ORIGINAL ARTICLE

Establishment success of invasive ring-necked and monk parakeets in Europe

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ABSTRACT

Aim Invasive alien species are a growing threat to biodiversity, and identifying the mechanisms that enable these species to establish viable populations in their new environment is paramount for management of the problems they pose. Using an unusually large number of both failed and successful documented introductions of parakeets (Aves: Psittacidae) in Europe, we test two of the major hypotheses on the establishment success of invading species, namely the climate-matching and the human-activity hypothesis.

Location European human population centres where ring-necked parakeet (*Psittacula krameri*) and/or monk parakeet (*Myiopsitta monachus*) introductions have occurred.

Methods Data on ring-necked and monk parakeet introductions in Europe were gathered from various sources, including published books and articles, but also from unpublished reports and local grey literature. Information was verified with experts from the region under consideration. In order to test the climate-matching hypothesis, we verified whether the climatic factors that determine the parakeets' native ranges also explain establishment success in Europe. Parakeet occurrence data from the native ranges were analysed using the presence-only modelling method MAXENT, and correlations between parakeet establishment and climatic and anthropogenic variables in Europe were assessed using both stepwise logistic regression and the information-theoretic model selection approach.

Results The establishment success of ring-necked and monk parakeets was found to be positively associated with human population density, and, both in the native and in the introduced regions, parakeet occurrence was negatively correlated with the number of frost days. Thus, parakeets are more likely to establish in warmer and human-dominated areas.

Main conclusions The large number of independent parakeet introductions in Europe allows us to test the often-used climate-matching and human-activity hypotheses at the species level. We show that both hypotheses offer insight into the invasion process of monk and ring-necked parakeets. Our results suggest that, in the future, parakeet establishment probability may increase even further because global warming is likely to cause a decrease in the number of frost days and because urbanization and human populations are still increasing.

Keywords

Climate-matching hypothesis, establishment success, Europe, human-activity hypothesis, invasive alien species, monk parakeet, *Myiopsitta monachus*, Psittacidae, *Psittacula krameri*, ring-necked parakeet.

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INTRODUCTION

Invasive alien species are a growing threat to biodiversity and ecosystem functioning (McKinney & Lockwood, 1999; Clavero & García-Berthou, 2005). Human activities continue to increase the number of species introduced to regions beyond their native distributions, and identification of the mechanisms that enable these species to establish viable populations in their new environment is paramount for future management of the problems they pose (Kolar & Lodge, 2001). Factors influencing the establishment success of non-native species can be grouped into three broad categories: species-level (e.g. life-history traits), location-level (e.g. climate at introduction site) and event-level (e.g. total number of individuals released) variables (Blackburn & Duncan, 2001a). In their meta-analysis of bird introductions, Cassey *et al.* (2005) found that event-level variables such as introduction effort are the most consistent predictors of establishment success. However, when relevant location- and event-levels variables have been accounted for, significant differences in establishment success among species remain (Cassey *et al.*, 2004).

A number of hypotheses relating to the role of location-level variables have been put forward, including the 'climate-matching' hypothesis and the 'human-activity' hypothesis (Williamson, 1996; Taylor & Irwin, 2004; Leprieur *et al.*, 2008). The former hypothesis states that species have a higher probability of establishing if they are introduced into regions with a climate similar to that in their native area, whereas the latter postulates that human activity facilitates the establishment of alien species. In South Africa, for example, Byrne *et al.* (2002) found that the establishment success of the tortoise beetle *Gratiana spadicea* was lower in areas where levels of cold and humidity stress were higher than those in the beetle's native range. Both mammals and birds that were successfully introduced to Australia had a larger range of climatically suitable habitat than those that failed (Duncan *et al.*, 2001; Forsyth *et al.*, 2004). The human-activity hypothesis is invoked to explain the often-found correlation between the presence of exotic species and human activities (Guo *et al.*, 2006; Leprieur *et al.*, 2008). Human population and activity can have direct and indirect effects on the establishment of invasive alien species. As a direct effect, human population and activity may increase the chance of repeated introductions and strengthen the introduction effort, which often remains unknown. Repeated introductions in particular can greatly enhance the establishment success of an invasive species, for example by overcoming Allee effects or by inducing rescue effects (Drake & Lodge, 2006; Drury *et al.*, 2007). Indirect effects include food provisioning, ecosystem disturbance and habitat fragmentation. Humans increase food availability either by direct food provisioning in parks and at backyard bird feeders, or by introducing a wide variety of (exotic) plant species in urban parks and gardens (Chace & Walsh, 2006). However, human activity may act as a surrogate for the degree of ecosystem disturbance, as there is a strong positive relationship between human population size and the threat level of native mammals and birds (McKinney, 2001). Human activity often leads to impoverished native faunas where niches become vacant for introduced species (biotic resistance; Levine, 2000), or where only a few predators are left (predator release; Newsome & Noble, 1986). In contrast, several studies have found a positive correlation between humans and both native and exotic species richness (although this pattern may be scale-dependent; reviewed in Luck, 2007). Human activity fragments the landscape and creates artificial habitats (e.g. urban parks) and this can lead to increased habitat heterogeneity, which creates opportunities for both native and exotic species to establish. Finally, the positive correlation between humans and species richness may be, at least partly, a result of both responding positively to the same driving factors, such as energy availability (Araújo, 2003; Evans & Gaston, 2005).

