

# Influences on the transport and establishment of exotic bird species: an analysis of the parrots (Psittaciformes) of the world

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## Abstract

Most studies of exotic species invasions only consider the factors that affect the establishment of populations following release, yet this is only one step on the invasion pathway. Different factors are likely to influence which species are transported and released. Here, we examine the influence of species traits on the successful transition of species through several stages in the introduction pathway (transport, release, and establishment), using parrots (Aves: Psittaciformes) as a model system. We use a species-level supertree of parrots to test for phylogenetic auto-correlation in the introduction process. Our analyses find that different sets of variables are related to the probability that a species enters each stage on the invasion pathway. The availability of individuals for transport and release seems to be most important for passage through these stages, but has no obvious effect on establishment following release. Rather, establishment success is higher for sedentary species, and species with broad diets.

*Keywords:* aliens, exotics, introduction, invasion, parrots, transport

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## Introduction

The introduction of non-native species outside their native geographic ranges represents a major and growing threat to the maintenance of global biodiversity, and has been described as a major component of human-induced global change (Vitousek *et al.*, 1996; Mack *et al.*, 2000). In most cases, we are unable to predict which species will successfully establish non-native populations. Consequently, the literature on biological introductions is increasingly populated with attempts to explain introduction outcomes by identifying the life history and ecological traits that predispose certain species to establish and spread outside their native range (Drake *et al.*, 1989; Williamson, 1996, 1999; Reichard & Hamilton, 1997; Daehler, 1999). Several

recent studies have found that species-specific traits are related to whether introduced birds will establish non-native populations, and whether they will become invasive (reviewed in Kolar & Lodge, 2001; see also Sol & Lefebvre, 2000; Blackburn & Duncan, 2001a; Cassey, 2002; Duncan *et al.*, 2003). Identification of such traits may allow us in future to target prevention measures against potential invaders that possess them.

Williamson (1996) identified a series of unique, but nested, stages of successful biological invasions. These include introduction, release, and establishment (cf. Vermeij, 1996). One stage precedes another, such that among all the species that establish, some larger proportion must first be released, and so on. Only those established species that spread widely beyond the site of release are termed 'invasive'. Some species in this group cause economic or ecological damage in their new environment. It is the size of this group that trait-based screening policies hope to reduce (Reichard & Hamilton, 1997; Mack *et al.*, 2000).

The failure of a species to pass through any one of the stages in the introduction pathway can be attributed to

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the possession of traits that do not favour a successful transition. However, the sequential nature of the introduction process raises the possibility that the influence of characteristics at earlier stages of the process can have carry-over effects on later stages. Moreover, because the social and biological mechanisms operating at each stage differ, the influence of any given trait may vary according to the stage at which it is evaluated (Kolar & Lodge, 2001). Notably, life history traits may either negate or reinforce one another across introduction stages. For example, migratory birds are less likely to become successfully established if released, but more likely to spread once established (Kolar & Lodge, 2001). The possibility of such across-stage interactions suggests that misleading conclusions about the correlates of invasiveness may easily be drawn (Lockwood, 1999; Blackburn & Duncan, 2001a), and that extreme caution must be exercised when interpreting the biological and policy significance of traits whose influence has only been evaluated at any single stage.

In response to these issues, we examined the influence of taxon-specific traits on the successful transition of parrot species (Aves: Psittaciformes) through different stages in the introduction pathway (transport, release, and establishment). Parrots are ideal for across-stage comparisons of invasion success. When looking for traits that influence successful transition through a stage in the invasion process, the proper comparison is between the set of species that were successful and the set that failed (Prinzing *et al.*, 2002). Thus, we must have knowledge of the species that failed to transit a stage in addition to those that succeeded. Together, these two groups of species (i.e. successful and failed) make up the species pool at any given introduction stage. Transporting and selling parrots is big business and records of the parrot trade are well kept. Parrots are large-bodied, gregarious, and frequently vocal, and so are easily spotted by amateur bird watchers. Consequently, we have unusually good regional (e.g., Johnston & Garrett, 1994; Garrett, 1997; Sol *et al.*, 1997; Pithon & Dytham, 2002) and global records (e.g., Long, 1981; Lever, 1987) of which species have been intentionally released from captivity and subsequently become established beyond their native distributional limits. Thus, there is unprecedented information concerning which species comprise the 'pool' at each separate introduction stage. This allows what is, as far as we are aware, the first global analysis of correlates of passage along the invasion pathway, from transport to establishment, for an entire clade of organisms (for a similar analysis of more restricted spatial extent, see Kolar & Lodge, 2002).

