Patterns of non-randomness in the exotic avifauna of Florida

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ABSTRACT

It is now generally recognized that human-mediated biological invasion is a multi-stage process, successively comprising transport, introduction, establishment, and spread, and that a complete understanding of the causes of invasion requires studies of all stages. However, while many studies address the characteristics that influence establishment, relatively few address the characteristics that influence whether or not a species transits the earlier stages of transport and introduction. Here, we use data on the rich exotic avifauna of Florida to assess non-randomness in the identities of species that have passed through the transport and introduction stages. Bird species transported and introduced to Florida are non-random with respect to their taxonomic affiliations, body mass, native geographical range size, and region of origin: introductions are more likely for widespread, large-bodied species from the Neotropics and belonging to the Anatidae, Psittacidae, Ciconiidae, and Passeridae. Data on the identities of species that have attempted to breed but failed, and on the breeding population size for most established species, also allowed us to assess the extent to which the same variables influenced various aspects of post-introduction establishment. Only native geographical range size and latitudinal range mid-point distinguish between these different classes of exotic species. Geographical range size is the most general correlate of different classes of invaders in our analyses.

Keywords

Birds, geographical range size, invasion pathway, non-native species.

INTRODUCTION

A large and growing number of species have invaded areas beyond the boundaries of their natural geographical distributions as a result of human activities (Elton, 1958; Crosby, 1993; Cohen & Carlton, 1998; Mack et al., 2000). The process of human-mediated invasion is typically divided into four stages (e.g. Lockwood, 1999; Kolar & Lodge, 2001; Duncan et al., 2003; Cassey et al., 2004b). First, the species must be transported from its native range to the alien environment (here termed ‘transport’). Second, it must be released or escape from captivity into the alien environment (‘introduction’). Third, the species must succeed in establishing a viable population in the alien environment (‘establishment’). Finally, the species may spread beyond the initial area of establishment, and so become invasive in the new area (‘invasion’), although the exotic distributions of many species have remained localized at the point of establishment. Invasive species may cause substantial environmental and economic damage in regions to which they have been introduced (Pimentel et al., 2000), and so there is a strong incentive to understand what determines whether or not species pass successfully through all four stages of the process.

However, invasion studies are not evenly distributed with respect to describing the various stages of the invasion process. Most studies focus on the third stage, attempting to determine the characteristics that predict whether or not a species will establish a viable population following introduction (e.g. Duncan et al., 2003; Puth & Post, 2005). Establishment is clearly a key stage, in as much as any species that fails the challenges posed by an alien environment is unlikely to be of economic or environmental concern. In contrast, the first two steps on the invasion pathway have been the subjects of comparatively few studies (Cassey et al., 2004b; Puth & Post, 2005; Jeschke & Strayer, 2006). Yet, transport and introduction constrain the characteristics of species that will face the subsequent steps of establishment and invasion. This in turn will influence the kinds of relationships and outcomes we will see expressed in the ecology and evolution of introduced species. Thus, understanding the determinants of transport and introduction is a key element in understanding the invasion process (Blackburn & Duncan, 2001b).

The relative lack of attention paid to transport and introduction is probably because data on which species have been transported beyond their native range, and which species have been transported but not introduced, are not available for most taxa (Cassey
et al., 2004a; but see Cassey et al., 2004b). Consequently, it has rarely been possible to compare successful and unsuccessful species at these two stages. Nevertheless, studies have been able to address the transport and introduction stages by concatenating them, and comparing the characteristics of species that have been introduced with those in the same taxon that have not (e.g. Lockwood, 1999; Blackburn & Duncan, 2001b; Jeschke & Strayer, 2005, 2006; Suarez et al., 2005; Ward et al., 2006).

Such studies are useful for at least three reasons. First, understanding non-randomness in the identities of the species in a given taxon that get introduced provides information on the constraints applied to the outcomes of introductions by the early invasion stages. These constraints may take the form of selectivity in terms of the taxonomic or geographical composition of introduced species, or in terms of life-history syndromes favoured in these stages. Second, such patterns of non-randomness also provide information on physical aspects of the introduction process, in terms of the identity and dynamics of likely dispersal vectors for introduced species. For example, they may allow changes in vectors to be identified, such as shifts from planned releases of exotic game species to unplanned releases or escapes of pet species. Third, studies that concatenate the transport and introduction stages may provide information that will aid in the analysis and interpretation of data in subsequent invasion stages. It will be necessary to understand how non-randomness at these stages is manifested in order to devise strategies to control for it.

