

# High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate

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## Summary

1. We investigated factors hypothesized to influence introduction success and subsequent geographical range size in 52 species of bird that have been introduced to mainland Australia.
2. The 19 successful species had been introduced more times, at more sites and in greater overall numbers. Relative to failed species, successfully introduced species also had a greater area of climatically suitable habitat available in Australia, a larger overseas range size and were more likely to have been introduced successfully outside Australia. After controlling for phylogeny these relationships held, except that with overseas range size and, in addition, larger-bodied species had a higher probability of introduction success. There was also a marked taxonomic bias: gamebirds had a much lower probability of success than other species. A model including five of these variables explained perfectly the patterns in introduction success across-species.
3. Of the successful species, those with larger geographical ranges in Australia had a greater area of climatically suitable habitat, traits associated with a faster population growth rate (small body size, short incubation period and more broods per season) and a larger overseas range size. The relationships between range size in Australia, the extent of climatically suitable habitat and overseas range size held after controlling for phylogeny.
4. We discuss the probable causes underlying these relationships and why, in retrospect, the outcome of bird introductions to Australia are highly predictable.

*Key-words:* Australian birds, biological invasions, climatic suitability, ecology of invasions, extinction, introduced species, introduction effort, range size.

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## Introduction

Many species have been deliberately or accidentally introduced to areas outside of where they naturally occur (Long 1981; Lever 1994). Some species have established populations successfully and spread, but others either failed to establish or established but have not spread. Although these introductions have often had disastrous consequences for indigenous biota (e.g. Savidge 1987), they also provide opportunities to improve our understanding of biological invasions and other ecological processes.

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The historical record of bird introductions to New Zealand has been used extensively to test hypotheses about the factors influencing introduction success and the subsequent spread of introduced birds (Veltman, Nee & Crawley 1996; Duncan 1997; Green 1997; Sorci, Møller & Clobert 1998; Duncan, Blackburn & Veltman 1999; Legendre *et al.* 1999). A similarly detailed record of bird introductions to Australia exists: at least 55 species have been introduced to mainland Australia, of which 19 have successfully established (Long 1981; Newsome & Noble 1986). Our aim in this study is to test hypotheses about factors thought to influence introduction success and geographical range size using this historical record. The hypotheses that we test can be divided into three groups:

1. Availability of climatically suitable habitat. One of the most frequently stated hypotheses in the biological

invasion literature is that species should have a greater chance of success if they are introduced to an area with a climate that closely matches that in their original range (Brown 1989; Mack 1996; Williamson 1996). This hypothesis has never been tested using a set of successful and failed introductions. Here we test the hypothesis that introduced species with a larger area of climatically suitable habitat in Australia should have both a higher probability of successful introduction and, if successful, should have a larger geographical range in Australia.

**2. Life history traits.** Certain life history traits are hypothesized to increase the probability of successful introduction and to be associated with larger geographical range sizes. In particular, species with a faster population growth rate should have higher introduction success because they will be less vulnerable to local extinction when their population is small and, following successful introduction, should be able to colonize more sites and thereby attain a larger range size (Gaston 1988; Hanski 1991; Hanski, Kouki & Halkka 1993; Holt *et al.* 1997). We test this hypothesis by searching for significant correlations between introduction success, geographical range size and biological traits that are probable correlates of population growth rate, including body size, clutch size, number of broods per season and incubation time. In addition, species with sexually dichromatic plumage, migratory species, solitary species and species with a narrow diet are hypothesized, or have been shown, to have a lower probability of successful introduction (Mayr 1965; Veltman *et al.* 1996; Sorci *et al.* 1998). Birds that are partial migrants in their natural range have also been shown to have a larger geographical range size following introduction to New Zealand (Duncan *et al.* 1999).

**3. Historical factors.** Greater introduction effort (number of introduction attempts, number of locations at which species are introduced or the total number of individuals introduced) is the strongest predictor of success for birds introduced to New Zealand (Veltman *et al.* 1996), and predicts the success of bird introductions to Australia (Newsome & Noble 1986). For introduced Australian birds, we extend this result by testing if greater introduction effort is associated with a larger geographical range, as is the case for birds introduced successfully to New Zealand (Duncan *et al.* 1999). We also test if successful introduction elsewhere and the overseas range size of a species predict introduction success in Australia, as has been found elsewhere (Moulton & Pimm 1986; Rejmánek 1996; Reichard & Hamilton 1997).

## Methods

### DATA SOURCES

We identified 55 bird species introduced to Australia from Newsome & Noble (1986) and Long (1981). We excluded two species that were introduced only to offshore islands (*Alopecurus aegyptiacus* (Linnaeus

1766) and *Meleagris gallopavo* (Linnaeus 1758)), and one species (*Lophura nycthemera* (Linnaeus 1758)) that established a population that was subsequently destroyed by humans. Our data set thus comprised a total of 52 species that have been introduced to mainland Australia, of which 19 species have successfully established (Fig. 1, Appendix 1).