We used two related approaches to understanding the passage of parrot species between successive stages

in the introduction pathway. First, we explored how taxonomic clustering of success on passing through different stages of the introduction pathway varies across the levels of the parrot taxonomic hierarchy. This information can be used to predict introduction success if it is found that taxonomically related species have similar probabilities of transiting a given stage. Second, we tested for specific characteristics that relate to successful passage through different stages of the introduction pathway. The analyses were based on the hypothesis that exotic species can be characterized by distinguishable traits that determine the probability of successful transit through different stages (e.g. see Lodge, 1993; Lockwood, 1999; Kolar & Lodge, 2001; Cassey, 2002).

## Materials and methods

### *Data sources*

We gathered information on all 350 extant parrot species, following the species list in Juniper & Parr (1998), but with *Aratinga holochlora* split into *A. holochlora* and *A. rubritorquis*. For consistency, the data were derived largely from del Hoyo *et al.* (1997) and Juniper & Parr (1998), supplemented by available unpublished information (P.M. Bennett, M. Cardillo, P. Cassey, and T.A. Mulliken). We defined the three different stages of the introduction pathway and the species that have transited them, as follows:

### *Transport*

Parrot species that are well recorded as having been commonly transported outside their natural geographic range are scored as 1; all other parrot species are scored as 0.

### *Release*

Parrot species that are well recorded as having been intentionally released outside their natural geographic range for purposeful introduction (a subset of those transported) are scored as 1; all other parrot species that have been transported but were not released are scored as 0.

### *Establishment*

Parrot species, following their intentional introduction, are well recorded as having established free-living exotic populations. As a species may be released on more than one occasion, but different releases may have different establishment outcomes, we analysed establishment success as a binomial variable  $R(x/y)$  for a species with  $x$  successes in  $y$  attempts (following the convention of Simberloff & Boecklen, 1991). Note that

successfully established species are a subset of those released.

Many studies have identified associations between the probability of establishment and species characteristics, but studies of characteristics of species transported vs. those not transported, and released vs. not released, are much rarer (Duncan *et al.*, 2003; but see Guix *et al.*, 1997). We analyse a set of variables that have been suggested in the literature as determinants of an exotic species' establishment following release. These can be broadly divided into four categories, related to: species' population size or extent, ecological flexibility, the likely extent to which species are subject to movements through human activities, and life history (listed in Table 1). It seems likely that at least some of these variables should also relate to the probability of transport and/or release. Transport has been shown to be more likely for species with larger population or range sizes (Blackburn & Duncan, 2001b). Transport outside the native region additionally seems likely to relate to the frequency with which species are traded

and kept in captivity, and with life history characteristics that make a species valuable for trade (for example, its size, longevity, and plumage). Which of the transported species then get released is less predictable *a priori*, but may conceivably relate to abundance in captivity, and hence to a similar set of factors that determine probability of transport.

#### *Variables relating to population size or geographical extent*

Threat status was defined following BirdLife International (2000) as; (0) for species that are not considered to be threatened, (1) near-threatened species, (2) vulnerable species, (3) endangered, and (4) critically endangered species. Extinct species were not included in these analyses. Range-restricted species were taken from del Hoyo *et al.* (1997). These are species with geographic ranges of < 50 000 km<sup>2</sup> as defined by BirdLife International (Stattersfield *et al.*, 1998). Pest parrot species were defined as; (0) for species that are not

**Table 1** Univariate analyses of the probability that a parrot species successfully transits a given stage in the introduction pathway