Given that studies of the early stages of the invasion process are still relatively rare, and that studies that concatenate the transport and introduction stages can provide useful information about the invasion process, here we present such an analysis for the set of exotic bird species recorded in Florida (Pranty, 2004). The exotic avifauna of Florida represents an ideal assemblage for such a study, as it comprises a large number of species (> 200) and has been the focus of several previous studies of features of the invasion process (e.g. James, 1997; Forys & Allen, 1999; Romagosa & Labisky, 2000; Tillman et al., 2000; Allen, 2006; Avery et al., 2006). We use this assemblage to test several aspects of non-randomness in the identities of species that have passed through the transport and introduction stages.

First, we assess whether Floridian exotics are a non-random subset of bird taxa. Several previous studies have shown that exotic birds tend to come from a limited range of families, with Anatidae, Phasianidae, Psittacidae, and Passeridae being consistently over-represented (Lockwood, 1999; Lockwood et al., 2000; Blackburn & Duncan, 2001b; Duncan et al., 2006; Kark & Sol, 2005). Second, we test for non-randomness in the life histories of Floridian exotics, using body mass as a proxy for life-history variation. Selectivity in the families of birds being introduced is expected to lead to non-randomness in their characteristics, since many life-history traits, including body size, are evolutionarily conserved within bird families (e.g. Bennett & Owens, 2002; Frecleton et al., 2002). To assess this effect, we also test for selectivity with respect to body mass while controlling for family membership.

Third, we test for non-randomness in the geographical range sizes of Floridian exotics. Previous studies have shown that bird species that are widespread and/or abundant in their native distributions are more likely to be transported and introduced than narrowly distributed and/or rare species (Blackburn & Duncan, 2001b; Cassey et al., 2004a,b; Jeschke & Strayer, 2006). We lack abundance data for all Floridian exotics, but abundance and range size are generally positively correlated in birds (Gaston & Blackburn, 2000; Gaston et al., 2000) and other organisms (Blackburn et al., 2006).

Fourth, we test for selectivity in the locations of origin of Floridian exotics. Previous studies have shown that high proportions of the exotic birds introduced to an area come from the same or nearby biogeographical regions, or from regions with which trade has traditionally been strong (e.g. Blackburn & Duncan, 2001b). Thus, we might expect Floridian exotics to derive primarily from the New World or from Europe. We also assess non-randomness in the latitudes of origin of Floridian exotics. If species are introduced at random with respect to their regions of origin, we might expect to see more exotic species from low latitudes, simply because this is where most bird species reside. Conversely, if people consciously release species that they expect to survive in the Floridian climate, we might expect exotics to derive from similar latitudes to those spanned by the Florida peninsula.

As well as listing all known exotic species recorded from Florida, Pranty (2004) provides information on the status of these species. He distinguishes between species whose occurrence in Florida has been verified by specimen evidence and those whose occurrence has not been so verified, and between species suspected of breeding and those not. For suspected breeders, he also distinguishes between established and extirpated species, and provides abundance estimates for most of the former. We use Pranty’s (2004) classifications to assess the extent to which non-randomness in the traits described above can be identified in the different categories of exotic bird species.

**METHODS**

**Data**

Our analyses are based on the set of exotic bird species recorded in Florida listed in Pranty (2004), excluding the records for the golden × Lady Amherst’s pheasant (Chrysophalus pictus × amherstiae) hybrid, for Aratinga rubritorquis (considered a subspecies of Aratinga holochlora), and for Lophura atricapilla (considered a subspecies of Lophura malacca). This gives a total of 207 non-indigenous bird species recorded in the wild in Florida.

A further four species were excluded from analyses of specific characteristics because their classification to a specific wild species was uncertain (Gyps sp., Streptopelia risoria, Aratinga solstitialis/jandaya, and Lophura cantsis/malabarica), although we used the generic assignments of these four in analyses of taxonomic selectivity (see below). Each species was assigned to a family on the basis of the classification in Sibley & Monroe (1990; 1993).

