Zealand were combined, a variable categorizing species as ungulate or bird was a highly significant predictor of introduction success, after variation in introduction effort was controlled. For a given number of individuals introduced, ungulates were much more likely to succeed than birds.

**Keywords:** biological invasions, bird introductions, extinction, mammal introductions, ungulates.

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The factors influencing the success of biological invasions have long interested ecologists (Elton 1958; Mooney and Drake 1986; Crawley 1987; Drake et al. 1989; Lodge 1993; Ruesink et al. 1995; Williamson and Fitter 1996). The number of individuals involved in the invasion, or “propagule

size,” has a strong theoretical basis for determining introduction success. Demographic stochasticity, the result of random and independent births and deaths, can lead to population extinction, the probability of which is inversely proportional to population size (Goel and Richter-Dyn 1974; Leigh 1981; Goodman 1987; Lande 1988, 1993, 1998; Legendre et al. 1999). The likelihood of extinction from random catastrophes and environmental stochasticity is also inversely related to population size (Hanson and Tuckwell 1978; Leigh 1981; Lande 1993). Thus, for any taxon, larger propagules can be expected to have a greater probability of successful introduction than smaller propagules. Comparisons of successful and unsuccessful introductions of insects (Beirne 1975; Ehler and Hall 1982; Hopper and Roush 1993; Memmott et al. 1998; Berggren 2001), birds (Griffith et al. 1989; Veltman et al. 1996; Green 1997; Wolf et al. 1998), and mammals (Crowell 1973; Ebenhard 1989; Griffith et al. 1989; Novellie et al. 1996; Wolf et al. 1998; Komers and Curman 2000) have identified increasing propagule size (or surrogates of propagule size) as a significant correlate of introduction success. Other factors associated with successful animal introductions have been habitat suitability (Novellie and Knight 1994) or quality (Griffith et al. 1989), an absence of migratory behavior (Veltman et al. 1996), plumage dichromatism (McLain et al. 1995; Sorci et al. 1998), a polygynous rather than a monogamous mating system (Legendre et al. 1999), and being introduced where fewer potential competitors (Ehler and Hall 1982; Moulton 1985; Moulton and Pimm 1987; Moulton and Lockwood 1992; Lockwood et al. 1993; Lockwood and Moulton 1994; but see Duncan 1997) or predators (Short et al. 1992; Schoener and Spiller 1995; Lovegrove 1996) were present.

Comparisons of invasion success have usually been conducted within broad taxonomic groups such as birds in Hawaii and New Zealand (Moulton and Pimm 1987; Veltman et al. 1996). Also of interest is the extent to which species in broad taxonomic groups might differ in their likelihood of introduction success (Williamson and Fitter 1996). Such differences could arise because taxa in different groups differ in traits likely to affect the probability of successful invasion (Lodge 1993; Ruesink et al. 1995).

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Modeling suggests that species with long life spans, relatively constant numbers over time, and high rates of population growth will have low probabilities of extinction (Richter-Dyn and Goel 1972; Leigh 1981). However, there have been few empirical tests of these predictions (Pimm et al. 1988; Ebenhard 1989; Schoener and Spiller 1992; Tracy and George 1992; Ryan and Siegfried 1994), and the relative importance of these life-history traits in determining invasion success is equivocal (Lawton and Brown 1986; Lodge 1993; Ruesink et al. 1995). Furthermore, since longevity, intrinsic rate of increase, and population variability are not independent life-history traits (Caughley and Krebs 1983; Gaillard et al. 1989; Stearns 1992), very different predictions can often be made about the invasion success of a taxonomic group. Because of their greater body size and longevity, large mammals should be more buffered from environmental extremes (Lindstedt and Boyce 1985) and consequently have a higher probability of successful invasion than most birds. Conversely, because of a low rate of population increase relative to birds, large mammals could take longer to attain population sizes at which extinction from environmental or demographic stochasticity is unlikely (Pimm 1991), thereby lowering their introduction success relative to birds. Clearly, quantitative comparisons are required before robust generalizations about the relative invasion success of different taxonomic groups can be made.

Mammals and birds have been frequently introduced to new locations (Long 1981; Lever 1994) with varying success (Williamson and Fitter 1996). The introduction of ungulate and bird species to New Zealand has been well documented (e.g., Thomson 1922; Donne 1924), and these records provide an opportunity to test hypotheses about the factors influencing invasion success in these two groups and to compare the outcomes. Recent analyses of exotic bird introductions to New Zealand have identified initial propagule size and the number of introductions (collectively, "introduction effort"), plumage dichromatism, and mating system as significant predictors of introduction success (Veltman et al. 1996; Williamson 1996; Duncan 1997; Green 1997; Sorci et al. 1998; Legehdre et al. 1999). The factors influencing the success of ungulate introductions to New Zealand have not yet been investigated.