Variables	Transport		Release		Establishment	
	Coefficient	SE	Coefficient	SE	Coefficient	SE
(a) Relating to population size/extent						
Threat status	-0.36	0.11**	-0.53	0.21*	0.37	0.27
Range restricted	-1.08	0.29***	-1.13	0.43**	-1.35	0.79 <sup>†</sup>
Pest	1.35	0.41**	0.76	0.18***	0.33	0.21
Population size	0.40	0.22 <sup>†</sup>	1.00	0.29**	0.60	0.25*
Geographic range size	0.71	0.13***	0.48	0.19**	-0.24	0.18
(b) Relating to ecological flexibility						
Diet breadth	0.45	0.20*	0.42	0.19*	0.54	0.20**
Altitudinal range	0.85	0.68	1.23	0.76	3.83	1.25**
Latitudinal range	1.04	0.25***	1.43	0.43***	-0.01	0.47
Median latitudinal midpoint	0.13	0.04***	0.11	0.03***	0.02	0.03
(c) Relating to movement						
Trade (local)	1.86	0.61**	-0.52	0.17*	-0.2	0.39
Trade (international)	2.11	0.59***	0.78	0.14***	0.32	0.12**
Captivity	1.69	0.42***	0.82	0.21***	-0.21	0.21
Pet	26.14	0.15***	1.60	0.32***	0.66	0.35 <sup>†</sup>
CITES	0.23	0.47	-0.69	0.55	-0.36	0.73
(d) Relating to life history						
Body mass	1.55	0.49**	0.24	0.39	0.51	0.39
Annual fecundity	1.67	1.09	1.46	0.84 <sup>†</sup>	-1.73	1.00 <sup>†</sup>
Age at maturity	-0.69	1.43	-1.19	1.02	1.56	1.02
Incubation period	3.00	4.12	-1.15	2.53	2.77	2.30
Fledging period	2.89	2.16	-0.20	1.22	4.82	1.85**
Migration	0.09	0.23	-0.51	0.25*	-0.88	0.28**
Dichromatism	0.02	0.30	0.68	0.34*	-0.60	0.34 <sup>†</sup>

SE, standard error.

For analyses, <sup>†</sup> $P \leq 0.10$ ; \* $P \leq 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

reported as pests in their native ranges, (1) for species reported as pests in their native ranges, and (2) for parrots that are either persecuted or officially listed as pest species in their native ranges (del Hoyo *et al.*, 1997; Juniper & Parr, 1998).

Population size was the arithmetic mean of available estimates of the number of individuals considered to comprise the total world population (estimates were taken from del Hoyo *et al.*, 1997; Juniper & Parr, 1998; BirdLife International, 2000). Geographical range size was an estimate of the total extent of the geographic distribution of a species. To derive the estimate for each species, we used a complete species-level geographic range digital database to obtain accurate measures of geographic range sizes (km<sup>2</sup>) and latitudinal and longitudinal extent. Ranges were first compiled using the species' extent of occurrence from the distribution maps in Juniper & Parr (1998). This was completed for all species except for *A. holochlora* and *A. rubritorquis*, whose distribution is not separated in Juniper & Parr (1998). For these two species, we used del Hoyo *et al.* (1997). All maps were digitized into a GIS (ArcGIS v8.3) and range sizes were calculated using the total extent of a species range, using the Behrmann global equal-area projection. Species' geographic ranges were logarithmically transformed for analysis.

#### *Variables relating to ecological flexibility*

Diet breadth was the composition of each species' diet scored with respect to the presence or absence of substantial amounts of four different food types: seeds, fruits, vegetative material, and animal material. Diet breadth was measured as the sum of these different food types in the diet (range 1–4).

Altitudinal range (metres) was the difference between the normal upper and lower altitudinal range limits of a species in its natural range, logarithmically transformed for analysis.

We used digitized parrot distributions to record the northern and southern limits of the geographical range of each species, in degrees of latitude. From these, we calculated two variables that may relate to ecological flexibility (Stevens, 1989; Daehler & Strong, 1993; Brooks, 2001). Latitudinal range was calculated as the difference in degrees between the latitude of the northern range limit and the latitude of the southern range limit and logarithmically transformed for analysis. Latitudinal range midpoint was calculated by subtracting half the latitudinal range from the latitude of the northernmost range limit. Midpoints south of the equator were arbitrarily designated as negative. These variables may relate to flexibility because species with broad latitudinal ranges or living at high latitudes may

encounter a broader range of climatic or environmental conditions.

