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CORRELATES OF INTRODUCTION SUCCESS IN EXOTIC NEW ZEALAND BIRDS

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Abstract.—Whether or not a bird species will establish a new population after invasion of uncolonized habitat depends, from theory, on its life-history attributes and initial population size. Data about initial population sizes are often unobtainable for natural and deliberate avian invasions. In New Zealand, however, contemporary documentation of introduction efforts allowed us to systematically compare unsuccessful and successful invaders without bias. We obtained data for 79 species involved in 496 introduction events and used the present-day status of each species as the dependent variable in fitting multiple logistic regression models. We found that introduction efforts for species that migrated within their endemic ranges were significantly less likely to be successful than those for nonmigratory species with similar introduction efforts. Initial population size, measured as number of releases and as the minimum number of propagules liberated in New Zealand, significantly increased the probability of translocation success. A null model showed that species released more times had a higher probability per release of successful establishment. Among 36 species for which data were available, successful invaders had significantly higher natality/mortality ratios. Successful invaders were also liberated at significantly more sites. Invasion of New Zealand by exotic birds was therefore primarily related to management, an outcome that has implications for conservation biology.

Increasingly, conservation practitioners are turning to population biologists for advice on how best to start new populations by translocation, where translocation means the intentional release on one or more occasions of animals to the wild to establish, reestablish, or augment a population (Griffith et al. 1989). Translocation mimics the natural process of colonization, which is defined as starting with the arrival of immigrants and ending when the extinction probability of the population is no longer dependent on the initial state (Ebenhard 1991). The small-population paradigm in conservation biology, with its focus on determining the viability of small populations (Caughley 1994), has not so far answered practitioners' questions.

Translocations of small numbers of animals of endangered species have had low success (Griffith et al. 1989). In New Zealand, for example, eight liberations involving 139 North Island weka (*Gallirallus gallirallus greyii,* an endemic flightless rail) failed to establish new populations between 1976 and 1986 (MacMillan 1990). In a similar manner, releases of small numbers of cheer pheasant (*Catreus wallichii*) in Pakistan (Garson et al. 1992) and marsupial mammals in Australia (Short et al. 1992) have failed.

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Analyses of past invasions have generated lists of invader-level traits associated with colonization success (Ehrlich 1986, 1989; Crawley 1987), including phylogeny, body size, fecundity, and diet. Concurrently, theoretical and empirical analyses of community assembly rules suggest that invasion resistance is a property of some communities (Case 1990; Drake 1990; Nee 1990). However, both approaches assume that the correlates of invasion success are independent of environmental context (Gilpin 1990).

A new approach to old invasions is required, in which the likelihood of success or failure of translocations is estimated in relation to the type of invasion (Ehrlich 1989; Gilpin 1990) as well as the intrinsic properties of the species or community. Four classes of invasion were listed by Ehrlich (1989): species that invaded without any deliberate human intervention, species that were deliberately translocated to new places by people without systematic thought to the consequences, species transplanted after significant evaluation of the organism and the community being invaded, and vertebrate species introduced as biocontrol agents. We studied the introductions of exotic bird species to New Zealand that occurred over the last century, an example of the second class.

The history of avian introductions to New Zealand was documented by Thomson (1922), working from records kept by Acclimatisation Societies. The result is a uniquely extensive account of acclimatization attempts and their outcomes (McDowall 1994). At least 137 exotic bird species were introduced on North, Kawau, South, and Stewart Islands by human colonists before 1907; of these species 28 (20%) have persisted to the present. Because unsuccessful introductions are generally less likely to be reported than those that result in viable populations (Herbold and Moyle 1986), the New Zealand experience provided a rare opportunity to analyze invasion outcomes without bias.

We used a multiple logistic regression model to predict the success of avian introductions to New Zealand. Predictor variables were life-history variables (taxon, body mass, body length, geographic range, clutch size, brood frequency, diet, migratory status, and habitat use) and introduction effort (number of release events, minimum number of individuals introduced). Because the number of release events explained so much of the variation in invasion success, we also used a simple null model of invasions as a stochastic sampling process.