For each species on the list, Pranty (2004) recorded whether the species’ occurrence has been verified by archived photographic or specimen evidence (verified species; n = 95), whether the species...
is reported to have bred in Florida outside captivity (breeding species; \( n = 68 \)), and for this last group, an estimate of the size of the species’ breeding population in Florida. Pranty (2004) assigned each breeding population estimate to one of six size classes: extirpated (reported to have bred but current breeding population size is zero; \( n = 30 \)), one pair (this category contains only a single species, the house crow \( Corvus splendens \), \( < 25 \) pairs \( n = 10 \), \( 25–99 \) pairs \( n = 15 \), \( 100–999 \) pairs \( n = 5 \), and \( 1000 + \) pairs \( n = 6 \). No breeding population size estimate was available for two species (\( Anser anser \) and \( Anser cygnoides \)). We combined the categories for \( 1, \ < 25, \) and \( 25–99 \) pairs to give a category for species that are established but rare breeders, and for \( 100–999 \) and \( > 1000 \) pairs to give a category for species that are established but common breeders. Thus, we have three abundance classes for exotic bird species that have been recorded breeding in Florida (extirpated, rare breeders, common breeders). Note that not all the identities of breeding species have been verified, so that the former set is not a subset of the latter.

For each Floridian exotic species whose identity was certain, we collated the following information:

Geographical range size (km\(^2\)) — a measure of geographical range extent (Gaston, 1991, 1994), extracted from the data set used in Orme \( et \ al \). (2006). The breeding ranges of all bird species were mapped as vectors or ‘polygons’ and converted to an equal area grid for analysis. The grid used a Behrmann projection and a cell size (96.3 km) that gives a scale identical to 1° grids at the 30° latitude of true scale. The vertical cell boundaries coincide with 1° lines of longitude but the horizontal boundaries vary systematically in their latitudinal separation, giving a grid with 360 columns and 152 rows. Species were scored as present in a grid cell if any of the available vector sources suggested that the breeding range fell within the cell boundaries. The geographical range sizes of individual species were estimated as the sum of the areas of the cells in which they were scored as occurring (Orme \( et \ al \)., 2006).

Latitudinal range mid-point (degrees) — the absolute value of the median latitude of the centre of the grid cells in which the species occurs.

Region of origin — the biogeographical region in which the native population of the exotic species was found. Biogeographical realms were delimited using the World Wildlife Fund ecoregions map (Olson \( et \ al \)., 2001). Species whose distributions span biogeographical region boundaries, and for which region of origin for individuals seen in Florida is therefore uncertain, were excluded. The numbers of native species in each biogeographical region were taken from Thomas \( et \ al \). (unpublished), derived from the database described by Orme \( et \ al \). (2005). We removed species that breed in Florida (Florida Fish and Wildlife Conservation Commission, 2003) from the Nearctic total as these cannot become Floridian exotics.

Body mass (g) — a measure of the size of the species, from data in Dunning (1992). See Gaston & Blackburn (1995) for details on how a value was calculated for each species.

Analyses

We used the simulation approach described in Lockwood \( et \ al \). (2000) and Blackburn & Duncan (2001b) to test for differences between the observed number of Floridian exotic species in each bird family, and the number that would be expected if Floridian exotics were a random selection of the world’s bird species. Each iteration of the simulation involved picking 207 species at random, and without replacement, from the total global avifauna (9702 species) and summing the number of these randomly chosen species in each family. A total of 10000 iterations of the simulation procedure were run, and the observed number of introduced species in any given family was judged significantly greater than expected if at least 5% of the randomly derived values for that family were less than the observed, where \( S = (B/2) \times 100 \). \( B \) is calculated by applying a sequential Bonferroni correction to \( \alpha \) (Rice, 1989), and \( \alpha = 0.05 \). The same simulation approach was also used to assess taxonomic selectivity in terms of the identities of exotic species suspected of breeding, given the family composition of exotic species, and in terms of the identities of exotic species with established breeding populations, given the family composition of species suspected of breeding.

Permutation tests were used to assess whether or not the geographical range sizes, latitudinal range mid-points, and body masses of exotic species differed from a random sample of bird species. For geographical range size, 207 species were chosen at random and without replacement from the list of 9614 species, for which estimates of geographical range size were available from the database described by Orme \( et \ al \). (2005). The geometric mean range size was calculated, and the procedure repeated 1000 times to produce a frequency distribution of expected mean range sizes, against which the observed mean range size was compared. The same methodology was used for latitudinal range mid-point, except that 1 was added to all mid-point values to avoid problems arising from the logarithm of zero in the algorithm for the geometric mean. The same methodology was also used for body mass, except that masses were only available for 170 of the Floridian exotic species, and for 6319 bird species in total. Hence, these were the subsets used for the body mass tests.