The minimum recorded number of separate introductions, the minimum number of introduction sites and the minimum total number of birds introduced for each species was collated from Long (1981) and Newsome & Noble (1986). We followed Newsome & Noble (1986) in grouping species into three categories: 20 or fewer individuals introduced (including species classed as unknown or cage escapees), 21–100 individuals introduced, or > 100 individuals introduced. Species that had been successfully introduced to locations outside Australia were identified from Long (1981).

For the successful species, two measures of geographical range size in Australia were taken from Blakers, Davies & Reilly (1984): (i) 'observed range size', the number of 1° blocks in which the species was confirmed sighted, and (ii) 'breeding range size', the number of 1° blocks in which the species was confirmed breeding. The overseas geographical range of each species (i.e. the geographical range excluding Australia) was calculated by digitizing the distribution maps in Long (1981).

Data on body mass, migratory behaviour, flocking behaviour, diet, clutch size, number of broods per season and incubation period (Appendix 1) were taken from Frith, McKean & Braithwaite (1976), Cramp & Simmons (1977–94), Goodwin (1982), Goodwin (1983), Bennett (1986), Goodwin (1986), Johnsgard (1986), Potts (1986), Urban, Fry & Keith (1986), Fry, Keith & Urban (1988), del Hoyo, Elliott & Sargatal (1992–97), Dunning (1993), Maclean (1993), Shurtleff & Savage (1996), Veltman *et al.* (1996), Baicich & Harrison (1997) and Sorci *et al.* (1998).

A binary variable coding for plumage dichromatism (i.e. a colour difference between males and females of the same species) was taken from Sorci *et al.* (1998) for those species introduced to both Australia and New Zealand. The remaining species were scored as monochromatic or dichromatic from illustrations in Heinzel, Fitter & Parslow (1984), or from descriptions in Long (1981).

We classed each species as associated with human-dominated habitats or not, from the habitat descriptions in Sibley & Monroe (1990). When a species was listed in Sibley & Monroe (1990) as occupying either towns, gardens, farmland, fields or pastures we classed that species as being associated with human-dominated habitats; species not listed as occupying those habitats were classed otherwise.

### AVAILABILITY OF CLIMATICALLY SUITABLE HABITAT

We used a climate-matching procedure to quantify the climatically suitable habitat available to each



**Table 1.** The 16 climate parameters (temperature and rainfall) used to estimate the extent of climatically matched habitat in the CLIMATE program (Pheloung 1996). Estimates of these parameters are derived from long-term averages of monthly minimum and maximum temperatures and rainfall for each of the approximately 8000 meteorological stations in the CLIMATE database

Temperature parameters (°C)	Rainfall parameters (mm)
Mean annual	Mean annual
Minimum of coolest month	Mean of wettest month
Maximum of warmest month	Mean of driest month
Average range	Mean monthly CV
Mean of coolest quarter	Mean of coolest quarter
Mean of warmest quarter	Mean of warmest quarter
Mean of wettest quarter	Mean of wettest quarter
Mean of driest quarter	Mean of warmest quarter

points. The 16 climate variables were generated for each grid point based on long-term data from meteorological stations in Australia (Nix 1986). For each of 16 climate variables at each of the input meteorological stations, the difference between the value for each input meteorological station and the value at each Australian grid point was divided by the global standard deviation for the variable to generate a standard score. A Euclidian distance was computed as the square root of the sum of the squares of the standard scores for each of the 16 climate variables, divided by 16. The resultant value was then compared to a normal distribution of reference scores that partition the normal distribution into percentage categories based on the area under the normal distribution curve. Scores within 10% of the mean score are those with the closest possible climate match, and scores of 80% or higher, which fall in the tails of the normal distribution, have the lowest climate match. CLIMATE repeats this matching process for all input meteorological stations. The closest matching score is then selected for each Australian grid square because, if a species occurs at an overseas location that closely matches the climate at a given Australian location, whether it also occurs at less well matched overseas locations is irrelevant. Hence, a close climate match is identified for an Australian grid square if at least one of the overseas locations where the species occurs closely matches that grid square. For each species, the number of Australian grid squares allocated to each climate matching class is a measure of Australia's land area in that climate matching class.

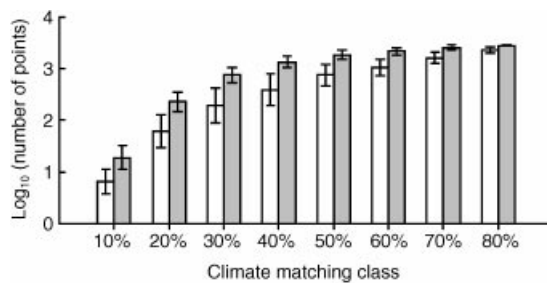
#### DATA ANALYSIS

The factors influencing introduction success (a binary variable) were modelled using logistic regression. We first included each predictor variable alone in a logistic regression model and then used a forward selection procedure to identify a subset of predictor variables that could independently predict introduction success. We then used a cross-validation procedure to test the ability of these variables to correctly predict

introduction outcomes. We estimated the probability that a particular species would have succeeded by removing that species from the dataset and constructing a logistic regression model using the data for the remaining species. The resulting model was then used to predict the probability that the removed species would have succeeded, a procedure that ensures that the data used to construct the model are independent of the data used to predict the probability of success. This procedure was repeated for all species and the predicted probabilities of introduction success compared with the actual outcomes. For geographical range size we used standard linear regression and analysis of variance to model relationships with predictor variables.