#### *Variables relating to extent of global movement*

The number of individuals of a species in international trade was recorded from the average net reported imports of parrot species (1983–1989) as listed in Thomsen *et al.* (1995). Data were logarithmically transformed for analysis. For the Moran's *I* analysis (see below), these data were converted into a binary variable: (0) species not known in international trade, or (1) species listed as traded in Thomsen *et al.* (1995). Species in local trade were specified as either: (0) species not known to be traded within its geographic range, or (1) species traded within its geographic range. Captive species were specified as either: (0) if they are unknown or rare in captivity, (1) if they are known and common in captivity, or (2) if greater than 10% of their world population is reported in captivity. Pet species were listed as either: (0) if the species is not reported as being kept in private captivity, or (1) for species that are so reported, from data in Vriens (1984). CITES species are those that are currently listed in CITES Appendix I.

#### *Variables relating to life history*

Body mass (g) was measured as the arithmetic mean of the adult ranges. Annual fecundity was estimated as the product of average clutch size and modal number of clutches. Age at maturity was taken as the time in months from hatching to adult plumage. We calculated the incubation period of parrot species as the mean time in days between egg laying and hatching. The fledging period was estimated as the mean time in days between hatching and leaving the nest. All life history variables were logarithmically transformed for analysis.

Sexual plumage was scored as dichromatic if there were any differences between sexes in the colour and/or pattern in the descriptions and illustrations from Juniper & Parr (1998). The degree of migration undertaken by parrot populations was scored as: (0) if species are resident with local movements only, (1) if they are nomadic species with irruptive seasonal movements, and (2) if they are species with regular altitudinal or geographical migrations.

#### *Data analyses*

We tested for predictability in parrot invasions in two ways. First, we explored how taxonomic clustering of introduction success varies across the levels of a species-level supertree of parrots (South and Wilkinson,

unpublished results). Using Moran's *I* statistic (Moran, 1950), we looked for correlation of human imposed binary traits within taxa at the levels of genus, tribe, sub-family, and family (see Lockwood *et al.*, 2002). The traits were transport, release, establishment, captivity, and trade. The first three traits were examined in a nested fashion, in that transport was examined using the set of all parrots, release was examined using the subset of all transported parrots, and establishment was examined using the subset of all released parrots. This is because only transported parrots can be released, and only released parrots can become established. Captivity and trade were examined using the set of all parrots.

We define the evolutionary distance between any two taxa as the number of steps in the taxonomic hierarchy required to move from one to the other. Phylogenetic autocorrelation (indicated by a positive *I*-value) is then the degree to which similar biological attributes (e.g., introduction success) tend to be clustered within closely related taxa. *I* has the usual form for a correlation, being a covariance divided by a variance. The variance is simply the variance of all the observations. The covariance uses a weighting value  $w_{ij}$  for each pair of species. Typically, these weights are binary, being set to one for pairs of observations separated by a specified distance or range of distances, and zero otherwise. Thus, we were able to measure autocorrelation at any level of phylogenetic interest or any stage of the introduction process.

To test the significance of the *I* statistic, we used Monte-Carlo simulations in which the trait of interest was distributed across species at random. These simulations generated a null distribution for *I* keeping the phylogenetic associations constant while randomly reshuffling the traits, an approved method for tests of phylogenetic inertia (Maddison & Slatkin, 1991). We tested the significance of *I* using a two-tailed approach, allowing the possibility of negative correlation. Some evolutionary processes, such as disruptive evolution, can give rise to negative correlations. In this case, our 'traits' are not evolutionary characters *per se*, but the outcome of an interaction between the environment (including human influences) and the organism as a whole. This presents other opportunities for negative correlations to arise, for example, if traders collect birds from a certain locality and related taxa tend to be allopatric, or if collectors desire a single representative of every higher taxon such that traders focus on the easiest-to-capture or most abundant species.