In Europe, the DAISIE project (http://www.europe-aliens.org/; DAISIE, 2009) has identified 375 terrestrial vertebrates that have been introduced. Almost half of these species are birds (171 species, 45%), and Chiron *et al.* (2009) identified 75 birds that have established stable populations in Europe. Owing in large part to their popularity as cage birds, Psittacidae (parrots) are well represented and account for almost 18% of Europe's established alien avifauna. In their global analysis of exotic parrot establishment success, Cassey *et al.* (2004) found that introduced parrots tend to be widespread species, pest species, and species that are traded and kept as pets, and this is certainly true for the ring-necked parakeet, *Psittacula krameri* (Scopoli, 1769), and the monk parakeet, *Myiopsitta monachus* (Boddaert, 1783). Of all Psittacidae, the ring-necked and monk parakeets are the most successful, having established at least 65 and 31 European populations, respectively. Population sizes range from only a few tens of birds to several thousands (Strubbe & Matthysen, 2007). Ring-necked parakeets originate from Africa and Asia, whereas the monk parakeet is native to South America (Forshaw, 1978). Both species are known to cause considerable agricultural damage in their native range (Bucher, 1992; Dhindsa & Saina, 1994), and monk parakeets are known to cause damage to human infrastructure on account of their bulky communal nests (Avery *et al.*, 2002). As typical of Psittacidae, ring-necked parakeets are secondary cavity-nesters and are known to compete with native species (Strubbe & Matthysen, 2007, 2009a). Therefore, the growing number and sizes of invasive parakeet populations are causing both economical and ecological concerns.

In order to cope with the threat that invasive alien species pose (Rooney *et al.*, 2007), information on the factors that promote establishment success is needed. Most studies on establishment success rely on databases comprising large number of species introductions, but with a low number of introduction events per species [e.g. Kark & Sol (2005): 180 introduction events for 121 species; Blackburn & Duncan (2001a): 1466 introductions for 389 species]. However, when pooling these data, it is necessary to account for the fact that species cannot be treated as independent data points because closely related species share some traits, as a result of common ancestry, that can influence their establishment success.

Moreover, patterns of establishment success may be biased because species are not randomly distributed among introduction locations and because some regions receive disproportionally more invaders, or a larger proportion of better (or poorer) invaders, than other regions (Blackburn & Duncan, 2001a; Duncan *et al.*, 2003; Kark & Sol, 2005). As we were able to collect an unusually large number of documented parakeet introductions in Europe, both failed and successful, we can model establishment success within, rather than among, species, thereby avoiding the difficulties associated with pooling data from different species. This allows us to test the importance of location-level variables, in particular in relation to the climate-matching hypothesis and the human-activity hypothesis.