In this article, we compare the factors affecting the introduction success of ungulate and bird species introduced to New Zealand. The objectives of our study were twofold: first, to identify which life-history and/or ecological variables predict the success of 14 ungulate species introduced to New Zealand and to determine whether introduction effort was a factor influencing introduction success and, second, to determine whether species of ungulates and birds differed in their probability of success when introduced to New Zealand.

## Methods

### *Data Sources*

We searched the literature for information on the introduction of ungulates into North, South, and Stewart Islands ("New Zealand"). Our primary sources were Thomson (1922), Donne (1924), Logan and Harris (1967), and King (1990). The purpose of nearly all introductions was to establish wild populations for hunting (Thomson 1922). Introductions were made between approximately 1851 and 1926; thereafter, the importation of ungulates to New Zealand ceased, although some animals captured from established herds were released (King 1990). We did not include species introduced primarily as domestic livestock that subsequently became feral (*Sus scrofa*, *Bos taurus*, *Capra hircus*, *Equus caballus*, and *Ovis avies*) or two unsuccessful species for which there was no information on the number of introduction events or the number of individuals introduced (a "South American deer," species unknown, and *Lama glama*; King 1990).

Introductions were defined as "successful" if the species had wild populations in New Zealand in 1996 or previously had a self-sustaining wild population that was eradicated by hunting. Only one species, *Axis axis*, met the latter criterion. Introductions not meeting these criteria were termed "unsuccessful." There is uncertainty as to whether moose (*Alces alces*) were extant in New Zealand in 1996 (Davidson and Tustin 1990), but based on the evidence in Tustin (1998), we concluded that a population was present.

To determine whether introductions failed because species were introduced into areas that lacked suitable habitat, we quantified the propensity of each species to utilize 10 major habitat types in New Zealand (table 1). Each habitat was scored as 1 for "suitable" and 0 for "unsuitable" based on descriptions of each species' habitat use outside New Zealand (see table 1 for data sources). In addition, for the species introduced successfully to New Zealand, we assumed that habitats currently used by these species would have been suitable for introductions. We then identified the habitats that were available at the locations where species were introduced and determined whether species had been introduced to areas that lacked suitable habitat. We acknowledge the difficulty of determining whether habitat is "suitable" for an exotic species. However, we judged only one introduction of three Himalayan tahr to the Rotorua district (Donne 1924) to have been made into unsuitable habitat, and we excluded this introduction from our analyses. Our results were unchanged when this introduction was assumed to have been into suitable habitat.

We collected data on the following life-history traits (see table 2 for data sources): body mass of adult males and females (kg), maximum life span of males and females (yr), youngest recorded age at which females wean young (yr),

Table 1: Suitability of habitats for ungulates introduced to New Zealand

Habitat	Area of habitat		Cervus										Dama		
	North Island (ha)	South Island (ha)	<i>Pseudis nayaur</i> (blue sheep)	<i>unicolor</i> (sambar deer)	<i>hemionus</i> (mule deer)	<i>timorensis</i> (rusa deer)	<i>rippon</i> (silka deer)	<i>rupicapra</i> (Alpine chamois)	<i>Alces alces</i> (moose)	<i>Axis axis</i> (chital deer)	<i>Cervus elaphus</i> (wapiti deer)	<i>virviniatus</i> (white-tailed deer)	<i>Hemitragus jemlahicus</i> (Himalayan tahr)	<i>dama</i> (fallow deer)	<i>elaphus scoticus</i> (red deer)
Pasture	5,795,500	4,106,200	1	0	1	1	1	0	0	1	1	0	1 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>
Swampland	72,800	145,500	0	1 <sup>a</sup>	1	1	1	0	1	1	1	0	1	1	1
Sand dunes	107,300	21,700	1	0	1	1	1	0	0	1	1	0	1	1	1
Low-altitude scrubland	322,600	129,100	1	0	1	1	1	0	1	1	1	0 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>
Tussock	205,100	3,423,700	1	0	1	1	1	0	0	1	1	0	1 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>
Indigenous forest/scrub	3,938,700	4,571,900	0	0	1 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>	0	1 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>	0	1 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>
Exotic forest/scrub	570,200	181,300	0	0	1	1	1	0	1	1	1	0	1	1	1 <sup>a</sup>
Semi-arid herb fields	0	60,800	1	0	0	1	0	0	0	1	1	0	0	0	1
Sub-alpine scrub/grasslands	68,600	1,403,800	1	1 <sup>a</sup>	0	1	0	1	1	1	1	0	1 <sup>a</sup>	1	1
Alpine herbs	33,000	248,100	1	1 <sup>a</sup>	0	0	0	1 <sup>a</sup>	0	1	1	0	1 <sup>a</sup>	0	1
Total	11,113,800	14,292,100													
Sources	1, 2	3-5	6-8	9	6, 10	6, 11-14	15	16	17-19	20, 21	22	23, 24	25	26-29	