The question we addressed using *I* was is there correlation of a given trait at *any* taxonomic distance? This requires us simultaneously to consider the tests at each of the four levels in our taxonomy (see Table 2). Because the tests are independent, we only considered there to be overall significance if one or more of

**Table 2** Summary of significance of Moran's *I* statistic for the variables in the first column across the taxonomic hierarchy for parrots

Trait	Separate level tests*				Overall test†
	Genus	Tribe	Sub-family	Family	
Transport	---			-	S
Release				--	S
Establishment					NS
Captive	---		+++	---	S
Traded	+++	---	---		S

'+' and '-' indicate positive and negative correlation, respectively.

-or + =  $P < 0.05$ , -- or ++ =  $P < 0.01$ , --- or +++ =  $P < 0.005$ .

S, significant; NS, nonsignificant.

\*Two-tailed,  $\alpha = 0.05$ .

†Bonferroni corrected  $\alpha = 0.0125$ .

the tests was significant at a sequentially derived Bonferroni critical value of  $\alpha = 0.05$  (Hommel & Bernard, 2000).

Second, we tested whether any of the variables described above correlates with the identity of parrot species present at different stages of the introduction pathway by comparing characteristics between species that have and have not achieved each stage. Although comparisons among taxa cannot determine causation, the analyses we present do provide insight into causes, and highlight potential evolutionary influences, that are related to the passage of parrot species along the introduction pathway. Because the introduction pathway is nested, this leads to successively smaller sets of species in each comparison. Thus, we compared the characteristics of species that have been transported outside their native range ( $n = 292$ ) with the characteristics of species that have not been so transported ( $n = 58$ ), and the characteristics of transported species that have been released into alien environments ( $n = 54$ ) with the characteristics of species that were transported but not released ( $n = 238$ ). For released species ( $n = 54$ ), we tested for correlates of establishment success.

Statistical analyses were conducted in SAS v.8.02. Generalized linear models were used to test the outcome of transported (a binary variable, 0 = not transported, 1 = transported), released (a binary variable, 0 = transported but not released, 1 = transported and released), and established (a binomial variable,  $R(x/y)$  for a species with  $x$  successes in  $y$  attempts) against the influence of predicted life history and ecological variables across parrot species. Each independent variable was first included alone in a logistic regression type model, and then the combined effects of

different variables were investigated using multivariate models. We addressed the problem of pseudoreplication consequent on the fact that species are introduced to multiple locations by adjusting the assumed binomial variance using a scale parameter, estimated as the  $\chi^2$  value divided by the effect degrees of freedom, and then determining significance values using the *F* statistic (e.g. Crawley, 2002; Blackburn *et al.*, 2004).

Multivariate models were used to investigate the independent influence of species-specific variables relating to population size, ecological flexibility, and life history. Note that we do not examine the variables relating to movement as these are indices of human selection and therefore represent the multiplicative influence of the species-specific variables rather than the variables themselves. A manual selection method was used to assess and remove nonsignificant terms manually from multivariate models until no further terms could be removed without reducing the model's explanatory powers (Olden & Jackson, 2000). This is termed the reduced adequate model.

## Results

### *Nonrandomness in the introduction pathway*

Results of the Moran's *I* tests are summarized in Table 2. Using Bonferroni-corrected  $\alpha$  levels as described in the Materials and methods, all but one of the overall tests (see Materials and methods) showed some form of correlation. Within the taxon-level tests, seven out of the nine significant tests (78%) showed a negative correlation with the trait in question, indicating less clustering of the trait within the taxonomic level than expected by chance.

Positive correlations were observed for trade status at the genus level and captive status at the sub-family level. Strong negative correlations were observed for transport and captive status at the genus level, trade at the tribe and sub-family levels, and captive at the family level. Weaker, but still significant, negative correlations were observed for transport and release at the family level. Only establishment showed no significant correlation at any level.