A significantly greater than expected range size or body mass for exotic bird species could result from the bias in the taxonomic composition of such species, if exotic species tended to come from families with larger than average range sizes or body sizes. To account for the effect of taxonomic composition, the permutation test was repeated, this time replacing the range size or body mass of each species with that of a species chosen at random from the same family. This approach constrains the family level composition of the list of randomly chosen species in each iteration of the model to be the same as that of the species actually introduced.

Within the set of Floridian exotic species, we compared the geographical range sizes and body masses of different subsets using nonparametric Kruskal–Wallis tests. All statistical analyses were performed in \( R \) version 2.0.1 (\( R \) Development Core Team, 2006).

RESULTS

Four bird families included significantly more exotic species in Florida than expected by chance: Anatidae, Psittacidae, Ciconiidae, and Passeridae (Table 1). Three of these families are frequently
over-represented in analyses of taxonomic non-randomness, but as far as we are aware, this is the first study to identify Ciconiidae as such. The excess of observed exotic species was particularly extreme for the Psittacidae. The 99.9th percentile of simulation outcomes was for 17 species vs. 75 exotic parrot species actually observed in a wild state in Florida. Other families with relatively large numbers of exotic species in Florida included the Phasianidae (8 species) and Fringillidae (15 species). However, neither of these higher numbers of species than expected given the global richness of these families, and indeed for the Fringillidae, 15 species is fewer than the median expectation from the simulations. There was no evidence that any bird family contained more species suspected of breeding in Florida if exotics were a random selection of the world’s bird species. The 99.9th percentile of the simulated distribution is also shown.

Table 1 Results of the simulations to assess the probability of observing as many or more introductions from a bird family given the number of species in the family and the number of non-native bird species that have been seen in the wild in Florida. Only families for which the probability was significantly lower than expected ($\alpha = 0.05$), once a sequential Bonferroni correction for multiple statistical tests (Rice, 1989) has been applied, are shown. Median expectation is the median (over 10,000 simulations) number of exotic species expected to have been recorded in Florida if exotics were a random selection of the world’s bird species. The 99.9th percentile of the simulated distribution is also shown.

<table>
<thead>
<tr>
<th>Family</th>
<th>Median expectation</th>
<th>99.9th percentile</th>
<th>Observed number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anatidae</td>
<td>3</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td>Psittacidae</td>
<td>8</td>
<td>17</td>
<td>75</td>
</tr>
<tr>
<td>Ciconiidae</td>
<td>0</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Passeridae</td>
<td>8</td>
<td>18</td>
<td>20</td>
</tr>
</tbody>
</table>

Within Floridian exotics, body mass does not vary between any of the different categories of invader. Thus, species whose presence has been verified by specimens or photographs do not differ significantly from those whose presence has not ($\chi^2 = 3.40$, d.f. = 1, $P = 0.065$), species that have been suspected of breeding in the State do not differ from those that have not ($\chi^2 = 0.23$, d.f. = 1, $P = 0.63$), those suspected breeding species with established populations do not differ from those species suspected of breeding but which are now extirpated ($\chi^2 = 0.16$, d.f. = 1, $P = 0.69$), and breeding species with different breeding population sizes also do not differ in mass ($\chi^2 = 0.66$, d.f. = 2, $P = 0.72$; Table 2).

The geometric mean geographical range size for bird species recorded in Florida as exotics is 2.88 million km$^2$, compared to 0.56 million km$^2$ for species not so recorded. A permutation test shows that the expected mean range size for a sample of 207 species is 0.60 million km$^2$, and the 99% confidence intervals of this estimate span the range of 0.39 million to 0.85 million km$^2$. Repeating the permutation test but controlling for family membership gives an expected mean range size of 0.64 million km$^2$, with 99% confidence intervals of 0.45 million to 0.90 million km$^2$. Thus, Floridian exotics have significantly larger range sizes than expected.