METHODS

The Data

Data on the size, diet, range, migratory behavior, habitat, and reproductive potential of each bird species in its endemic range were obtained from published sources. Sufficient published data were available for analysis of 79 species involved in 496 introduction events (table 1). Measurements of adult female body size were used throughout, to control for sexual size dimorphism in some species (Nee et al. 1991). Values for average adult female body length (millimeters) from bill to tail, and average female body mass (grams) in spring and summer were obtained from published literature. In a few cases, the sex of measured individuals was not given, and we have assumed the measurements represent adults of both

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TABLE 1

AVIAN SPECIES INTRODUCED TO NEW ZEALAND BEFORE 1907 AND THEIR PRESENT-DAY STATUS SCORED AS PRESENT (1) OR ABSENT (0)

		Predictor Variables													
Species	Status	A	B	C	D	E	F	G	H	I	J	K	L	M	Sources*
Anatidae:															
Cygnus olor	1	1,520	9,600	1.21	1	12	2	6.0	1	0	0	1	6	29	1, 2
Cygnus atratus	1	1,250	5,000	.56	1	0	1	6.0	1	0	0	1	10	85	1, 3, 4
Cereopsis novaehollandiae	1	870	3,360	.07	1	0	1	4.0	1	0	0	1	3	8	1, 5, 6
Anser caerulescens	0	720	2,517	1.10	3	12	2	3.8	1	0	0	1	1	10	1, 2, 7
Anser anser	0	820	3,170	3.45	3	0	1	5.9	1	0	0	1	2	7	2
Branta canadensis	1	770	4,390	2.96	2	0	1	5.9	1	0	0	1	10	60	1, 2
Branta sandvicensis	0	50	1,930	.01	1	0	1	4.0	2	0	0	0	1	2	1, 8
Alopochen aegyptiacus	0	680	2,040	2.71	1	. . .	2	8.5	1	0	0	1	1	8	2
Anas platyrhynchos	1	570	1,020	9.01	2	6	2	12.6	1	0	0	1	17	1,539	2
Anas acuta	0	580	910	7.90	3	6	2	8.3	1	0	0	1	3	102	2
Anas penelope	0	480	590	4.33	3	0	1	8.7	1	0	0	1	5	32	2
Aix sponsa	0	470	539	1.04	3	12	2	13.5	2	1	0	1	5	10	1, 9, 10
Aythya ferina	0	450	940	2.17	3	12	2	9.5	1	0	0	1	3	9	2
Aythya fuligula	0	435	684	4.81	3	12	2	10.1	1	0	0	1	2	5	2
Phasianidae:															
Oreortyx pictus	0	275	230	.31	1	3	1	9.5	1	1	1	0	9	398	1, 11
Lophortyx californicus	1	256	162	.24	1	3	1	14.2	2	0	0	0	15	1,420	1, 11
Colinus virginianus	1	230	170	.77	1	3	1	13.7	1	0	0	0	17	1,156	1, 11, 12, 13
Alectoris graeca	1	330	501	2.23	1	3	1	15.5	1	0	1	0	15	362	14
Alectoris rufa	0	330	439	.22	1	3	2	11.2	2	0	0	0	2	20	14
Perdix perdix	0	300	386	2.40	1	3	1	14.6	1	0	1	0	24	676	14
Coturnix pectoralis	0	182	95	.33	3	. . .	2	7.5	1	0	0	0	3	. . .	1, 3, 11
Coturnix australis	1	180	95	.69	2	12	2	11.0	1	0	0	1	11	601	1, 3
Lophura nycthemera	0	800	1,150	.28	1	12	2	5.0	1	1	1	0	4	6	1, 15
Phasianus colchicus	1	710	850	1.25	1	12	2	11.8	1	1	0	0	27	244	1, 14
Syrmaticus reevesii	0	750	949	.20	1	12	2	9.5	1	1	1	0	2	9	1, 15, 16
Tetraonidae:															
Tetrao tetrix	0	470	900	4.17	1	3	1	7.9	1	1	1	0	2	13	1, 14
Lagopus lagopus	0	390	517	7.29	1	0	1	7.5	1	1	1	0	2	4	1, 14
Pedioecetes phasianellus	0	440	815	1.83	1	3	1	12.3	1	1	0	0	1	22	1, 17, 18, 19
Tympanuchus cupido	0	435	770	.26	1	4	1	12.0	1	0	0	0	3	57	1, 17, 18, 20