Sources: Data on habitat suitability: 1, Franklin 1982; 2, G. Davis unpublished data; 3, Wilson 1981; 4, Harris and Miller 1995; 5, Oli 1996; 6, Whitehead 1972; 7, Lewis et al. 1990; 8, Porwal et al. 1996; 9, Wallmo 1981; 10, Stewart 1985; 11, Takatsuki 1990; 12, Endo and Doi 1996; 13, Chadwick et al. 1996; 14, Putman 1996; 15, Von Elsner-Schaack 1985; 16, Franzmann and Schwartz 1997; 17, Khan 1994; 18, Moe and Wege 1994; 19, Bhat and Rawat 1995; 20, Boyce and Hayden-Wing 1979; 21, Boyce 1989; 22, Halls 1984; 23, Caughley 1970a; 24, Bauer 1990; 25, Chapman and Chapman 1975; 26, Georgii 1980; 27, Catt and Staines 1987; 28, Clutton-Brock and Albon 1989; 29, Albon and Langvatn 1992.

Note: The 10 habitat types were taken from Blaschke et al. (1981). Habitats were scored 1 for "suitable" and 0 for "unsuitable." Data were probably incomplete for red and fallow deer because not all of the introduction sites were documented. The areas of habitat on Stewart Island were unavailable.

<sup>a</sup> Habitat into which the species was introduced.

number of offspring born per adult female per annum, and maximum lifetime reproduction (the product of reproductive life span [maximum female life span minus age at first reproduction] and number of offspring born per annum). Mating systems were classified according to Weckerly (1998): "tending," males did not herd or follow more than two females simultaneously; "harem," males did herd more than two females simultaneously; and "territorial," males exhibited polygyny based on a territory defended against other males. The most common system was used for species exhibiting multiple mating systems (Weckerly 1998). We also categorized species as migratory (defined as consistent seasonal shifts of individuals between geographic areas; McCullough 1991) or nonmigratory.

Estimates of annual survival based on capture-mark-recapture models are preferable to observed maximum life spans (Krementz et al. 1989), but these data were unavailable for most ungulates introduced to New Zealand. We caution that observed maximum life span represents a best-case survival estimate.

#### *Statistical Procedures*

Introduction success was used as the response variable in a logistic regression model with the remaining variables fitted individually as predictors. Body mass, maximum longevity, maximum lifetime reproduction, minimum number of introduction events, and minimum number of individuals introduced were  $\log_{10}$  transformed, and dummy categories were constructed for mating system. A problem arose for two variables (maximum life span of males and minimum number of introduction events) in that the logistic regression model failed to converge because the model provided an exact fit to certain observations and so was overfitted (see Collett 1991, p. 82). We therefore tested whether successful and unsuccessful species differed in maximum male life span and number of introduction events using a Kruskal-Wallis approximate  $\chi^2$  test. The problem of overfitting became acute when we attempted to model introduction success as a function of two or more predictor variables using multiple logistic regression. To overcome this problem, we used principal components analysis (PCA) to extract two axes that explained most of the variation in species traits. We included all  $\log_{10}$ -transformed variables except migratory tendency (because it contained missing values) in the PCA and then examined how successful and unsuccessful species were arranged along the first two PC axes.

It became apparent that the relationship between present-day status and introduction effort was confounded with other species traits. This makes it difficult to argue for a causal relationship between introduction effort and introduction success because that relationship could have

arisen indirectly. Those species with traits that make them successful invaders may just happen to have been introduced more times and in greater numbers. We could overcome this problem by statistically controlling for the influence of other traits in multiple regression (e.g., Veltman et al. 1996) or by incorporating phylogenetic information into our analysis and thereby testing only for differences between closely related species that share potentially confounding life-history traits in common (Harvey and Pagel 1991). However, the small size and sparseness of our data set precluded either approach.