We repeated the analyses using the method of independent contrasts (Felsenstein 1985) to control for phylogenetic relatedness among species. This is important because the birds introduced to Australia are not a random sample of all birds. The families Phasianidae and Anatidae, for example, contain just over 3% of the world's bird species (following Sibley & Monroe 1990), but species in these families comprise 27% of the birds introduced to Australia. Hence, relationships in our data could be biased by the over-representation of certain taxa as a result of the introduction process (Lockwood 1999). The effect of this taxonomic bias will be reduced if we test for relationships independent of phylogeny.

We constructed a phylogeny for the birds introduced to Australia (Fig. 1) from data in Sibley & Ahlquist (1990), Sibley & Monroe (1990), Martin & Clobert (1996) and Livezey (1997). The method of independent contrasts requires a fully resolved phylogeny, but our phylogeny contained several unresolved nodes. We therefore used a model (Comparative Analysis by Independent Contrasts (CAIC); Purvis & Rambaut 1995) which applies the method of independent contrasts to data sets for which only approximate phylogenies are known. Because we lacked data for all branch lengths, we set these as equal. The independent contrasts for continuous variables were calculated using the CRUNCH option in CAIC (Purvis & Rambaut 1994). Relationships between these sets of contrasts were then analysed using ordinary least squares regression, with the regression line forced through the origin (Garland, Harvey & Ives 1992). Where one variable was dichotomous (e.g. introduction success) and the second variable was continuous, the independent contrasts were calculated using the BRUNCH option (Purvis & Rambaut 1994). If there is no relationship between two variables then, under this option, the independent contrasts should show no significant tendency to be either positive or negative. We tested for such a tendency using a one-sample *t*-test against an expected value of zero (Purvis & Rambaut 1994). Where one variable was dichotomous and the second variable was categorical we also used the BRUNCH option, treating the categorical variable as continuous by assigning a rank order score to its categories. In all cases the categories could be ranked sensibly.



**Fig. 2.** The mean ( $\pm$  95% confidence limits) of the  $\log_{10}$ (total number of target points) in climate matching classes below a progressively higher threshold ( $\leq 10\%$ ,  $\leq 20\%$ ,  $\leq 30\%$ , and so on), for bird species that were successfully (shaded bars) and unsuccessfully (open bars) introduced to Australia.

## Results

### INTRODUCTION SUCCESS

#### *Availability of climatically suitable habitat*

For the successful and failed bird species introduced to Australia, we compared the mean of the (log-transformed) number of target points allocated to climate matching classes below a progressively higher threshold ( $\leq 10\%$ ,  $\leq 20\%$ ,  $\leq 30\%$  and so on). Successfully introduced species had a significantly greater number of target points in climate matching classes

below all but the highest threshold ( $\leq 80\%$ ; Fig. 2). This difference was greatest in climate matching classes below a threshold of about 50%. Indeed, there was a significant relationship between the probability of successful introduction and the total number of target points in the  $\leq 50\%$  climate matching classes, both across-species and having controlled for phylogeny (Table 2). The greater the extent of more strongly climatically matched habitat that was present in Australia, the greater the probability that a species was successfully introduced. Of the nine species with 25 or fewer points in the first two climate matching classes, none were introduced successfully.

#### *Life history traits and historical factors*

The number of broods per season, and diet, were significant but weak predictors of introduction success across-species, and body mass and diet were significant predictors having controlled for phylogeny (Table 2). Species producing more broods per season, species with omnivorous or carnivorous diets and species with larger body mass tended to have a higher probability of introduction success.