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Charadriidae:															
Vanellus vanellus	0	300	226	3.93	2	12	3	3.8	1	0	0	0	8	124	1, 21
Pluvialis squatarola	0	285	318	1.67	3	12	3	4.0	1	0	0	1	2	3	21
Pteroclididae:															
Pterocles alchata	0	350	225	1.21	2	0	1	2.5	2	0	0	0	1	8	22
Columbidae:															
Phaps chalcoptera	0	320	350	.60	1	12	2	2.0	2	1	0	0	8	42	1, 3
Ocyphaps lophotes	0	330	205	.76	1	0	1	2.0	7	1	0	1	4	23	1, 3
Leucosarcia melanoleuca	0	372	. . .	.07	1	12	2	2.0	1	1	0	0	6	34	1, 3
Strigidae:															
Athene noctua	1	220	176	4.84	1	12	3	3.6	1	1	0	0	7	221	1, 22
Tytonidae:															
Tyto alba	0	340	298	8.90	2	0	3	5.7	2	1	0	0	1	7	22, 23
Alcedinidae:															
Dacelo novaeguineae	1	460	382	.34	1	12	3	2.0	1	1	0	0	7	21	3, 23, 24
Alaudidae:															
Lullula arborea	0	150	32.1	1.78	2	4	2	3.9	2	1	0	0	1	5	1, 25
Alauda arvensis	1	185	38.9	5.19	2	12	2	3.7	3	0	0	0	11	391	1, 25
Prunellidae:															
Prunella modularis	1	145	20.5	1.95	2	12	2	3.4	2	1	0	0	14	245	1, 25, 26
Turdidae:															
Erithacus rebecula	0	140	15.8	2.31	2	12	2	5.0	2	1	0	0	11	123	1, 25
Luscinia megarhynchos	0	161	19.4	1.88	3	12	2	4.7	2	1	0	0	4	7	1, 25
Turdus merula	1	255	82.6	3.30	2	12	2	3.8	3	1	0	0	16	596	1, 26, 27, 28
Turdus philomelos	1	230	67.3	4.84	2	12	2	4.7	2	1	0	0	12	343	1, 25, 26, 29, 30
Sylviidae:															
Sylvia communis	0	140	12.8	3.39	3	12	2	4.6	2	1	0	0	1	2	1, 31, 32, 33
Sylvia atricapilla	0	142	17.5	2.43	2	5	2	4.6	1	1	0	0	1	5	1, 34, 35, 36, 37
Meliphagidae:															
Manorina melanophrys	0	180	. . .	.04	1	12	3	1.9	5	1	0	0	1	2	38, 39, 40, 41
Manorina melanocephala	0	265	59.0	.25	1	12	2	2.6	. . .	1	0	0	1	80	1, 23, 42, 43
Grallinidae:															
Grallina cyanoleuca	0	275	128.0	.83	1	12	3	3.0	2	1	0	1	1	. . .	1, 23, 44
Cracticidae:															
Gymnorhina tibicen	1	400	380.0	.82	1	12	3	4.0	1	1	0	0	15	448	1, 45, 46
Corvidae:															
Corvus monedula	0	335	203.0	3.40	2	12	2	4.5	1	1	0	0	2	3	1, 47, 48, 49, 50
Corvus frugilegus	1	400	425.0	3.73	1	12	2	3.6	1	1	0	0	10	182	1, 51, 52, 53
Sturnidae:															
Sturnus vulgaris	1	222	79.8	3.33	2	6	2	4.8	2	1	0	0	14	653	1, 54, 55, 56, 57
Acridotheres tristis	1	230	111.3	.56	1	12	2	3.7	1	1	0	0	5	88	1, 58, 59, 60, 61

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TABLE 1 (*Continued*)