The lack of taxonomic clustering in whether or not species pass through different stages on the invasion pathway mean that in subsequent analyses we use species as independent data points. While it is now almost standard practice to perform phylogenetic controls (Harvey & Pagel, 1991; Garland *et al.*, 1999; Freckleton *et al.*, 2002; but see Harvey & Rambaut, 2000), there is no phylogenetic association to control for in this case.

### *Correlates of passage along the introduction pathway*

Independent variables related to the geographical extent or population abundance of parrot species in their native environment were found frequently to be significantly correlated with whether species were transported beyond their native range, and then whether or not they were subsequently released at a novel location (Table 1a). Species with larger range sizes and species that were pests in their native range were more likely to be transported and subsequently released. Range-restricted and threatened species were less likely to be transported, and if transported, less likely also to be released. Species with larger population sizes were more likely to be released, but population size was unrelated to probability of transport. Following release, only population size was (negatively) correlated with establishment success (Table 1a).

Independent variables likely related to the environmental tolerance of species in their native environment were frequently found to be significant correlates of whether or not species were transported beyond their native range, whether or not they were subsequently released at a novel location, and then their success in establishing a non-native population (Table 1b). Species with broader diets and latitudinal extents, and species with higher latitudinal midpoints were more likely to be transported and released. Altitudinal range and diet breadth correlated with establishment success following release: species with broader altitudinal distributions and broader diets were more likely to succeed (Table 1b).

Independent variables related to the extent to which species may be subject to movements through human activities were generally good correlates of whether or not parrot species were transported (Table 1c). Unsurprisingly, species more often kept in captivity, as pets, and more heavily traded species, were all more likely to have been transported beyond their native range. Species kept in captivity and as pets were also more likely to have been released into alien environments. Species in international trade were more likely to establish once released.

Life history characteristics of parrots were poorer correlates of a species' passage along the introduction pathway than other variable classes (Table 1d). Body mass was positively related to transport. Migratory and dichromatic species were less likely to be released, and once released, migratory species were less likely to establish. Fledging period was positively related to establishment success.

We performed stepwise multiple regression analyses to assess the extent to which the various correlates of

transport, release, and establishment explained variation independent of each other. The reduced adequate model for transport included only  $\log_{10}$  geographic range size (coefficient = 0.81, SE = 0.26) and  $\log_{10}$  fledging time (coefficient = 5.44, SE = 2.62): species with larger range size and longer fledging times were more likely to be transported. The model for release included  $\log_{10}$  population size (coefficient = 1.82, SE = 0.48),  $\log_{10}$  body mass (coefficient = 1.97, SE = 0.81), and dichromatism (coefficient = -1.46, SE = 0.65): species are more likely to be released if they have large population and body sizes, and are monochromatic. The reduced adequate model for establishment included migratory status (coefficient = -0.69, SE = 0.30) and diet breadth (coefficient = 0.43, SE = 0.21): species are more likely to establish if they are sedentary and have broader diets. Unlike for transportation and release, the reduced adequate model for establishment has a significant change in deviance from the full model ( $\Delta\text{Dev} = 32.96$ ,  $\text{df} = 10$ ,  $P < 0.001$ ). This indicates that the model lacks terms and does not adequately explain the variability in the data.

## Discussion

A decade ago, the global trade in parrot species was estimated at \$1.4 billion annually (Thomsen & Brautigam, 1991). Subsequently, Thomsen & Mulliken (1992) estimated that nearly four million individual parrots were harvested from the wild each year in order to supply the burgeoning pet bird industry. Consequently, almost two-thirds of parrot species have been recorded as commonly transported beyond the limits of their natural geographic distributions, and many other species are traded locally. Almost one quarter of all transported species find their way into exotic environments, and 10% of parrot species have established exotic populations. Parrots tend not to be associated with acclimatization – the deliberate transport of species for release in exotic environments (McDowall 1994) – suggesting that their releases are more likely to be unplanned. This implies that the characteristics of exotic parrot species may be those of whichever species are at hand, and hence characteristics of species favoured for trade.