A better way of dealing with this problem is to investigate the outcome of independent introductions of the same species to different locations. If propagule size is a key factor influencing introduction success, then introductions of the same species to different locations should be more likely to succeed if a greater number of individuals are introduced. By comparing the outcome of independent introductions of the same species, we sidestep the problem that across-species comparisons are confounded with variation in life-history traits. We therefore collated the available data for independent introductions of each species to different locations in New Zealand and examined whether introductions that succeeded consistently involved more individuals than introductions of the same species that failed.

Complete data on the number of individuals involved in each introduction were available for all species except fallow deer (*Dama dama dama*) and red deer (*Cervus elaphus scoticus*). For this last species, data on the number of individuals were available for all introductions to a region of the northern South Island (Clarke 1971). We can discount two factors that could confound our analysis. First, when several introductions of the same species were made to the same location within a short space of time, we considered them to be a single introduction. The introductions that we considered were then sufficiently separated in time or space that they could be reasonably regarded as independent events. Second, people might have introduced more individuals to locations where they were more likely to succeed in the first place or, when they introduced a large number of individuals, may have modified the site to make success more likely. Although we lack data to test this possibility, the large majority of introductions occurred in unmodified indigenous habitats. Range expansions from successful introductions have also included sites where unsuccessful introductions of the same species (e.g., Himalayan tahr in the Southern Alps; Tustin 1990) or species with similar habitat requirements (e.g., expanding red deer and unsuccessful white-tailed deer at Takaka Valley; Challies 1990a; Davidson and Challies 1990) were made. At least in these cases, it is unlikely that habitat modifications or a lack of suitable habitat were

Table 2: Ungulate species introduced to New Zealand and their present-day status scored as successful (1) or unsuccessful (0)

Species	Status	Body mass		Maximum life span		Youngest recorded year that		Migration <sup>c</sup>	Min. no. of introduction events	Min. no. of individuals introduced	Sources		
		Adult		Females		females							
		males (kg)	males (kg)	(yr)	(yr)	wean young	no. of offspring <sup>b</sup>					Max. lifetime reproduction	
<i>Lama pacos</i> (alpaca)	0	70	70	23	28	2	2	1	14 <sup>d</sup>	0	1	2	1-5
<i>Pseudis naysaur</i> (blue sheep)	0	54	40	15	20	0	2	1	18	0	1	3	1, 2, 6-10
<i>Cervus unicolor unicolor</i> (sambar deer)	1	192	146	12	17	2	2	1	15	0	2 <sup>e</sup>	4	1, 2, 6, 11-17
<i>Odocoileus hemionus</i> (mule deer)	0	93	69	19	22	0	1	2	42	1	1	5	1, 2, 6, 18-20
<i>Cervus timorensis</i> (rusa deer)	1	73	53	12	20	1	2	1	18	ND	1	8	1, 2, 6, 21, 22
<i>Cervus nippon</i> (sika deer)	1	63	50	11	15	2	1	1	14	1	2 <sup>e</sup>	9	1, 6, 23-25
<i>Rupicapra rupicapra rupicapra</i> (Alpine chamois)	1	35	29	14	19	0	2	1	17	1	2	9	1, 6, 5, 26
<i>Alces alces</i> (moose)	1	633	500	15	19	0	2	2	34	1	2	14	1, 2, 6, 27-32
<i>Axis axis</i> (chital deer)	1	89	50	12 <sup>f</sup>	18 <sup>g</sup>	0	1	1	17	ND	3	17	1, 2, 6, 33
<i>Cervus elaphus nelsoni</i> (wapiti)	1	233	120	13	21	1	2	1	19	1	1	18	1, 2, 34-38
<i>Odocoileus virginianus</i> (white-tailed deer)	1	54	40	12	20	0	1	2	38	1	3	23	1, 6, 19, 39-46
<i>Hemitragus jemlahicus</i> (Himalayan tahr)	1	63	31	14	22	0	2	1	20	0	4	21	1, 2, 6, 47-49
<i>Dama dama dama</i> (fallow deer)	1	67	47	8	12	2	2	1	10	1	24	126	1, 2, 6, 50-52
<i>Cervus elaphus scoticus</i> (red deer)	1	119	75	12	20	1	1	1	19	1	214	849	1, 6, 53-60
Statistical tests:													
Δ deviance		.70	.13	—	5.93*	1.67	.01	.30	.37	1.92	—	9.98**	
Kruskall-Wallis $\chi^2$					6.52*						4.74*		