Both ring-necked and monk parakeets have established several populations in temperate parts of Europe, and this has led to the conclusion that they are tolerant of cold conditions (Spreyer & Bucher, 1998; BBC, 2007). For the ring-necked parakeet this has been linked to its occurrence in the foothills of the Himalayas, whereas the monk parakeet's communal roosting in woven stick-nests is regularly used as an explanation for its apparent tolerance of cold. Using parakeet occurrence data from Asia and South America, we investigated the role of climatic factors in determining parakeet distributions in their native ranges, and then examined whether these climatic features can explain the success of ring-necked and monk parakeets in Europe, thereby testing a fundamental premise of the climate-matching hypothesis. Human activity covers several mechanisms that may co-act to promote exotic species richness (see above), and we thus expect higher parakeet establishment success in more densely populated areas.

MATERIALS AND METHODS

Ring-necked and monk parakeet occurrences

Introduction events in Europe

Data on ring-necked and monk parakeet introductions were gathered from various sources, beginning with the works of Long (1981) and Lever (1987, 1997, 2005). However, information from these sources is sometimes outdated, and we updated and confirmed this information using regional and local literature. Information was extracted from several published books and papers, regional or country-level bird atlases, unpublished reports and local 'grey' literature and websites. Wherever necessary, information was verified with experts from the region under consideration (see Appendix S1).

An introduction event was included in the database only if a breeding attempt was recorded (monk and ring-necked parakeet) or if at least one male and one female parakeet were seen or released together (ring-necked parakeet only, as monk parakeet sexes are similar). An introduction was considered successful when the parakeets established a breeding population. Smaller populations (< 100 birds) were included in the

database only when there was evidence of breeding in the 2007 breeding season, which was verified by contacting regional experts or ornithological societies (Appendix S1). Larger parakeet populations were excluded from the dataset (i.e. not used in any analysis) only when there were indications of a population crash in recent years. Introduction events after the year 2000 were not used, as it may be too early to determine whether these introductions have been successful. Each introduction event had to be pinpointed to a certain human settlement (i.e. release site) (e.g. 'Palermo' would be accepted, but not 'Sicily'). We did not encounter data on introduction events outside human settlements. Wherever available, we also noted the introduction date (year) and the number of individuals released or escaped (introduction effort). In total, we collected data on 167 ring-necked parakeet introductions, of which 123 matched the criteria mentioned above. For the monk parakeet, we found 90 introductions, of which 58 were suitable for analysis (Fig. 1).

Data from the native range

Data on the native distribution of ring-necked and monk parakeets were obtained from the GBIF database (http://www.gbif.org/; accessed 31 August 2008). As no occurrences of African ring-necked parakeet subspecies are known in Europe, we used data only on the Asiatic subspecies *P. krameri borealis* and *P. krameri manillensis*. However, the GBIF database yielded only 17 Asiatic parakeet occurrences, and to increase ring-necked parakeet sample size we used the Google website, on 31 August 2008, and entered the search terms '*Psittacula krameri*' OR 'rose-ringed parakeet' OR 'ring-necked parakeet' AND 'trip report'. Out of the 1440 hits, we extracted 44 Asiatic ring-necked parakeet observations that were detailed enough to be georeferenced (*sensu* Chapman & Wieczorek, 2006). For monk parakeets, we grouped all subspecies, and the GBIF yielded 64 monk parakeet observations in South America.