If it is true that international trade is driving the invasion pathway in parrots, then we might expect to see taxonomic clustering in the set of species entrained. If a set of characteristics makes one species desirable for trade, then closely related species should also possess many of these characteristics. Our analyses of taxonomic autocorrelation using Moran's  $I$  did indeed find that there was a strong clustering of traded species at the genus level: most species in some genera, such as

*Ara* macaws and *Aratinga* parakeets, tend to be traded, whereas most species in other genera, such as *Micropsitta* pygmy parrots, tend not to be. Nevertheless, this clustering disappeared at higher levels, and indeed Moran's  $I$  became significantly negative. This suggests that desirable genera are distributed evenly among higher-level taxonomic levels, such that traded species are clustered within no single higher-level group.

Notably, the taxonomic clustering found within genera with respect to trade was not repeated for species in any stage on the introduction pathway. Where Moran's  $I$  was significant, the relationship was always negative, suggesting a more even distribution of species among taxa than expected from chance processes alone. The reason for this is unclear, although we can propose at least two plausible interpretations. First, the patterns reflect a tendency to trade a highly selected sub-set of species on international markets but transport a much wider range of global parrots. Note that trade here only includes species that are traded internationally (see Materials and methods) but not locally, and locally traded species are still likely to be transported, or even illegally traded, on occasion outside their native geographic range. Indeed, the set of internationally traded species ( $n = 136$ ) and locally traded species ( $n = 79$ ) are not identical (more than 75% of locally traded species are transported but not internationally traded), and so some degree of selection must be involved in deriving one set from the other.

The second possible reason for the lack of taxonomic clustering is that those species that are transported may tend to be species that are most readily captured in sufficient numbers for transport, which may in turn be abundant and widespread species (e.g. see Blackburn & Duncan, 2001b). Since abundance and distribution tend not to be phylogenetically conserved traits (Gaston & Blackburn, 1997; Blackburn *et al.*, 1998; Gaston, 1998; Webb *et al.*, 2001), transport would not then be taxonomically associated. Whatever the explanation, however, the key issue here is that we do not find evidence for consistent taxonomic clustering on the invasion pathway. Indeed, in many cases we find exactly the reverse, while for establishment there is no taxonomic relationship at all.

The first step on the introduction pathway is transport. Compared with other parrot species, those that are transported outside their natural distributions tend to be widespread species, pest species, species that are traded, and kept as pets (it is likely that cause and effect are reversed here), and large-bodied species (Table 1). It is plausible that most of these patterns are a consequence of the readiness with which species can be captured and transported for the cage bird trade. Widespread species are more likely to be encountered

by trappers. Many parrots are captured on, or removed from, the nest. For example, a survey of nests of *Amazona brasiliensis* in south-east Brazil found that 41/49 nests had been robbed (Martuscelli, 1994). Species with long nesting periods may be particularly susceptible to trapping. Therefore, the significance of large body mass could be a simple consequence of the strong correlation between mass and both incubation ( $r = 0.57$ ,  $n = 143$ ,  $P < 0.001$ ) and fledging periods ( $r = 0.71$ ,  $n = 135$ ,  $P < 0.001$ ), although it is not unreasonable that large-bodied species may be particularly prized as 'home décor'. Nevertheless, only geographic range size and fledging period explain independent variation in whether or not a species is transported in our multivariate model.

The role of opportunity also seems to determine which parrot species are released following transport. Widespread and abundant species are those that most often get released (Table 1). Widespread species are also the most commonly found parrots in captivity ( $r = 0.12$ ,  $n = 350$ ,  $P = 0.023$ ). This may influence release probability in two ways. First, by chance alone, we would expect more commonly held species to be more commonly liberated, either accidentally or deliberately. Second, more commonly held species may be less expensive or valuable, and so less care may be taken in keeping them captive. The corollary of this second point is that more valuable species will have more care taken over their captivity. This may be why we find that threatened and range restricted species are less often released than expected (Table 1). Consistent with these ideas is the near significant relationship between fecundity and release. Highly productive species may again be more commonly liberated either by chance, or as a way of disposing of excess individuals of commercially, relatively valueless species. Whatever the precise mechanism, however, the point remains that the species that get liberated are those for which availability for release is likely to be greater.