Sources: Data for predictor variables: 1, Thomson 1922; 2, Weckerly 1998; 3, G. Davis, unpublished data; 4, Nowak 1991; 5, Fernandez-Baca 1993; 6, Donne 1924; 7, Ren and Yu 1990; 8, Schaller 1973; 9, Wegge 1979; 10, Wang and Hoffman 1987; 11, Douglas 1990b; 12, G. Moore, unpublished data; 13, Harris 1971; 14, Lewis et al. 1990; 15, S. Kelton, unpublished data; 16, Achariyo and Misra 1971; 17, P. Taylor, unpublished data; 18, Anderson and Wallmo 1984; 19, Wallmo 1981; 20, McNay et al. 1994; 21, Douglas 1990a; 22, Le Bel et al. 1997; 23, Feldhamer and Marcus 1994; 24, Davidson 1973; 25, Davidson 1990; 26, Clarke 1990; 27, Van Ballenberghe and Ballard 1997; 28, Ballard et al. 1991; 29, Sand and Cederlund 1996; 30, Schwartz and Hundertmark 1993; 31, Davidson and Tustin 1990; 32, Tustin 1998; 33, Graf and Nichols 1966; 34, Challies 1990b; 35, Strohmeier and Peek 1996; 36, Boyce and Hayden-Wing 1979; 37, Boyce 1989; 38, Banwell 1966; 39, Davidson and Challies 1990; 40, Harris 1981; 41, Beier and McCullough 1990; 42, McCullough 1990; 43, Ozoga and Verme 1982; 44, Tierson et al. 1985; 45, Forsyth 1985; 46, Verme 1965; 47, Tustin 1990; 48, Caughley 1970b; 49, Caughley 1971; 50, Davidson and Nugent 1990; 51, Nugent 1994; 52, Sterba and Klusak 1984; 53, Logan and Harris 1967; 54, Clarke 1971; 55, Challies 1990a; 56, Challies 1978; 57, Daniel 1963; 58, Staines 1974; 59, Catt and Staines 1987; 60, Albon and Langvatn 1992.

Note: Species are listed in ascending order of the minimum number of individuals introduced. The results of statistical tests of a difference between successful and unsuccessful species in the predictor variables are shown below each data column: Δ deviance is the change in deviance when the predictor variable is added to a logistic regression model with status as the response variable. A dash indicates that a logistic regression model could not be fitted, and the difference was tested using a Kruskal-Wallis approximate  $\chi^2$  test. ND = no data.

<sup>a</sup> Mating system categorized as tending (0), harem (1), or territorial (2).

<sup>b</sup> Median number of offspring per adult female per annum in conditions of high food quality.

<sup>c</sup> Migration categorized as nonmigratory (0) or facultatively migratory (1).

<sup>d</sup> Females give birth every other year (Nowak 1991).

<sup>e</sup> Subsequent introductions from established herds occurred but are not included (e.g., King 1990, p. 471).

<sup>f</sup> Extrapolated based on sexual-size dimorphism reported in Weckerly (1998).

\*  $P < .05$ .

\*\*  $P < .01$ .

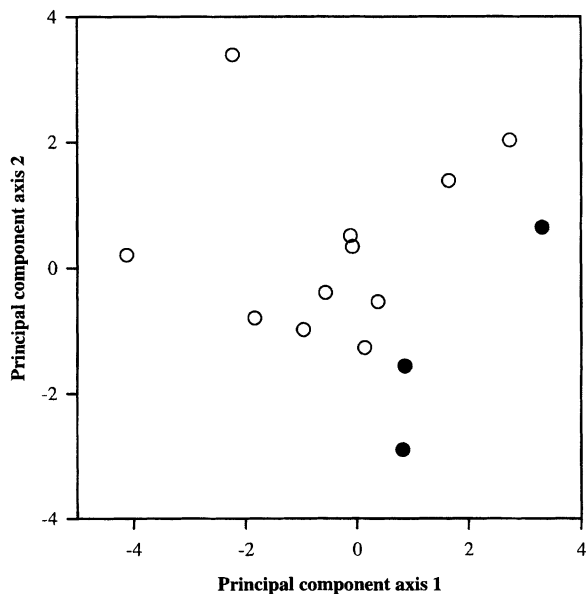


Figure 1: Plot of the first two axes from a principal components analysis using the traits in table 2 (excluding migration). Successfully introduced species are shown as open circles; unsuccessful species are shown as closed circles.

responsible for the success or failure of introductions (see "Results").