Environmental and climatological data

Data on environmental and climatological variables were extracted from several global GIS (Geographic Information System) grid databases. In Europe, all variables were extracted using polygons describing the extent of the urban area corresponding to the release site (ESRI, 2005). For some smaller settlements, these polygons were not available but were derived from recent satellite images available in Google Earth. In order to test the climate-matching hypothesis, we extracted a number of climatic variables from the WorldClim dataset (Hijmans *et al.*, 2005) and from New *et al.* (1999). We considered the maximum temperature of the warmest month, the minimum temperature of the coldest month, and mean winter and mean spring temperature (winter defined as November–January, spring defined as February–May). From New *et al.* (1999), we obtained data on the total number of frost days/year (FD). The number of frost days is the mean yearly number of days with subzero minimal temperatures from the
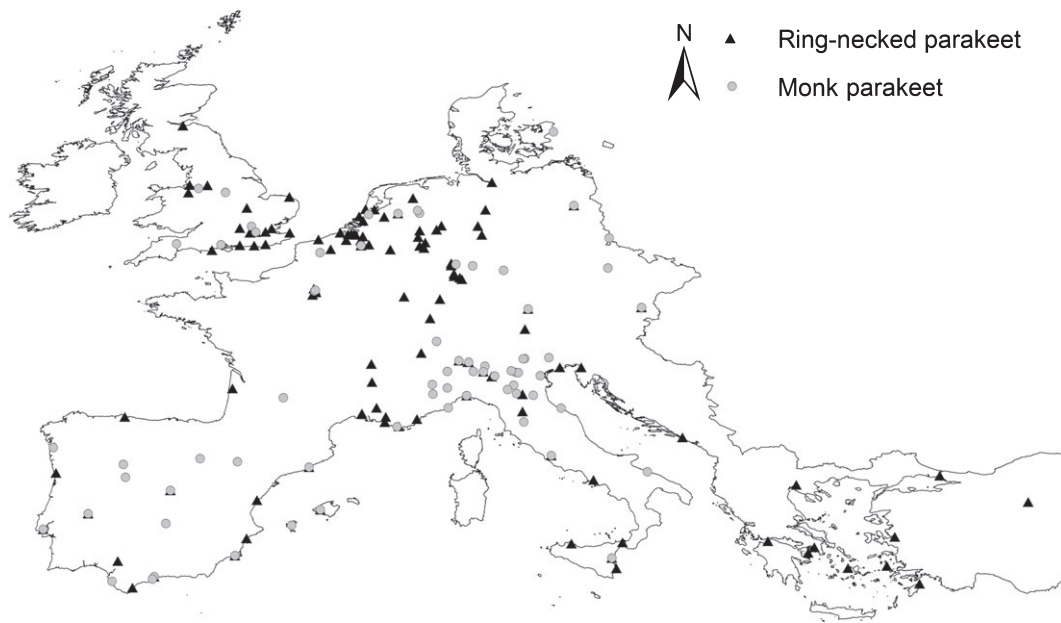
Figure 1 Locations of ring-necked (*Psittacula krameri*, n = 123) and monk (*Myiopsitta monachus*, n = 58) parakeet release sites in Europe.

period 1961 to 1990. However, for all our analyses, these temperature variables were highly correlated ($r > 0.70$), and we opted for FD as an indicator of climate. FD is often incorporated in analyses designed to identify the factors that promote exotic bird establishment and subsequent range expansion (e.g. Murgui & Valentin, 2003; Muñoz & Real, 2006; Nyari *et al.*, 2006; Real *et al.*, 2008), and, although ring-necked and monk parakeets are known to be somewhat cold-tolerant (Butler, 2003; Lever, 2005), freezing temperatures do pose a threat by causing frostbite (Ernst, 1995; Franz, 2008). There are indications that parakeets may suffer from the combination of cold and wet winters (Temara & Arnhem, 1996), and in order to further unravel the climatic factors that determine parakeet establishment success, we also extracted mean winter precipitation (WP) from the WorldClim database.

Many non-native species that have established populations in new regions benefit from human activity (Mooney & Cleland, 2001), and to verify whether this is true for invasive Psittacidae, we related parakeet introduction success to the human population density (number of humans/km^2; PD) and the Global Human Footprint (GHF) at the release site (Sanderson *et al.*, 2002). The latter is a global GIS map that depicts the human influence on terrestrial ecosystems using the best available datasets on human settlements, access, land transformation and electric power infrastructure (Sanderson *et al.*, 2002). Data on human population density were taken from the Gridded Population of the World database (year 2000, Balk & Yetman, 2004). We consider both measures of human activity to verify whether parakeets respond to the ecosystem disturbance and land modifications brought about by human activity (e.g. Laliberte & Ripple, 2004) or if their establishment success relates more directly to human presence (i.e. human population density). Several studies have shown

that both human population density and (exotic and native) species richness respond positively to measures of energy availability (Araújo, 2003; Gaston & Evans, 2004). In order to control for the possible confounding effect of energy availability, we included the Normalized Difference Vegetation Index (NDVI) as an environmental variable, as NDVI is a close correlate of plant productivity and can be used as a proxy for the amount of resources available for consumers such as birds (Evans *et al.*, 2006). Mean spring and winter NDVI values were obtained from Los (2004).