Species	Status	Predictor Variables													Sources*
		A	B	C	D	E	F	G	H	I	J	K	L	M	
Passeridae:															
Passer domesticus	1	149	28.8	6.50	1	6	2	3.9	3	1	0	0	12	416	1, 62, 63, 64, 65, 66
Passer montanus	0	133	22.0	6.80	1	6	2	4.7	3	1	0	0	3	14	1, 64, 67
Estrildidae:															
Aegintha temporalis	0	120	. . .	.17	1	6	2	4.7	3	1	0	0	3	14	1, 3, 68
Emblema guttata	0	120	19.0	.15	1	4	1	5.0	3	0	0	0	4	112	1, 3, 23, 68
Poephila guttata	0	100	12.4	.75	1	4	1	4.7	3	0	0	0	1	12	1, 23, 38, 69, 70
Lonchura punctulata	0	110	13.5	1.06	1	0	1	5.0	3	0	0	0	1	8	1, 3, 23, 38, 68
Lonchura castaneothorax	0	100	. . .	.13	1	4	1	5.0	. . .	0	0	1	4	45	1, 38, 68
Padda oryzivora	0	160	. . .	.09	1	0	1	5.0	. . .	0	0	0	2	6	1, 71, 72, 73
Fringillidae:															
Fringilla coelebs	1	160	23.5	2.61	2	12	2	4.9	2	1	0	0	17	449	1, 74, 75
Fringilla montifringilla	0	146	21.4	3.09	3	10	2	6.0	. . .	1	0	0	7	121	1, 74, 76, 77
Carduelis chloris	1	147	29.0	2.09	2	7	2	4.8	2	1	0	0	6	65	1, 74, 78, 79
Carduelis spinus	0	117	12.0	2.09	3	3	1	4.0	2	1	0	0	3	54	1, 74, 77
Carduelis carduelis	1	120	15.5	2.85	2	4	1	4.4	3	1	0	0	14	626	1, 74, 77, 80
Acanthis flammea	1	115	11.5	5.54	2	6	1	5.0	2	1	0	0	10	607	1, 74, 77, 81, 82
Acanthis flavirostris	0	133	17.0	1.67	2	0	1	5.0	3	0	1	0	3	61	1, 77
Acanthis cannabina	0	136	18.5	2.52	2	6	1	4.7	2	1	0	0	12	209	1, 74, 77, 82, 83
Pyrrhula pyrrhula	0	142	23.5	3.57	1	4	1	4.0	3	1	0	0	2	. . .	1, 63, 74, 77

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Emberizidae:															
Emberiza citrinella	1	160	28.2	4.11	2	8	2	3.3	3	1	0	0	14	656	1, 84, 85
Emberiza hortulana	0	163	21.6	2.75	3	12	2	5.0	1	0	0	0	1	6	1, 86, 87
Emberiza cirlus	1	160	23.6	.62	1	12	2	3.5	2	1	0	0	3	29	1, 88, 89
Emberiza schoeniclus	0	150	20.7	5.42	1	12	2	5.1	2	0	0	1	2	9	84, 90
Piranga rubra	0	170	31.0	.55	3	12	2	4.0	...	1	0	0	1	2	1, 91, 92
Icteridae:															
Agelaius phoeniceus	0	210	36.9	2.00	2	8	2	3.7	1	0	0	1	1	2	92, 93, 94, 95
Sturnella neglecta	0	225	106.5	1.20	2	12	2	4.8	2	0	0	0	1	2	1, 92, 95, 96

Note.—Data used in analyses are tabulated in columns A–M: A, female body length (mm); B, female body mass (g), measured to ± 1 g in all orders except Passeriformes, which were measured to ± 0.1 g; C, geographic range (% area of Australia); D, migration scored as sedentary (1), sedentary and migratory (2), or migratory (3); E, number of months in year with insects in diet; F, diet scored as herbivorous (1), omnivorous (2), or carnivorous (3); G, clutch size; H, number of broods per season; I, use of woodland scored as frequent (1) or infrequent (2); J, use of upland scored as frequent (1) or infrequent (0); K, use of water scored as frequent (1) or infrequent (2); L, minimum number of release events; M, minimum number of individuals introduced.