All of the historical factors that we considered were significant predictors of introduction success across-species and, with the exception of overseas range size, having controlled for phylogeny. Relative to species that

**Table 2.** Across-species and phylogenetically independent predictors of avian introduction success to Australia. The results of the across-species analyses are the change in deviance resulting from adding each predictor variable in the left-hand column to a logistic regression model with introduction outcome (success or failure) as the response variable. d.f. = the degrees of freedom associated with adding each variable to the model. The results of the analyses of phylogenetically independent contrasts are *t*-tests of the tendency for the independent contrasts associated with the variable in the left-hand column to be significantly positive or negative. A significant positive *t*-value indicates that larger values of the variable in the left-hand column are associated with greater introduction success, a significant negative *t*-value indicates the opposite. *n* = the number of independent contrasts associated with each *t*-test

Variable	Across-species		Independent contrasts	
	d.f.	Change in deviance	<i>n</i>	<i>t</i>
<b>Habitat availability</b>				
$\log_{10}$ (total number of points in the $\leq 50\%$ climate matching classes)	1	8.95**	15	2.81*
human-modified habitat use	1	1.29	2	-0.27
<b>Life history traits</b>				
$\log_{10}$ (body mass)	1	0.16	15	2.78*
$\log_{10}$ (clutch size)	1	2.75	15	0.52
$\log_{10}$ (broods per season)	1	5.47*	15	1.84
$\log_{10}$ (incubation period)	1	0.02	14	1.73
plumage dichromatism	1	2.09	8	-1.42
migration	2	4.91	8	-1.20
flocking	1	0.71	3	0.26
diet	1	4.53*	6	5.02**
<b>Historical factors</b>				
$\log_{10}$ (overseas range size)	1	8.57**	15	2.01
$\log_{10}$ (number of introduction events)	1	22.65***	14	7.02***
$\log_{10}$ (number of introduction sites)	1	22.85***	15	6.53***
number of individuals introduced	2	7.00*	10	10.57***
introduced successfully elsewhere	1	8.49**	9	3.01*

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

failed, the species introduced successfully to Australia tended to have larger overseas range sizes, to be released at more sites, to be released more often and in greater numbers, and to have been introduced successfully elsewhere.

In addition to the above relationships, there was a marked taxonomic bias in introduction success: of 11 species of gamebird (Order: Galliformes) introduced, only one succeeded (peafowl, *Pavo cristatus* (Linnaeus 1758)); we also excluded a twelfth species of gamebird, *Lophura nycthemera*, that failed but whose population was destroyed by humans). As a group, gamebirds had a significantly lower success rate than other species (change in deviance = 5.34,  $P = 0.02$ ).

#### Modelling introduction success

We coded the number of sites to which species were introduced as a binary variable (introduced to  $\leq 2$  or  $> 2$  sites) because only two of the 30 species introduced to  $\leq 2$  sites succeeded, while 17 of the 22 species introduced to  $> 2$  sites succeeded. Five variables were then significant predictors of introduction success in a forward selection model (Table 3). Species that were introduced to  $> 2$  sites, that were not gamebirds, that had a greater area of climatically suitable habitat available in Australia, that had been introduced successfully elsewhere, and that had a larger body mass were more likely to have been introduced successfully. Body mass was the only variable that was not a significant predictor of introduction success when included alone in logistic regression, although it was a significant predictor having controlled for phylogeny (Table 2).

Remarkably, the forward selection model that included these five variables explained all of the variation in introduction success (Table 3). The results from the cross-validation procedure indicate how well the model performs in prediction: it correctly predicted the outcome for 47 of the 52 species introduced to Australia. Of the five species that were misclassified in cross-validation, three were predicted to succeed but failed (*Branta canadensis* (Linnaeus 1758), *Numida meleagris* (Linnaeus 1758) and *Plectropterus gambensis* (Linnaeus 1766)), while two were predicted to fail but succeeded (*Lonchura punctulata* (Linnaeus 1758) and *Pavo cristatus*).

#### GEOGRAPHICAL RANGE SIZE

For analyses of geographical range size we excluded three predictor variables (human-modified habitat use, flocking behaviour, and whether or not birds were introduced successfully elsewhere) because in each case all but one of the successfully introduced birds used human-modified habitats, flocked or were introduced successfully elsewhere.

#### Availability of climatically suitable habitat

The observed and breeding range sizes were most strongly correlated with the number of points in the

**Table 3.** Results of a forward selection multiple logistic regression model with introduction outcome as the response variable (success or failure) and the variables listed in Table 2 as predictors, for 52 bird species introduced to mainland Australia. Ordered = the change in deviance associated with adding each predictor variable to the model in the order of inclusion; Last = the change in deviance associated with adding each predictor variable to the model last, with the remaining predictors already included; coefficient = the estimated regression coefficients. For the continuous variables (climate suitability and body mass), the positive coefficients indicate that species with more area of suitable climate and species with larger body mass had a higher probability of successful introduction. For the categorical variables, a negative coefficient indicates that species in that category had a lower probability of successful introduction relative to species in the category with a 0 coefficient. The total deviance explained by the model, the residual deviance, and the associated degrees of freedom (d.f.) are also shown. The residual deviance is 0 which indicates that the model explains perfectly the patterns in introduction success

Predictor variable	d.f.	Ordered	Last	Coefficient
Intercept	1			-3696.3
Number of introduction sites	1	30.0***	36.8***	
$\leq 2$				-1239.5
$> 2$				0
Gamebird	1	7.6**	32.8***	
Yes				-1806.1
No				0
Log <sub>10</sub> (total points in $\leq 50\%$ climate matching class)	1	6.4*	20.3***	898.6
Introduced successfully elsewhere	1	5.5*	20.0***	
No				-988.3
Yes				0
Log <sub>10</sub> (body mass)	1	18.8***	18.8***	759.4
Total deviance explained	5	68.3***		
Residual deviance	46	0.0		

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

closest matched climate class ( $\leq 10\%$ ), both across-species and having controlled for phylogeny (Table 4, Table 5).