Data analysis

Data preparation

Normality of all variables was verified using a Shapiro–Wilk test, and all variables with $W < 0.90$ were transformed to achieve normality. For the ring-necked parakeet analysis, PD and WP had to be log-transformed; for the monk parakeet analysis, this was necessary only for PD. For all analyses, Pearson correlation coefficients among variables were calculated, but no correlations with $r > 0.70$ were observed (see Appendix S2). Before analysis, all variables were standardized using the SAS proc stdize statement. Data were analysed using two distinct approaches: a 'traditional' stepwise logistic regression, and a more recent information-theoretic approach (see Burnham & Anderson, 2002; Stephens *et al.*, 2005, 2007; Lukacs *et al.*, 2007).

Climate analysis of native distribution data

If climate-matching is one of the drivers of establishment success, we would expect parakeets in the native and the

introduced regions to respond similarly to climate. In the native regions, only data on parakeet presence are available, ruling out the use of presence–absence analysis techniques such as logistic regression (Hirzel et al., 2002). In order to assess the response of native ring-necked and monk parakeets to our indicator of climate (i.e. FD), we used the presence-only modelling technique Maxent (version 3.3, free download at http://www.cs.princeton.edu/~schapire/maxent/; Phillips et al., 2006). Maxent applies a set of linear, quadratic, product, threshold and discrete functions to estimate the probability distribution of a species across the study area, by finding the probability distribution of maximum entropy – or closest to uniform – subject to the values of the locations where the species has been detected (for more details on Maxent, see Phillips et al., 2006; Phillips & Dudík, 2008). In order to fully capture the climatic determinants of the parakeets' native ranges, and thus avoid truncated response curves in the models (Austin & Gaywood, 1994; Thuiller et al., 2005), we therefore designated broad study areas, encompassing the ranges of the parakeets as depicted in Juniper & Parr (2003).

For the ring-necked parakeet, the study area consisted of Pakistan, India, Bangladesh and Myanmar, and the monk parakeet area comprised Bolivia, Paraguay, Uruguay and the provinces of Brazil and Argentina where monk parakeets have been observed. The Maxent algorithm was implemented with the parakeet presence data and the number of frost days in the study areas, and response curves depicting the probability of parakeet presence as a function of the number of frost days were obtained. Maxent performance was evaluated using the area under the receiver operating characteristic curve (AUC), a statistic that ranges from 0.5 to 1 (the closer to 1, the better the model performance). In order to verify whether the Maxent models obtained differ significantly from what would be expected by chance, we followed the null-model method of Raes & ter Steege (2007). This method involves testing the AUC of the parakeet models against a null distribution of AUC values based on random data. Null models were generated by randomly taking localities without replacement from the geographical areas for which the parakeet distributions are modelled. The number of randomly drawn localities was equal to the actual number of presence data for that species (i.e. 61 for the ring-necked and 64 for the monk parakeet). This was repeated 999 times to generate the frequency distribution of AUC values that would be expected if the null hypothesis were true. The 95% confidence interval upper limit AUC value of this distribution was then compared with the AUC of the parakeet model to assess whether the parakeet model has an accuracy that is significantly higher than expected by chance alone (P < 0.05, Raes & ter Steege, 2007).

Logistic regression of European data

For both species in the introduced regions, we performed a logistic regression to identify the variables that influence establishment success. Multivariate logistic regression models were constructed following the methods of Hosmer & Lemeshow (2000). First, univariate logistic models were created, and only variables with a P-value < 0.25 were retained for multivariate analysis. All remaining variables were included in a multivariate regression model, together with the interaction FD × (log) WP. A backward stepwise regression was performed, and the significance level required to remain in the model was set to 0.05. In tables, statistics and P-values of significant terms are from the minimal model (all significant terms included), whereas statistics and P-values of non-significant terms were obtained by fitting each non-significant term separately into the minimal model.