Correlates of release that seem unlikely to be explained by opportunity include diet breadth, latitudinal range midpoint, monochromatism, and sedentari-ness. There is no obvious collinearity of these traits with variables that are related to opportunity. Latitudinal range midpoint, for example, is unrelated to latitudinal range (cf. Stevens, 1989; Gaston *et al.*, 1998). While monochromatic species tend to be larger-bodied, with longer breeding periods and lower fecundities, none of these relationships would generate a relationship between monochromatism and probability of release. Moreover, multivariate analysis shows that monochromatism explains significant independent variation in probability of release, together with body mass and population size. Perhaps, monochromatic species are

less valuable than dichromatic species, and so again less care may be taken in keeping them captive. Why larger-bodied species should also be more likely to be liberated, controlling for population size and dichromatism, remains unclear although it may relate to their extended longevity and thus the effort required to maintain the species in captivity.

Once released, a parrot species may or may not go on to establish a viable population. Multivariate analysis reveals significant independent effects of diet breadth and migratory habit, with sedentary species again more likely to establish. The significance of migratory habit concurs with previous studies of avian establishment, which find that migratory species are generally more likely to fail (reviewed by Kolar & Lodge, 2001). The significance of diet breadth suggests that a generalist diet may increase the chances that a species can utilize resources in the environment, and so establish successfully.

One characteristic that has frequently been found to relate to establishment success in birds is introduction effort, or 'propagule pressure' (the number of separate release events, or number of individuals released: Pimm, 1991; Veltman *et al.*, 1996; Duncan, 1997; Green, 1997; Duncan *et al.*, 2001). We do not have sufficient data on effort to include it in these analyses. However, it has been shown for other introduced bird assemblages that effort is positively related to the abundance and/or distribution of the species in their native ranges (Blackburn & Duncan, 2001b; Duncan *et al.*, 2001), which was argued again to be a consequence of opportunity (widespread and abundant species are more likely to be available for introduction in larger numbers). Interestingly, we find the converse result, that species with smaller global population sizes are more likely to establish exotic populations. This may be explained by the role of an interaction with migratory habit, as migratory parrots that are released have larger global population sizes (Wilcoxon  $Z = 1.79$ ,  $n = 18$ ,  $P = 0.037$ ), but are also less likely to establish (Table 1d). The influence of propagule pressure may, nevertheless, be indicated by the near significant positive correlation between establishment probability and pet status, considering that species that are commonly held as pets are liberated more often and in larger numbers (Mulliken, 1995).

Our analyses of transport are necessarily based on those parrot species that are currently being, or have recently been, transported beyond the boundaries of their natural geographic distributions, as these are the data that are available to us. However, which parrot species are transported seems likely to have changed considerably over time. For example, the current rarity of some species may be a consequence of excessive

transport in the past, which may in turn have led to the imposition of trade bans. In particular, species listed on Appendix I of CITES are so listed because their populations are so low that it is important that they are not further threatened by trade. In that regard, it is interesting that CITES listing is unrelated to transport, suggesting that if listing has reduced a previous trade in such species, it has not reduced it enough to produce a negative relationship between listing and transport.

The issue of temporal changes in patterns in transport does not invalidate any of the results we have reported. However, it may affect our conclusions about the influence of different traits between the stages of transport and release, as most releases occurred at least several decades ago (Long, 1981). That said, we think that our conclusions are likely to be robust. The principal characteristics influencing which species are both transported and released relate to the availability of individuals for entry into these stages. If some species used to be transported, but are no longer transported because of their rarity, our conclusions that availability is important for transport would remain unchanged.

In summary, we find that different sets of variables are related to the probability that a species enters each stage in the invasion pathway, from transport to release to establishment. This highlights the value of assessing the factors that lead to a successful biological invasion at each stage in the pathway. Although only species that get transported and released have the opportunity to establish, the characteristics of species that establish are not typical of those associated with passage through the two prior stages. This suggests that detailed study of the introduction pathway for different taxa will allow identification of characteristics of potential invaders that can subsequently reduce current rates of biotic homogenization, without necessitating the unrealistic aim of preventing the transport of every species in the group.

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