#### Life history traits and historical factors

Three life history traits were significantly correlated with observed and breeding range size across-species; more widely distributed birds tended to have small body masses, short incubation times and to produce more broods per season (Table 4). The correlations were generally weaker after controlling for phylogeny (Table 5).

Introduced species with a larger geographical range outside Australia tended to have a larger geographical range inside Australia. After controlling for phylogeny, introduced birds that were partial migrants in their natural range also had a significantly larger observed range size in Australia, although this relationship was

**Table 4.** Results of across-species analyses (Pearson correlation coefficients,  $r$ , for the continuous variables or ANOVA  $F$ -values (Type 1 SS) for the categorical variables) comparing the  $\log_{10}$ -transformed observed and breeding range sizes in Australia with the variables in the left-hand column, for the 19 successfully introduced species

Variable	Log <sub>10</sub> (observed range size)		Log <sub>10</sub> (breeding range size)	
	$r$	$F$	$r$	$F$
Total number of points in climate matching class ( $\log_{10}$ transformed)				
≤10%	0.762***		0.704***	
≤20%	0.643**		0.573*	
≤30%	0.533*		0.469*	
≤40%	0.497*		0.430	
≤50%	0.519*		0.453	
≤60%	0.540*		0.483*	
≤70%	0.547*		0.472*	
≤80%	0.516*		0.442	
Life history traits				
log <sub>10</sub> (body mass)	-0.594**		-0.651**	
log <sub>10</sub> (clutch size)	-0.396		-0.388	
log <sub>10</sub> (broods per season)	0.543*		0.567*	
log <sub>10</sub> (incubation period)	-0.543*		-0.634**	
plumage dichromatism		0.00		0.16
migration		2.38		1.95
diet		0.30		0.62
Historical factors				
log <sub>10</sub> (overseas range size)	0.665**		0.636**	
log <sub>10</sub> (number of introduction events)	0.024		0.246	
log <sub>10</sub> (number of introduction sites)	-0.128		0.073	
number of individuals introduced		0.69		2.11

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .**Table 5.** Results of analyses of phylogenetically independent contrasts (Pearson correlation coefficients,  $r$ , for the continuous variables or  $t$ -tests for the categorical variables) comparing the  $\log_{10}$ -transformed observed and breeding range sizes in Australia with the variables in the left-hand column, for the 19 successfully introduced species.  $n$  = the number of independent contrasts

Variable	Log <sub>10</sub> (observed range size)		Log <sub>10</sub> (breeding range size)		$n$
	$r$	$t$	$r$	$t$	
Total number of points in climate matching class ( $\log_{10}$ transformed)					
≤10%	0.643**		0.624**		18
≤20%	0.526*		0.519*		18
≤30%	0.526*		0.535*		18
≤40%	0.560*		0.563*		18
≤50%	0.554*		0.542*		18
≤60%	0.545*		0.521*		18
≤70%	0.566*		0.513*		18
≤80%	0.582**		0.531*		18
Life history traits					
log <sub>10</sub> (body mass)	-0.315		-0.255		18
log <sub>10</sub> (clutch size)	-0.167		-0.200		18
log <sub>10</sub> (broods per season)	0.380		0.484*		18
log <sub>10</sub> (incubation period)	-0.231		-0.265		18
plumage dichromatism		1.21		1.35	6
migration		2.84*		1.91	6
diet		-0.16		-0.18	2
Historical factors					
log <sub>10</sub> (overseas range size)	0.563*		0.569*		18
log <sub>10</sub> (number of introduction events)	0.215		0.336		18
log <sub>10</sub> (number of introduction sites)	0.088		0.188		18
number of individuals introduced		-		-	

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

**Table 6.** Results of a forward selection regression model with  $\log_{10}$  (observed range size) as the response variable, for the 19 bird species successfully introduced to mainland Australia. The predictor variables in the left-hand column are shown in order of their inclusion in the model. Coefficient = the estimated regression coefficients ( $\pm$  one standard error);  $t$  and  $P$  = the  $t$ -value and the associated probability for each regression coefficient, respectively; partial  $r^2$  = the increase in  $r^2$  associated with successively adding each variable to the model

Predictor variable	Coefficient (SE)	$t$	Partial $r^2$
$\log_{10}$ (total points in $\leq 10\%$ climate matching class)	0.91 (0.218)	4.2***	0.58
$\log_{10}$ (body mass)	-0.32 (0.136)	2.4*	0.11

\* $P < 0.05$ , \*\*\* $P < 0.001$ .

not significant across-species. None of the remaining historical or life history variables significantly predicted Australian range size.