Introduction effort is a strong predictor of success for birds introduced to New Zealand (Veltman et al. 1996; Duncan 1997; Green 1997). We tested whether, for a given level of introduction effort, ungulates tended to be more or less successful than birds. To do this, we combined the data in Veltman et al. (1996) for the success of introduced birds, the number of introduction events, and the number of individuals introduced with our equivalent data for ungulates. Using logistic regression, we then tested whether the categorical variable taxonomic class (ungulate or bird) was a significant predictor of introduction success having adjusted for the number of introduction events and the number of individuals introduced.

## Results

### *Introduction Success of Ungulates*

Eleven of the 14 ungulate species were successfully introduced to New Zealand (table 2). Of the three unsuccessful species, none were apparently introduced into areas with unsuitable habitat (table 1), so we can tentatively exclude lack of suitable habitat as an explanation for their failure.

Three factors predicted whether introductions of ungulates succeeded (table 2). Species with greater maximum

life spans and species that were introduced more often and in greater numbers were more likely to succeed. The first two principal components explained 53% of the total variation in the species traits listed in table 2 (excluding migration). Successful and unsuccessful species were separated along these first two axes (fig. 1); unsuccessful species occurred toward the lower right of the ordination, with higher axis 1 and lower axis 2 scores. Axis 1 separated species along a gradient of maximum life span, number of offspring per adult female, maximum lifetime reproduction, mating system (tending or not), and introduction effort (number of introduction events and number of individuals introduced). Axis 2 separated species along a gradient of introduction effort (table 3). Hence, successful species tended to have a shorter maximum life span, a lower number of offspring per adult female, lower maximum lifetime reproduction, were nontending, and were introduced more often and in greater numbers.

### *Within-species Variation in Ungulate Introduction Effort*

Introduction effort was significantly related to introduction success across-species, but this relationship was confounded with other life-history traits. For example, the total number of individuals introduced and maximum male life span both significantly predicted introduction success (table 2), but these two variables were themselves correlated ( $r = -0.59$ ,  $n = 14$ ,  $P = .028$ ). We therefore examined whether independent introductions of the same

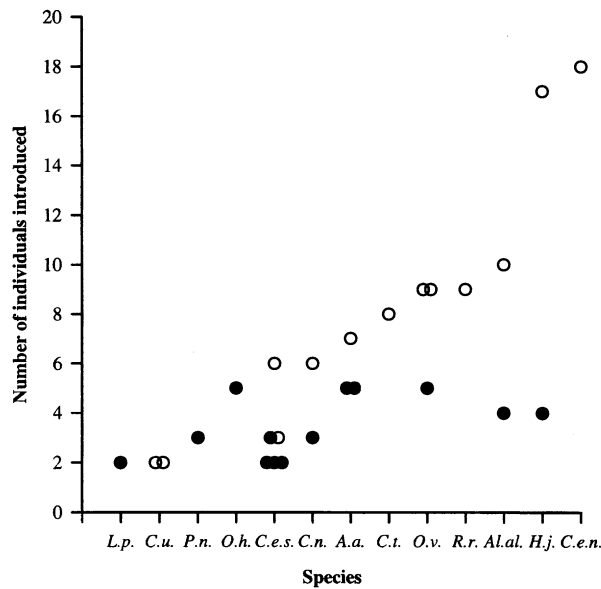
Table 3: Correlations of trait values with scores on the first two principal component axes for the 14 species of ungulates introduced to New Zealand

Trait	Axis 1	Axis 2
Body mass of adult males	.224	.466
Body mass of adult females	.267	.365
Maximum life span of males	.753**	-.338
Maximum life span of females	.662**	-.180
Mating system:		
Tending	.685**	.093
Harem	-.269	.398
Territorial	-.513	-.464
Youngest year that females wean	-.065	-.480
Number of offspring per female per annum	.714**	.459
Maximum life time reproduction	.833***	.485
Minimum number of introduction events	-.598*	.620*
Minimum number of individuals introduced	-.540*	.768**

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .



**Figure 2:** Relationship between the number of individuals introduced and introduction success for independent introductions of ungulate species to New Zealand. Successful introductions are shown as open circles, unsuccessful introductions as closed circles. Data for *Cervus elaphus scoticus* (red deer) are available for only a small subsample of introductions (Clarke 1971); red deer propagules of greater than six individuals were apparently always successful (Logan and Harris 1967). Two data points include more than one introduction event; *Hemitragus jemlahicus* was successful from three separate introductions at the same site in 1904 (five individuals), 1909 (eight), and 1919 (four), and *Rupicapra rupicapra* was successful from two separate introductions at the same site in 1907 (eight individuals) and 1914 (one female). Species are shown in ascending order of maximum propagule size: L.p. = *Lama pacos*; C.u. = *Cervus unicolor unicolor*; P.n. = *Pseudois nayaur*; O.h. = *Odocoileus hemionus*; C.e.s. = *C. elaphus scoticus*; C.n. = *Cervus nippon*; A.a. = *Axis axis*; C.t. = *Cervus timorensis*; O.v. = *Odocoileus virginianus*; R.r. = *R. rupicapra rupicapra*; Al.al. = *Alces alces*; H.j. = *H. jemlahicus*; C.e.n. = *Cervus elaphus nelsoni*.

species were more likely to succeed when a greater number of individuals were introduced.

For five of the six species with both successful and unsuccessful introductions, the successful introductions always involved more individuals than the unsuccessful introductions (fig. 2). Only for red deer (*Cervus elaphus scoticus*) was there a mixed outcome, where introductions of three individuals both succeeded and failed. For all of the independent introductions shown in figure 2, there was a highly significant relationship between the number of individuals introduced and introduction success (logistic regression,  $\Delta$  deviance = 12.0, df = 1,  $P < .001$ ). All 10 introductions involving six or more individuals succeeded while 13 of the 16 introductions involving fewer than six individuals failed. This suggests there was a thresh-

old introduction size of about six individuals, below which ungulate introductions to New Zealand were likely to fail and above which they were likely to succeed.

### Ungulates and Birds

Among species introduced to New Zealand for which propagule size data are available, ungulates were relatively more successful (11 of 14 established, 79%) than birds (29 of 79 established, 34%; Veltman et al. 1996). Our finding, that the number of individuals introduced was a significant predictor of ungulate introduction success, parallels the finding for introduced New Zealand birds (Veltman et al. 1996; Duncan 1997; Green 1997). We ask whether, for a given level of introduction effort, ungulates were more or less likely to succeed than birds.

For birds and ungulates combined, the number of introduction events, the number of individuals introduced, and taxonomic class were all significant predictors of introduction success when included alone in a logistic regression model (table 4). Taxonomic class was an even stronger predictor after controlling for introduction effort, and there was no significant interaction between either measure of introduction effort and taxonomic class. Ungulates were therefore much more likely than birds to establish when introduced to New Zealand in low numbers (fig. 3).

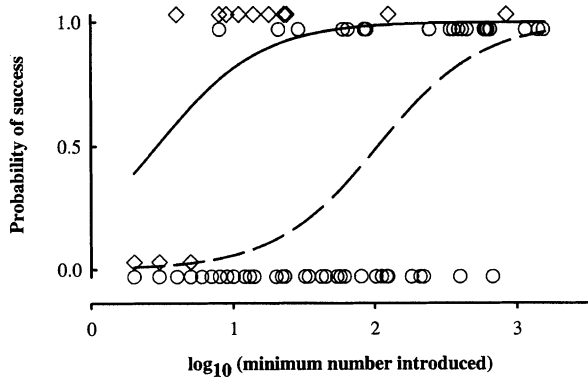
**Table 4:** Results of logistic regression models with introduction success as the response variable and the two pairs of variables in the left-hand column as predictors, using the data for birds and ungulates introduced to New Zealand

Variable	df	Alone	Last
Introduction events:			
Log <sub>10</sub> number of introduction events	1	33.8***	55.1***
Taxonomic class (bird or ungulate)	1	9.8**	31.1***
Individuals introduced:			
Log <sub>10</sub> number of individuals introduced	1	30.0***	47.1***
Taxonomic class (bird or ungulate)	1	9.8**	26.3***

Note: "Alone" shows the change in deviance when each predictor variable was added to the model alone. "Last" shows the change in deviance when a predictor variable was added to the model after a second predictor variable (the alternative of the pair) was already included. df = number of degrees of freedom.  $N = 93$  for the number of introduction events,  $N = 90$  for the number of individuals introduced.

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .



**Figure 3:** Relationship between introduction effort (measured as  $\log_{10}$  minimum number of individuals introduced) and introduction success for 14 ungulate species (diamonds; three unsuccessful, 11 successful) and 76 bird species (circles; 51 unsuccessful, 25 successful) introduced to New Zealand and the logistic regression lines modeling the probability of success (solid line = ungulates, dashed line = birds).