Information-theoretic approach of European data

The information-theoretic approach (Burnham & Anderson, 2002) allows the consideration of non-exclusive candidate models, and we used the second-order Akaike information criterion corrected for small sample size (AIC$_c$) to rank candidate models. All possible subsets of all variables plus the interaction between FD and (log) WP were modelled using logistic regression, and corresponding AIC$_c$ values were calculated from log-likelihood statistics provided in R by the 'all.regs algorithm' (part of the hier.part package; Walsh & Mac Nally, 2008). For each possible model, a likelihood weight w_i is calculated, and this w_i is the probability (or 'weight of evidence', also termed 'AIC$_c$ weight'), for the set of models under consideration, that model i is the best model. For a set of models the likelihood weights total to one. When no single model attains overwhelming support (likelihood weight $w_i \geq 0.90$), inference can be made on the whole set of models, rather than on only the best-ranked model (termed 'model averaging'). In our analyses, no model clearly outperformed the others, and we used the model averaging procedure to present models that built up at least 95% of the sum of the AIC$_c$ weights within each set (termed 'the confidence set'; Burnham & Anderson, 2002). The relative importance of variables was assessed by summing the likelihood weights of all models in which the variable under consideration was present. Important variables are characterized by a high AIC$_c$ weight and model-averaged estimates that are higher than their standard errors (Anderson, 2008).

To control for the possible effects of event-level factors, we repeated the analyses described above on the subset of our data for which information on introduction year and effort was known. Changes in establishment rate over time have been found (García-Berthou et al., 2005), and year of introduction was included to account for this possibility. Alternatively, because parakeets are thought to be long-lived birds (Forshaw, 1978; Collar, 1997), there might be an apparent increase in establishment probability over time, as recently introduced populations have had less time to go extinct. For the ring-necked parakeet, introduction year was known for 114 releases, and introduction effort was known in 36 cases. For the monk parakeet, introduction year was known
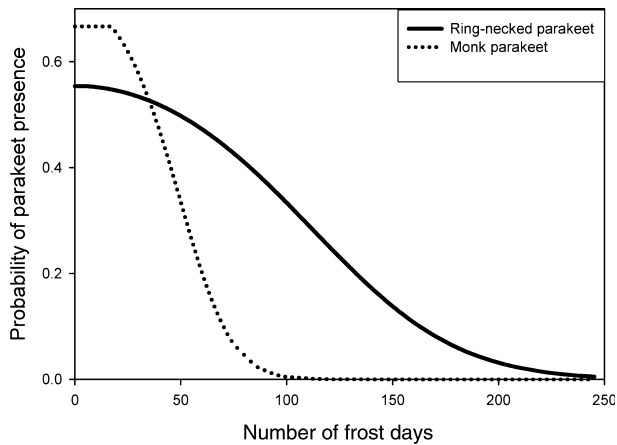
Figure 2 Probability of parakeet occurrence in relation to the number of frost days in the native ranges (ring-necked parakeet, *Psittacula krameri*: Southeast Asia, *n* = 61; monk parakeet, *Myiopsitta monachus*: South America, *n* = 64). Curves were obtained from the presence-only modelling method Maxent (Phillips *et al.*, 2006).

in 46 cases, but data on introduction effort were too sparse to analyse (*n* = 13).

RESULTS

Climate analysis of native distribution data

Maxent model performance was 0.64 for both ring-necked and monk parakeet models, and the 95% confidence interval upper limit of the randomly drawn null-models was 0.60 for the ring-necked parakeet and 0.61 for the monk parakeet, indicating that the correlation between parakeet presence localities and frost days, as identified and interpolated by Maxent, deviates significantly from random (*P* < 0.05; Raes & ter Steege, 2007). Figure 2 shows that in the native ranges, the probability of parakeet occurrence declines with increasing number of frost days. Monk parakeets appear to be more sensitive to frost than do ring-necked parakeets, as monk parakeet presence probability declined sharply with increasing number of frost days, whereas for ring-necked parakeets the decrease was more gradual. Ring-necked parakeet presence probability dropped below 0.5 at ± 50 frost days, whereas monk parakeet presence probability had by then already declined to ± 0.3.