* Sources are given for data in columns A–K: 1, Long 1981; 2, Cramp 1977; 3, *Reader's Digest* 1976; 4, Wilmore 1974; 5, Guiler 1967; 6, Marriott and Forbes 1970; 7, Jackson et al. 1988; 8, Kear and Berger 1980; 9, Armbruster 1982; 10, Naylor 1960; 11, Johnsgard 1988; 12, Schroeder 1985; 13, Klimstra and Roseberry 1975; 14, Cramp 1980; 15, Johnsgard 1986; 16, Delacour 1977; 17, Evans 1968; 18, Johnsgard 1983; 19, Pepper 1972; 20, Prose 1985; 21, Cramp 1983; 22, Cramp 1985; 23, Blakers et al. 1984; 24, Parry 1973; 25, Cramp 1988; 26, Niethammer 1971; 27, Snow 1988; 28, Snow 1958; 29, Simms 1978; 30, Snow 1955; 31, Bergmann 1976; 32, Emmrich 1974; 33, Persson 1971; 34, Cody and Walter 1976; 35, Terrill and Berthold 1990; 36, Garcia 1989; 37, Bairlein 1978; 38, Pizzey 1980; 39, Clarke and Heathcote 1988; 40, Clarke 1988; 41, Smith and Robertson 1978; 42, Dow 1978; 43, Dow 1975; 44, Robinson 1947; 45, Ford et al. 1986; 46, Veltman 1989; 47, Dwenger 1989; 48, Richford and Lawman 1978; 49, Richford 1978; 50, Gooders 1986; 51, Patterson et al. 1988; 52, Patterson and Grace 1984; 53, Holyoak 1972; 54, Bährmann 1978; 55, Taitt 1973; 56, Tiainen et al. 1989; 57, Wright and Cuthill 1990; 58, Ali and Ripley 1987; 59, Baker and Moeed 1980; 60, Brooke 1976; 61, Sengupta 1968; 62, O'Connor 1972; 63, Cheke 1972; 64, Seel 1968; 65, Seel 1969; 66, Keil 1972; 67, Seel 1964; 68, Immelmann 1965; 69, Clayton et al. 1991; 70, Frith and Tilt 1959; 71, Baptista and Atwood 1980; 72, MacKinnon 1988; 73, Robinson 1927; 74, Newton 1967; 75, Svensson 1978; 76, Jenni and Jenni-Eiermann 1987; 77, Newton 1972; 78, Monk 1954; 79, Hinde 1954; 80, Middleton 1970; 81, Pulliainen and Peiponen 1981; 82, Ernst 1988; 83, Tast 1970; 84, Prys-Jones 1977; 85, Parkhurst and Lack 1946; 86, Campbell and Lack 1985; 87, Conrads 1969; 88, Groh 1975; 89, Barba and Lopez 1990; 90, Haukioja 1970; 91, Nørgaard-olesen 1974; 92, Terres 1980; 93, Ewald and Rohwer 1982; 94, Nero 1956; 95, Orians and Angell 1985; 96, Lanyon 1957.

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sexes. Whenever two or more published values for a body size trait were discovered, the median value was used. Diet was measured in two ways. "Insect months" referred to the number of months in the year in which insects composed part of the diet of birds within the species' endemic range. For the second measure, we categorized each species as herbivore, omnivore, or carnivore. Geographical range for species not originating in Australia was estimated by the method developed by Moulton and Pimm (1986), in which range as depicted for each species in Long (1981) was scaled to the size of Australia. For Australian species, the number of primary blocks (grid blocks in which a species was present) recorded as containing the species in the range maps of Blakers et al. (1984) was converted to a percentage of the total area of Australia. Migratory behavior was categorically scored as sedentary, sedentary and migratory, or migratory. Use of habitat in the endemic range for each species was classified with scores of one or zero for obligate use (with one indicating use and zero indicating nonuse) of woodland, water, and uplands.