#### Modelling geographical range size

A forward selection model included two variables that explained 69% of the variation in geographical range size across-species: the number of target points in the  $\leq 10\%$  climate matching class and body mass (Table 6). Species with a greater area of closely matched climate and species with smaller body mass tended to have larger geographical ranges, although the area of closely matched climate alone could explain most of the variation (58%).

## Discussion

### INTRODUCTION SUCCESS

Our results support the claim by Williamson (1996) that 'propagule pressure, habitat matching and previous success at invasion' are robust predictors of introduction success. For birds introduced to Australia, these three factors significantly predicted introduction success both across-species and having controlled for phylogeny, and all three factors emerged as independent predictors in our forward selection model (Table 3). Introduction effort (or propagule pressure) was the strongest predictor in our study and is consistently a strong predictor in other retrospective and experimental studies with data to quantify this effect (Crowell 1973; Ebenhard 1989; Griffith *et al.* 1989; Pimm 1991; Hopper & Roush 1993; Veltman *et al.* 1996; Williamson 1996; Duncan 1997; Green 1997; Memmott, Fowler & Hill 1998; Forsyth & Duncan 2001). Introduction effort is important because the introduction of more individuals to any one site lowers the chance of stochastic extinction (MacArthur & Wilson 1967), while introductions to multiple sites increase the probability that at least one population will escape stochastic extinction and will encounter habitat suitable for establishment (Crawley 1989). The probability of successful introduction will be enhanced if a species is both introduced

to multiple sites and if a large proportion of those sites contain suitable habitat. This is precisely what we found: the number of introduction sites and the extent of climatically suitable habitat independently predict introduction success (Table 3).

Climate matching is reported to have mixed success in predicting introduction outcomes because there are examples of species that have been introduced successfully to areas outside their original climatic range (Mack 1996; Williamson 1996). Despite this, the degree of climate matching significantly predicted the success or failure of birds introduced to Australia. To our knowledge, this is the first time this hypothesis has been tested quantitatively (but see Nix & Wapshere 1986). However, climate matching alone would have failed to predict the success of several birds introduced to Australia. Repeating the cross-validation procedure using the number of target points in the  $\leq 50\%$  climate matching class as the only predictor results in 19 of the 52 introductions being misclassified, including 11 species predicted to fail that actually succeeded.

The low success rate in gamebirds, independent of other variables, suggests that an additional factor limited introduction success in this group. Several species of gamebird introduced to New Zealand have similarly failed to establish despite persistent efforts to introduce them (Heather & Robertson 1996). In Australia, one explanation for the high failure rate is human hunting. We excluded from our analysis one species of gamebird (*Lophura nycthemera*) whose population was destroyed by humans, and other gamebird populations may have been reduced by hunting. The one species that did succeed (peafowl, *Pavo cristatus*) is an ornamental species that is not typically hunted.

Overseas range size significantly predicted introduction success across-species but not having controlled for phylogeny or in multiple regression, suggesting that its predictive power derived from correlations with other traits. Wide overseas range could indicate flexible or generalist species that, relative to specialist species, have a high chance of success because they are likely to encounter conditions suitable for establishment (Williamson 1996). As we would predict if this were the case, introduced Australian birds with larger overseas range sizes had a greater area of climatically suitable habitat available in Australia (Spearman  $r = 0.35$ ,  $n = 52$ ,  $P = 0.01$ ). However, widespread species will also be readily available for capture and may therefore be introduced more often and in greater numbers to any one location, increasing their success rate. This holds for birds introduced to Australia: overseas range size is significantly correlated with the number of introduction events, the total number of individuals introduced, and the number of introduction sites (Spearman  $r = 0.29$ ,  $0.44$  and  $0.30$  respectively,  $n = 52$ ,  $P$  all  $< 0.03$ ). Hence, an indirect relationship between overseas range size and introduction success could arise via two different pathways, the first associated with habitat availability and the second associated with the introduction process.



Of the remaining traits that we considered, only diet showed a consistent relationship with introduction success both across-species and having controlled for phylogeny. Nevertheless, diet failed to explain, independently, significant variation in multiple regression, suggesting that its relationship with introduction success may derive from correlations with other traits. We found no evidence to support the hypotheses that species with a faster population growth rate, species that are non-migrants, species with dichromatic plumage and species that are gregarious were more likely to be introduced successfully.

#### GEOGRAPHICAL RANGE SIZE IN AUSTRALIA

A larger geographical range size in Australia is associated with a greater extent of climatically suitable habitat, suggesting that, at a broad scale, climate constrains the distribution of introduced birds. In European birds, changes in the timing (Crick *et al.* 1997) and success (Visser *et al.* 1998) of reproduction, and shifts in species northern range-margins (Thomas & Lennon 1999), have been related to changes in climate, mechanisms which could underlie a relationship between climate and geographical range size.