### Discussion

Despite the small sample size, our results (both across and within species) suggest that introduction effort, particularly the number of individuals introduced, was an important determinant of the success of ungulate introductions to New Zealand. We excluded two species (a “South American deer” and *Lama glama*) from our analyses because there was no data on the number of introduction events or the number of individuals introduced. This lack of information most likely reflects a low introduction effort. Both species were unsuccessful, and their inclusion, if we knew their details, would almost certainly reinforce our finding that species introduced in fewer numbers were less likely to succeed.

Both theoretical (Lande 1993, 1998) and empirical studies (Crowell 1973; Ebenhard 1989; Griffith et al. 1989; Berger 1990; Tracy and George 1992) have shown that the probability of extinction increases with decreasing population size, and our results further support this pattern (fig. 2). However, few individuals were required to establish ungulate populations. Of the independent introductions we considered, all of those with six or more individuals succeeded (fig. 2), and in two instances, populations of sambar deer (*Cervus unicolor unicolor*) established following the introduction of only a single pair (Harris 1971; King 1990).

The comparison of ungulate and bird introductions suggests that taxa vary with regard to the minimum number of individuals required for introductions to have a high chance of success. For a given number of individuals introduced, ungulates were much more likely to succeed than birds (table 4; fig. 3). This outcome parallels the

findings of Griffith et al. (1989) and Wolf et al. (1996), who showed that, having controlled for other variables, including introduction effort, mammals translocated for conservation purposes were more likely to establish populations than translocated birds. Wolf et al. (1998) subsequently reanalyzed these data using the method of independent contrasts to control for phylogenetic relatedness and found no difference in the success rate of mammal and bird translocations. However, controlling for phylogenetic relatedness is unnecessary if the aim is to compare the success rate of introductions in two monophyletic groups. Our results and those of Wolf et al. (1996) therefore reveal a consistent difference in the relative success of mammal and bird introductions.

Several factors could explain the greater success rate of ungulates relative to birds for a given introduction effort in New Zealand. First, more care may have been taken with ungulate introductions. Agencies responsible for the introduction of ungulates apparently matched species with suitable habitat on all but one occasion (table 1) while bird introductions appeared to be more haphazard (Thomson 1922). Second, introduced ungulates lacked both predators and competitors while birds did not. Except for humans, ungulate predators were absent from New Zealand whereas birds faced a suite of indigenous and introduced avian predators plus three species of mustelid, three species of rat, and feral cats (King 1984, 1990). Ungulates also initially faced few potential competitors because native species, such as moa, had been extirpated (Caughley 1989), and because different species were rarely introduced to the same location. Even when more than one species of ungulate was introduced to the same location, the effects of competition became important only when one species attained high density (e.g., Himalayan tahr and Alpine chamois; Forsyth and Hickling 1998), long after the introduction might have failed for other reasons. There is little evidence that introduced birds compete to any extent with native birds in New Zealand (Diamond and Veitch 1981), but birds were often introduced to the same location and competition between introduced birds has been implicated as a factor increasing extinction rates following avian introductions on other islands (e.g., Moulton and Pimm 1987; Moulton and Lockwood 1992; but see Simberloff and Boecklen 1991). Third, ungulates, and mammals in general, differ from birds in aspects of their life history (Gaillard et al. 1989) that could influence introduction outcomes. In particular, the survival rate for adult ungulates is higher and perhaps more constant (Gaillard et al. 1998) than for birds (Sæther 1989; Karr et al. 1990), so that small populations of long-lived mammals should be more strongly buffered against demographic stochasticity (Legendre et al. 1999) and environmental extremes (Lindstedt and Boyce 1985). Likewise, the proportionately greater variance associated with the higher intrinsic



rate of increase ( $r_m$ ) of many small birds (Pimm et al. 1988) relative to ungulates (McCorquodale et al. 1988; Choquenot 1990) could place colonizing bird populations at greater risk of extinction (Leigh 1981; Lande 1993).

We conclude that introduction effort was a critical factor in the success of ungulate introductions to New Zealand. Our findings suggest that, if six or more individuals of the unsuccessful species had been introduced, then it is likely that they would have succeeded, given that they were introduced into suitable habitat. This finding applies also to bird introductions (Veltman et al. 1996; Duncan 1997; Green 1997), although more individuals of each species of bird would have to be introduced to achieve a success rate comparable with ungulates.

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