The minimum known number of introductions and the minimum known number of birds released for each species were obtained from Thomson (1922), by summing the values given for each liberation event for each species. Once we had extracted the data in this way, we compared our values to those summarized from the same source by Long (1981), as a check for errors in interpretation. The clarity of Thomson's (1922) account meant there were few cases in which our values differed from Long's (1981), and when they did, we used our own interpretation. Some additional data were obtained from shipping lists published as appendices to Lamb (1964)—when an importation of birds in Lamb (1964) was not documented by Thomson (1922), we added the values from the shipping list to the values in Thomson. Thus, the data in table 1 sometimes exceed the values in Long (1981).

Two species of introduced birds that still occur in New Zealand today had to be omitted from the data set because no information could be found on the number of introductions or number of propagules. They were peafowl (*Pavo cristatus*) and rock dove (*Columba livia*). A further 56 species of introduced birds that did not invade successfully were omitted from the data set because it was not clear just which species they were, or because quantitative information about their introductions could not be extracted from Thomson (1922).

Statistical Procedure

The present-day status of each species in New Zealand, categorized as present (successful) or absent (unsuccessful), was used as the response variable in fitting a multiple logistic regression model using generalized linear models (McCullagh and Nelder 1989; Crawley 1993). A binomial probability distribution was specified. A maximal model using 14 predictor variables was constructed. The minimal adequate models were found by deleting variables with no significant effect from the maximal model, which left those factors whose deletion significantly reduced the goodness-of-fit in the model (χ^2). At all stages, control of the model was manual (i.e., an automatic stepwise procedure was not used).

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TABLE 2

PARAMETER ESTIMATES, χ^2 VALUES FOR GOODNESS-OF-FIT TESTS, AND VARIANCE FOR EACH FACTOR IN THE MAXIMAL MODEL AND MINIMAL ADEQUATE MODEL

	MAXIMAL MODEL				MINIMAL MODEL			
SOURCE	% Variance	χ^2	df	P	% Variance	χ^2	df	P
Number of releases	2.2	2.13	1	ns	43.4	42.4	1	.001
Number of propagules	8.7	8.52	1	.005	38.0	37.1	1	.001
Migration	5.1	5.02	2	.05	16.0	15.7	2	.001
Body length	.1	.16	1	ns				
Body mass	6.3	6.20	1	.025				
Taxon (order)	9.9	9.70	7	ns				
Insect months	6.1	5.99	1	.025				
Range	.04	.04	1	ns				
Clutch size	3.2	3.13	1	ns				
Number of broods	3.1	3.08	1	ns				
Diet	4.1	4.06	2	ns				
Use of woodland	3.2	3.13	1	ns				
Use of upland	1.4	1.46	1	ns				
Use of water	.08	.08	1	ns				

NOTE.—Model involves stepwise deletion from a logistic regression with a binary response variable: present (successful) or absent (unsuccessful); ns, nonsignificant.

RESULTS

Scope of the Data

Approximately half of the species in the sample were Passeriformes, while the remainder were from seven other avian orders (table 1). Of the 91 possible pairwise correlations between the 14 predictor variables, 35 (38%) were significant (Pearson's product moment correlations, $P < .05$). This meant that there was a moderate amount of overlap between measures. However, all variables were entered initially in the model.

Relationships between Variables Using Multiple Logistic Regression

Two minimal adequate models for describing systematic variation in the data were discovered through a multiple logistic regression procedure (table 2). Because one model included the variables "number of releases" and "migration" and the other included "number of propagules" and "migration," the two models varied only in the way in which the introduction effort was quantified. The changes in residual deviance and degrees of freedom as each factor was removed from the maximal model are shown as χ^2 statistics in table 2. There was greater variance in number of propagules, which explains why this variable accounted for more of the variance in the maximal model.