Within Floridian exotics, the subset of species whose presence has been confirmed by specimen or photographic evidence has significantly larger range sizes than the subset of species that have not been so confirmed (geometric means 3.83 million and 2.26 million km$^2$, respectively, $\chi^2 = 4.93$, d.f. = 1, $P = 0.026$). However, there is no difference in the range sizes of species that have or have not been suspected of breeding in the State (geometric means 2.92 million and 2.85 million km$^2$, respectively, $\chi^2 = 0.01$, d.f. = 1, $P = 0.94$). Among those exotic species that have been recorded breeding in Florida, the range sizes of those that currently have breeding populations are higher than those that bred once but have since been extirpated (geometric mean range sizes of 3.88 million vs. 1.92 million km$^2$, $\chi^2 = 4.13$, d.f. = 1, $P = 0.042$). Range sizes also differ between different population size classes for these breeders (Table 2; $\chi^2 = 8.64$, d.f. = 2, $P = 0.013$). Mean range sizes are ordered with respect to population size in Florida, with the largest mean native range size for those currently extant species that have the largest breeding population sizes (Table 2).

The geometric mean latitudinal range mid-point for bird species recorded in Florida as exotics is 13.74°, which is similar to the value of 11.96° for species not so recorded. The expected mean latitudinal mid-point for a sample of 207 bird species is 12.02°. The 99% confidence intervals for this mean span the range 10.04° to 14.17°, but the 97.5th percentile of the distribution of estimates is 13.64°. Thus, the observed mean mid-point for Floridian exotics would be judged significantly different from random expectation at the 5% level, but not at the 1% level. Repeating the permutation test but controlling for family gives

Table 2 Geometric mean values of geographical range size (km$^2$), body mass (g), and absolute latitudinal range mid-point for exotic bird species recorded as breeding in Florida with different estimates of breeding population sizes.

<table>
<thead>
<tr>
<th>Population size class</th>
<th>Geographical range size</th>
<th>Body mass</th>
<th>Absolute latitudinal mid-point</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 (extirpated in Florida)</td>
<td>$1.92 \times 10^6$</td>
<td>187.45</td>
<td>12.09</td>
</tr>
<tr>
<td>1–99 (rare breeders)</td>
<td>$2.73 \times 10^6$</td>
<td>289.34</td>
<td>11.64</td>
</tr>
<tr>
<td>&gt; 100 (common breeders)</td>
<td>$9.16 \times 10^6$</td>
<td>189.45</td>
<td>26.43</td>
</tr>
</tbody>
</table>
an expected mean mid-point of 12.44°, with 95% confidence intervals of 11.15° and 13.82°. Thus, Floridian exotics do not have latitudinal range mid-points that differ significantly from expectation when accounting for their non-random family membership.

The latitudinal mid-points of the native distributions of exotics whose presence in Florida has been verified by specimen or photographic evidence do not differ from those of species whose presence is unverified ($\chi^2 = 0.26$, d.f. = 1, $P = 0.61$). Similarly, there are no differences between the range mid-points of suspected breeders vs. those for which breeding has never been seen ($\chi^2 = 2.31$, d.f. = 1, $P = 0.13$), or between those species with current breeding populations vs. those that bred once but have since been extirpated ($\chi^2 = 0.85$, d.f. = 1, $P = 0.36$). Latitudinal range mid-points do differ between different population size classes for these breeders ($\chi^2 = 10.88$, d.f. = 2, $P = 0.004$). Species with breeding population sizes in Florida > 100 have range mid-points further from the equator than those exotics with small breeding populations, or that were recorded breeding but have been extirpated (Table 2). Florida spans latitudes in the range of 24–30° N, which is similar to the mean values for the birds with the largest exotic populations there. We thus repeated the analyses for range mid-point, using instead the distance of the mid-point of a species’ latitudinal range from the latitude of Miami (25° N). However, none of these relationships were significant ($P > 0.15$ in all cases).

Floridian exotics derive from six different biogeographical regions (Table 3). The Neotropics is the primary source for Floridian exotics, both in terms of total numbers of species introduced (and hence the proportion of all exotics that derive from a region) and the proportion of the native avifauna introduced. A test for equality of proportions shows that the proportion of native species introduced differs between regions ($\chi^2 = 21.3$, d.f. = 5, $P < 0.001$). The same is true excluding the Nearctic, which has a low number and proportion of Floridian exotic species ($\chi^2 = 16.5$, d.f. = 4, $P = 0.002$).