The availability of climatically suitable habitat also appeared to account for the strong but indirect relationship between overseas and Australian range size. Species with larger overseas range sizes had more climatically suitable habitat available in Australia and hence a larger Australian range size. Consequently, the number of target points in the closest climate matching class entirely accounted for the relationship between overseas range size and Australian range size in multiple regression.

Introduced species possessing traits associated with fast population growth rate (small body size, short incubation period and multiple broods per season) were significantly more widely distributed, and body mass remained a significant predictor of range size in multiple regression (Table 6), although these relationships were generally weaker having controlled for phylogeny. Similar relationships between range size and traits associated with population growth rate were found for introduced New Zealand birds and for British breeding birds (Duncan *et al.* 1999), highlighting a consistent pattern in range size variation.

#### Conclusions

This is the first published study confirming that climatic suitability significantly predicts introduction success and the subsequent geographical range size of introduced birds. While many studies stress the unpredictability of biological invasions (Williamson 1999), the outcome of bird introductions to Australia were highly predictable, possibly because we included attributes that are typically unknown, such as introduction effort and climatic suitability, and that

were important predictors of introduction outcomes. Further studies in which these factors can be quantified are required to test the generality of these conclusions.

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**Appendix 1.** Bird species introduced to mainland Australia. Nomenclature follows Sibley & Monroe (1990). AUS, species was successfully (1) or unsuccessfully (0) introduced to Australia; A, 'observed' range size in Australia (1° blocks); B, 'breeding' range size in Australia (1° blocks); C, female body mass (g); D, plumage dichromatism, scored as no (0) or yes (1); E, migration, scored as sedentary (1), sedentary and migratory (2), or migratory (3); F, flocking, scored as no (0) or yes (1); G, diet, scored as herbivorous (1), omnivorous (2), or carnivorous (3); H, clutch size; I, number of broods per season; J, days to incubate; K, do not (0) or do (1) use human-dominated habitats; L, overseas range size ( $\times 10^6$  km<sup>2</sup>); M, minimum number of individuals introduced; N, minimum number of introduction events; O, minimum number of introduction sites; P, successfully introduced elsewhere, scored as yes (1) or no (0). n.d. indicates no data available

Species	AUS	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
<b>Struthionidae</b>																	
<i>Struthio camelus</i>	1	1	1	9950	1	1	1	2	7	1	45.5	0	8	> 500	4	5	0
<b>Odontophoridae</b>																	
<i>Callipepla californica</i>	0	.	.	162	1	1	1	1	14.2	2	n.d.	1	3	267	6	5	1
<b>Numididae</b>																	
<i>Numida meleagris</i>	0	.	.	1388	0	1	1	2	8	1	n.d.	1	20	170	3	6	1
<b>Phasianidae</b>																	
<i>Alectoris barbara</i>	0	.	.	376	0	1	1	2	13	1	25	1	3	2	1	1	1
<i>Alectoris graeca</i>	0	.	.	501	0	1	1	2	15.5	1	25	0	23	48	5	2	1
<i>Alectoris rufa</i>	0	.	.	439	0	1	1	2	11.2	2	23.5	1	1	9	1	1	1
<i>Gallus gallus</i>	0	.	.	850	1	1	1	2	5.5	1	19	1	6	4	2	2	1
<i>Lophura ignita</i>	0	.	.	1600	1	1	0	2	6	1	24	0	1	2	1	1	1
<i>Lophophorus impejanus</i>	0	.	.	2000	1	1	1	2	4.5	1	27	0	1	2	1	1	0
<i>Pavo cristatus</i>	1	2	2	3375	1	1	1	2	6	1	25.5	1	4	33	10	9	1
<i>Perdix perdix</i>	0	.	.	386	1	1	1	2	14.6	1	24.5	1	32	4	2	2	1
<i>Phasianus colchicus</i>	0	.	.	850	1	1	0	2	11.8	1	n.d.	1	34	750	12	12	1
<b>Anatidae</b>																	
<i>Aix galericulata</i>	0	.	.	635	1	2	1	2	9	1	29	1	3	2	1	1	1
<i>Anas platyrhynchos</i>	1	81	13	1020	1	2	1	2	12.6	1	27.5	1	95	86	4	3	1
<i>Branta canadensis</i>	0	.	.	4390	0	2	1	1	5.9	1	29	1	38	4	2	1	1
<i>Cygnus olor</i>	1	1	1	9600	0	1	1	2	6	1	36	1	11	12	5	5	1
<i>Plectropterus gambensis</i>	0	.	.	4700	0	1	1	2	11	1	31.5	1	16	4	2	2	0
<b>Psittacidae</b>																	
<i>Agapornis roseicollis</i>	0	.	.	55.5	0	1	1	1	3.5	1	23.3	1	2	3	2	1	0
<b>Columbidae</b>																	
<i>Columba livia</i>	1	304	89	296	0	1	1	2	2	5	17.5	1	80	> 500	2	2	1
<i>Oena capensis</i>	0	.	.	39.5	1	1	1	1	2	2.5	14.5	1	20	2	1	1	1
<i>Streptopelia chinensis</i>	1	89	31	160.5	0	1	0	2	2	5	14	1	11	57	10	7	1
<i>Streptopelia senegalensis</i>	1	34	13	99	0	1	1	2	2.5	5.5	13	1	44	4	3	3	1
<i>Streptopelia turtur</i>	0	.	.	132	0	2	1	1	2	2.5	13.5	1	34	8	1	1	0
<b>Pteroclididae</b>																	
<i>Pterocles exustus</i>	0	.	.	248	1	1	1	2	2.5	3	23	1	15	2	1	1	0
<b>Ardeidae</b>																	
<i>Bubulcus ibis</i>	1	172	14	357	0	2	1	3	3.5	2	23.7	1	54	18	1	1	1
<b>Corvidae</b>																	
<i>Corvus splendens</i>	0	.	.	307	0	1	1	2	4.5	1	16.5	1	5	53	4	2	1
<b>Muscicapidae</b>																	
<i>Erithacus rubecula</i>	0	.	.	15.8	0	2	0	2	5	2	14	1	25	47	3	1	0
<i>Luscinia megarhynchos</i>	0	.	.	19.4	0	3	0	2	4.7	2	13	1	16	4	1	1	0
<i>Turdus merula</i>	1	117	78	82.6	1	2	1	2	3.8	3	13.5	1	31	102	8	4	1
<i>Turdus philomelos</i>	1	4	4	67.3	0	2	1	2	4.7	2	11.5	1	31	129	8	5	1
<b>Sturnidae</b>																	
<i>Acridotheres tristis</i>	1	55	20	111.3	0	1	1	2	3.7	1	17.5	1	11	277	11	9	1
<i>Sturnus vulgaris</i>	1	246	157	79.8	1	2	1	2	4.8	2	14.5	1	58	292	9	4	1
<b>Pycnonotidae</b>																	
<i>Pycnonotus cafer</i>	0	.	.	35.5	0	1	1	2	3	3	14	1	6	4	2	2	1
<i>Pycnonotus jocosus</i>	1	11	4	32.5	0	1	1	2	3	3	13	1	6	8	3	3	1
<b>Alaudidae</b>																	
<i>Alauda arvensis</i>	1	88	37	38.9	0	2	1	2	3.7	3	11.5	1	57	526	13	8	1