Large positive residuals were observed for cirl buntings (*Emberiza cirlus*), mute swans (*Cygnus olor*), and kookaburras (*Dacelo novaeguineae*). These species became established in spite of low numbers of introductions and propagules. In contrast, there was a large negative residual for European partridge (*Perdix per-*

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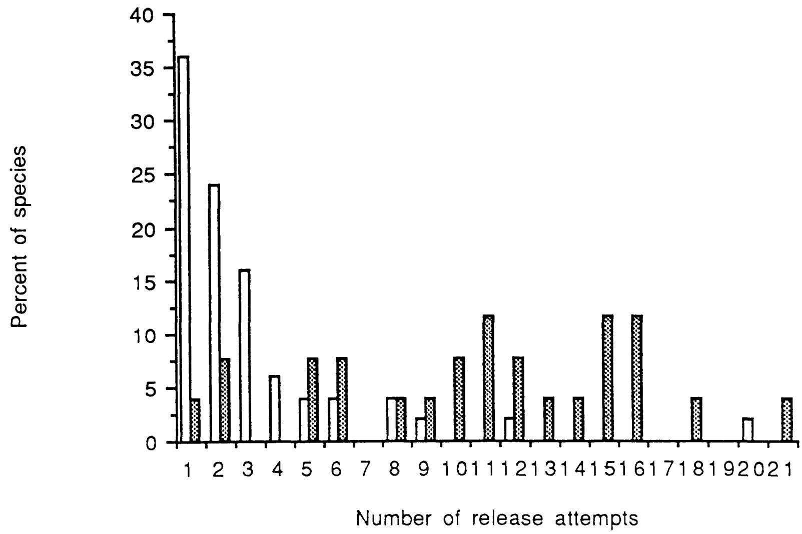

FIG. 1.—Frequency distribution of numbers of releases made of successful bird colonists (*shaded bars*) and unsuccessful colonists (*unshaded bars*) in New Zealand.

dix), which failed to colonize New Zealand despite at least 676 individuals being released in 24 introduction attempts.

The frequency distribution of introduction attempts for successful invaders and colonist populations that became extinct is given in figure 1.

Null Model for Investigating Success of Translocations

Figure 1 conveys the clear visual impression that species that were released more times are more likely to have become established, and the minimal model shows that this factor explains most of the variation in establishment success. A natural null model is that each release attempt has a probability p of resulting in the successful establishment of the species in New Zealand and that this probability is the same for all species. A species will become established if at least one of the releases is successful; hence the probability that a species that is released N times does *not* become established is

$$(1 - p)^N .$$

This is simply the probability that all the species fail. The probability that the species becomes established is, then,

$$1 - (1 - p)^N .$$

If K species are each released N times and S become established while F do not (so $S + F = K$), then the probability of observing this outcome is

$$\binom{K}{F}(1 - p)^{NF}[1 - (1 - p)^N]^S .$$

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Therefore, the expected number of species that fail to invade is

$$K(1 - p)^N.$$

For these data, the maximum likelihood estimate of p is 0.0924. For each number of releases, N, we compared the observed and expected numbers of species that failed to become established, where the expected number is $K(1 - p)^N$. The null hypothesis was rejected ($\chi^2 = 15.47$, df $= 6$) because too many of the species that were released more times had a higher probability per release of successful establishment.

Reproductive Potential of Species Liberated More Often

To account for the differences in establishment probabilities, we obtained adult survival estimates for 36 of the species and calculated the ratio of natality (number of broods multiplied by clutch size) to mortality (proportion of adults not surviving to the next season in the endemic range). Among the 36 species for which we had data, there was a significant correlation between the natality/mortality ratio and the number of translocations that were done ($r = 0.371$, $P < .05$).

Number of Release Localities

A feature of the New Zealand introduction effort is that birds were liberated by Acclimatisation Societies representing each of the four provinces of the time. It was therefore likely that species with more releases were released at many sites rather than repeatedly liberated at one or a few sites. We found that successful species had been introduced to significantly more localities (median $= 5$, $n = 25$) than unsuccessful species (median $= 2$, $n = 52$, Mann-Whitney $W = 1{,}379.5$, $P < .0001$).

DISCUSSION

Colonization Success and Introduction Effort

The New Zealand experience conforms to an emerging generalization that most translocations fail, even when there is some deliberation (Ehrlich 1989). A much lower proportion of birds were successful colonists in New Zealand (20%) compared with an estimated minimal 35% establishment rate in other countries (Lodge 1993). This likely reflects the greater completeness of the contemporary record compiled by Thomson (1922).