There is no relationship between the latitudinal mid-point of the geographical range and the range size for species recorded as exotics in Florida (Spearman rank correlation, $rho = 0.071$, $n = 203$, $P = 0.31$), nor between latitudinal range mid-point and body mass ($rho = 0.072$, $n = 170$, $P = 0.34$). Floridian exotics with larger range sizes do tend to have larger body masses ($rho = 0.203$, $n = 170$, $P = 0.008$), and mean range size also varies between regions of origin (Kruskal–Wallis test, $\chi^2 = 34.9$, d.f. = 5, $P < 0.001$). However, there is no relationship between the mean range size of species in a region and either the number ($rho = -0.33$, $n = 6$, $P = 0.52$) or the proportion ($rho = -0.27$, $n = 6$, $P = 0.59$) of species in the region recorded as exotics in Florida.

### Discussion

Florida is home to a wide diversity of exotic species, including plants (Gordon & Thomas, 1997), insects (Frank et al., 1997), freshwater (Warren, 1997) and marine invertebrates (Carlton & Ruckelshaus, 1997), fish (Courtenay, 1997), amphibians and reptiles (Butterfield et al., 1997), and mammals (Layne, 1997). Previous studies have considered the pathways by which exotic species arrive in Florida (e.g. Frank et al., 1997), the taxonomic composition of these exotics (e.g. Gordon & Thomas, 1997), their geographical origin (e.g. Butterfield et al., 1997), and the influence of climate matching on success (Curnutt, 2000), but no previous study has analysed non-randomness in Floridian exotics across several stages in the invasion pathway (Williamson, 1996) in a quantitative manner.

The species of bird recorded in Florida as exotic introductions differ from a random sample of bird species in a number of respects. They are on average larger bodied, and with substantially larger geographical range sizes than expected. Four bird families are significantly over-represented on this species list (Table 1), most notably the Psittacidae (cf. Lockwood, 1999; Lockwood et al., 2000; Blackburn & Duncan, 2001b; Duncan et al., 2006; Kark & Sol, 2005). However, the body mass and range size relationships are not a simple consequence of the family level composition of Floridian exotics, because tests that control for this composition confirm these effects. Floridian exotics derive mainly from the Neotropics, and while this region is also the richest in bird species, the proportion of Neotropical species introduced to Florida is higher than for any other region (Table 3). However, Floridian exotics are a random sample of the global avifauna with respect to their latitudinal range mid-points. Overall, these relationships concur with previous studies (Blackburn & Duncan, 2001b; Cassey et al., 2004b; Jeschke & Strayer, 2005, 2006) in revealing that there is considerable non-randomness in the characteristics of bird species that have been introduced.

By and large, the characteristics that we analyse here do not differentiate those species that have or have not passed through the transport and introduction stages. The one exception is geographical range size, as species with larger ranges are more likely to have had their presence in the State confirmed, and are more likely to have established breeding populations. Moreover, range size also relates systematically to the size of the breeding population

#### Table 3

<table>
<thead>
<tr>
<th>Region of origin</th>
<th>No. native species</th>
<th>No. Floridian exotics</th>
<th>Prop. Floridian exotics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australasia</td>
<td>1691</td>
<td>18</td>
<td>0.011</td>
</tr>
<tr>
<td>Afrotropics</td>
<td>2091</td>
<td>36</td>
<td>0.017</td>
</tr>
<tr>
<td>Indo-Malaya</td>
<td>1825</td>
<td>22</td>
<td>0.012</td>
</tr>
<tr>
<td>Nearctic*</td>
<td>719</td>
<td>5</td>
<td>0.007</td>
</tr>
<tr>
<td>Neotropics</td>
<td>3628</td>
<td>85</td>
<td>0.023</td>
</tr>
<tr>
<td>Palaearctic</td>
<td>1745</td>
<td>25</td>
<td>0.014</td>
</tr>
</tbody>
</table>

*Excluding Nearctic species that breed in the native state in Florida.
for species known to have bred in Florida (Table 2). Native geographical range size seems to be a consistent correlate of which bird species will be introduced (Blackburn & Duncan, 2001b; Cassey et al., 2004b; Jeschke & Strayer, 2006), and has also been shown to relate to establishment success (Moultou & Pimm, 1986; Blackburn & Duncan, 2001a; Duncan et al., 2001; Cassey et al., 2004c) and range size in the exotic environment (Duncan et al., 1999, 2001). The former association is argued to derive from the likelihood that species with large ranges will be encountered by bird collectors, and so be available for international trade. Also consistent with this explanation is the tendency for significant effects of abundance on introduction probability in analyses for which, unlike here, such data are available (e.g. Blackburn & Duncan, 2001b; Cassey et al., 2004b). Indeed, the effect of range size is sometimes superseded by that of abundance, although the two variables tend to be positively correlated in birds (Gaston & Blackburn, 2000; Gaston et al., 2000).