Appendix 1. *Continued*

Species	AUS	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
<b>Passeridae</b>																	
<i>Euplectes albonotatus</i>	0	.	.	17.6	1	1	1	2	2.5	1	13	0	6	2	1	1	0
<i>Euplectes orix</i>	0	.	.	24.5	1	2	1	2	3.5	2	12.5	0	13	4	2	2	1
<i>Lonchura malacca</i>	0	.	.	12.5	0	1	1	1	5.5	3	12.5	1	7	2	1	1	1
<i>Lonchura punctulata</i>	1	41	19	13.5	0	1	1	1	5	3	16	1	9	8	4	4	1
<i>Padda oryzivora</i>	0	.	.	24.8	0	1	1	1	5	3	13.5	1	1	255	2	2	1
<i>Passer domesticus</i>	1	330	185	28.8	1	1	1	2	3.9	3	12.5	1	110	414	20	20	1
<i>Passer montanus</i>	1	20	14	22	0	1	1	2	4.7	3	13	1	70	68	4	3	1
<b>Fringillidae</b>																	
<i>Carduelis cannabina</i>	0	.	.	18.5	1	2	1	1	4.7	2	13.5	1	25	32	4	4	0
<i>Carduelis carduelis</i>	1	123	77	15.5	0	2	1	1	4.4	3	13	1	31	223	5	4	1
<i>Carduelis chloris</i>	1	55	23	29	1	2	1	2	4.8	2	13	1	21	133	7	4	1
<i>Carduelis spinus</i>	0	.	.	12	1	3	1	1	4	2	13	1	22	80	3	1	0
<i>Emberiza citrinella</i>	0	.	.	28.2	1	2	1	2	3.3	3	13	1	47	34	3	3	1
<i>Emberiza hortulana</i>	0	.	.	21.6	1	3	1	2	5	1	11.5	1	30	16	1	1	0
<i>Fringilla coelebs</i>	0	.	.	23.5	1	2	1	1	4.9	2	12.5	1	27	498	4	2	1
<i>Fringilla montifringilla</i>	0	.	.	21.4	1	3	1	2	6	2	14	1	31	78	1	1	0
<i>Pyrrhula pyrrhula</i>	0	.	.	23.5	1	1	1	1	4	3	14	1	41	14	1	1	0
<i>Serinus canarius</i>	0	.	.	16.5	1	1	1	1	4	2	12.5	1	0.1	20	2	2	1