Introduction effort was the most important correlate of colonization success. Management by humans thus appeared to be the crucial factor for most of the introduced birds that have become established in New Zealand. Introduction of a greater number of individuals significantly increased the colonization success of birds introduced to Australia (Newsome and Noble 1986), birds introduced in Europe (unpublished data, cited in Ebenhard 1991), and of a variety of mammals and birds translocated in Pacific countries in recent times (Griffith et al. 1989; but note that $P = .15$ in their analyses). These earlier results were loosely interpreted as evidence that demographic stochasticity in small populations pushes them toward extinction. A single, small founder population may indeed fail to

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establish because of random fluctuations in the fates of individuals (Wilcox and Murphy 1985), but the finding here that the probability of establishment can depend on the number of introductions or on the number of propagules indicates that a successful outcome might be achieved through appropriate management. This is a novel result, although it was anticipated by Niethammer (1971). Data on the number of introductions have not been available for historic introductions elsewhere and were not considered by Griffith et al. (1989) in their analysis of contemporary translocations.

Repeated invasions occurred before bird species established themselves without deliberate human intervention in Great Britain (O'Connor 1986). In biocontrol studies, establishment rates also increased as more individuals were released (Ehler and Hall 1982; Crawley 1987).

Colonization Success and Life-History Attributes

The only life-history attribute of the introduced birds that significantly influenced the outcome was migration. Species that migrated within the endemic range were less likely to establish in New Zealand than nonmigratory species with similar introduction efforts. This result was predicted by Thomson (1922) and is intuitively sensible. A small number of birds "programmed" to fly long distances on a compass bearing will likely succumb at sea, given New Zealand's geography. Another reason why migrating species may fail to establish is that they disperse so far that few find each other in the breeding season.

To explore why species in the set of successful invaders had a higher probability *per release* of a release's being successful, we reasoned that the successful species must have possessed at least one trait not included in our analysis of life-history attributes or that some aspect of the way that the translocations were carried out differed between successful and unsuccessful species. Our data support both interpretations.

Common to all the models summarized in Ebenhard (1991; table 1) is the prediction that species with a high intrinsic rate of increase (r), or more precisely, a high ratio of natality to mortality (λ/μ) (Ehrlich 1986; Lawton and Brown 1986), should invade new habitats more readily than species with lower rates. Where birds are concerned, this means that species with big clutch sizes or several broods per breeding season might be expected to persist after translocation if mortality factors are not severe. What we discovered was a tendency for people in New Zealand to have made more releases of birds with such characteristics. Given that the suite of species taken to New Zealand was a somewhat predictable sample of British commensals and overlaps the lists for Australia (Newsome and Noble 1986) and Hawaii (Moulton and Pimm 1986), the apparent correlations between life-history attributes and invasion success in those places may have been confounded with the (unknown) number of translocations.

Invasion Outcome and Number of Release Sites

The question of whether, given 50 birds for liberation, a conservation practitioner should release all birds at one site or 10 birds at each of five sites (Pimm et al. 1988) may be addressed empirically from our data. Successful invaders were released at more sites than were unsuccessful ones. The New Zealand

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archipelago spans 13 degrees of latitude and offers landscapes ranging from sea level to 3,000 m in altitude. A large number of release sites necessarily equated to a variety of abiotic and biotic conditions, so that species with more propagules sampled a greater variety of environments. However, some species failed to colonize New Zealand in spite of very many introductions, so it would be unwise to infer a general rule from our results.

We focused on species that were deliberately translocated to a new place without systematic thought to the consequences (Ehrlich 1989). Conservation practitioners, on the other hand, evaluate both the organism and the community into which it is being translocated and may take some consolation from the observation that introductions into the core of a species' former range are more likely to succeed than introductions elsewhere (Griffith et al. 1989; Lawton 1993). While it will never be possible to specify with confidence the outcome of any particular translocation (Ehrlich 1989), the strategy of releasing animals simultaneously in different sites is one that also might be considered in the light of our results.

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