Associations between range size and establishment success could arise either because species with broad native ranges can tolerate a broad range of environmental conditions, and so are more likely to tolerate the conditions they encounter in the exotic environment (Williamson, 1996; Blackburn & Duncan, 2001a; Duncan et al., 2001), or because native range size is correlated with some other variable that directly influences establishment. In the latter regard, Cassey et al. (2004c) showed that range size was positively correlated to propagule pressure for global bird introductions, and that range size was only a significant predictor of establishment success if propagule pressure was excluded from the analysis (see also Jeschke & Strayer, 2006). Propagule pressure is the most consistent predictor of establishment success identified to date (Lockwood et al., 2005), while species with large range sizes have been shown to be released more often and in larger numbers (Blackburn & Duncan, 2001b). Unfortunately, data on propagule pressure are lacking for the exotic birds of Florida, making it impossible to assess the effect of range size independent of this potential confounding variable. Nevertheless, it seems likely that species with larger native ranges would have been introduced to Florida in larger numbers, and this could explain why species whose presence in Florida has been confirmed by specimen evidence have larger range sizes.

Alternatively, if species with broad native ranges can tolerate a broad range of environmental conditions, that might explain not only why range size relates to establishment probability, but also why it is that common Floridian exotics have larger ranges than rare exotics, which in turn have larger ranges than exotics that bred once but have since been extirpated (Table 2). Nevertheless, whether species with large ranges do in fact have broader tolerances is controversial, with current evidence perhaps suggesting not (Gaston, 2003).

As well as having the largest native range sizes, common Floridian exotics also have higher latitudinal range mid-points than other species recorded breeding in the State (Table 2). Interestingly, the mean range mid-point for this group of species is around 26°, close to the latitude of Miami. We found no evidence that species with latitudinal mid-points close to Miami’s latitude were more likely to be introduced or to establish, but it may be that such species are better able to spread through Florida if they do establish. Presumably, species from such latitudes find the Floridian environment to be a close match to that of their native distribution: such matching has previously been shown to predict the extent of spread by exotic birds (Duncan et al., 1999, 2001). Note that there is no relationship between latitudinal range mid-point and range size in this data set.

Analyses of avian introductions have shown that most exotic species derive from regions that are close to, or conduct large amounts of trade with, the region of introduction (Blackburn & Duncan, 2001b; Duncan et al., 2006). Florida derives a disproportionate number of its exotic birds from the Neotropics, which agrees in part with this pattern, but relatively few from the Nearctic, which does not. Florida can be considered part of the Nearctic, although elements of its flora and fauna are Neotropic in origin. Nevertheless, removing species breeding in Florida from the Nearctic total does not affect the relative under-representation of Nearctic species on the Floridian list. The taxonomic composition of Floridian exotics, and especially the large number of species from the families Psittacidae and Passeridae, suggests that species derive from the release or escape of cage birds. Since Floridian exotics are a random sample of birds with respect to their latitudinal mid-points, it follows that most exotic species must be tropical in origin. It is possible that Nearctic species are not as valued as cage birds as are truly ‘exotic’ tropical species.

Finally, it is interesting to note that the vector for exotic bird introductions appears to be changing (see also Butterfield et al., 1997; Gordon & Thomas, 1997). The deliberate introductions by acclimatization societies prevalent throughout the nineteenth and early twentieth centuries, for the purposes of hunting, aesthetics, and biocontrol (see, e.g. Long, 1981), have been superseded by unplanned releases or escapes of species imported for the cage bird trade. As the reasons for introduction change, we still expect selectivity but aspects of the patterns of selectivity could also change. Nevertheless, it seems as though some elements, and notably the influence of geographical range size on the availability of native species for capture and transport to exotic areas, are constant.

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**REFERENCES**