Establishment success in Europe

Ring-necked parakeet

The establishment success of ring-necked parakeets was 53% (65 out of 123 introduction events). Following Hosmer & Lemeshow (2000), we first conducted a univariate logistic regression for each habitat variable and selected only variables with *P* < 0.25 for multivariate analyses, and, because for the
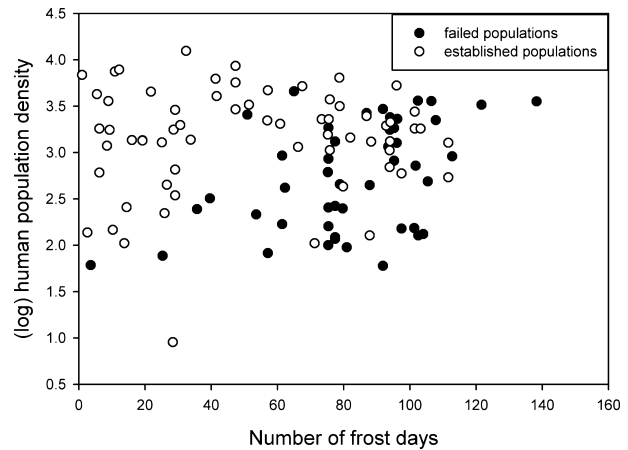

Figure 3 Success and failure of introduced ring-necked parakeet (*Psittacula krameri*, *n* = 123) populations in Europe in relation to the log human population density and the number of frost days.

full dataset and the introduction date subset the variables GHF and mean spring NDVI had a *P*-value larger than 0.25, these variables were removed and not included in the stepwise multivariate analysis. Whereas the multivariate logistic regression on the full dataset showed establishment success to be negatively associated with FD but positively associated with log PD (Fig. 3), the interaction of FD with log WP was also significant (Table 1), indicating that the negative effects of frost and rain reinforce one another. The max-rescaled R^2 of this minimal model was 0.44. The analysis of the subset of the data with known introduction year (*n* = 114) confirmed FD and log PD as significant variables, whereas FD × log WP was non-significant (*P* = 0.13). There was an indication for a change in establishment rate, as year of introduction was marginally significant (*P* = 0.08), and max-rescaled R^2 of this model was 0.42. Analysis of the subset with known introduction effort (*n* = 36) similarly yielded support for FD, log PD and mean spring NDVI. Introduction effort was not included in the analysis because of a univariate *P* > 0.25, and it remained insignificant when added to the minimal model (*P* = 0.28). Even when introduction effort was added to the minimal model, FD, log PD and mean spring NDVI remained significant predictors of parakeet establishment success (all *P* < 0.0315, max-rescaled R^2 = 0.55).

The information-theoretic approach identified a model containing the variables FD, log PD, log WP, FD × log WP, GHF and mean spring NDVI as the highest-ranking model (AIC$_c$ value = 127.7). The AIC$_c$ weight of this model was, however, only 0.18, indicating that there was a probability of only 18% that this was the best possible model. In order to assess the relative importance of predictor variables, we first created a confidence set (i.e. the smallest subset of candidate models for which the AIC$_c$ weights sum to 0.95). This set represents a set of models for which we have 95% confidence that it contains the best model (Burnham & Anderson, 2002). Thirteen models were needed for the confidence set to reach a cumulative probability of 0.95, and relative variable impor-

Table 1 Results of logistic regression on the establishment success of ring-necked parakeets (*Psittacula krameri*) in Europe according to the stepwise backward model selection.

	All data ($n = 123$)			Subset introduction year ($n = 114$)			Subset introduction effort ($n = 36$)		
	Estimate	SE	*P*-value	Estimate	SE	*P*-value	Estimate	SE	*P*-value
FD	**−1.58**	**0.33**	<0.0001	**−1.37**	**0.31**	<0.0001	**−2.87**	**1.21**	0.0172
Log PD	**0.91**	**0.26**	0.0004	**0.97**	**0.26**	0.0002	**2.39**	**0.69**	0.0120
GHF	–	–	–	–	–	–	−0.17	0.77	0.83
FD × log WP	**−0.59**	**0.31**	0.05	−0.46	0.30	0.13	–	–	–
Spring NDVI	–	–	–	–	–	–	**1.52**	**0.95**	0.0285
Winter NDVI	0.34	0.25	0.19	0.27	0.27	0.30	−0.45	0.76	0.56
Introd. year	n.a.	n.a.	n.a.	0.62	0.36	0.08	–	–	–
Introd. effort	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	–	–	–

FD, number of frost days; PD, human population density; GHF, Global Human Footprint; WP, mean winter precipitation; winter/spring NDVI, mean winter/spring NDVI; probability being modelled is 1 (establishment). Bold variables were included in the final model; '–' means that the variable was removed in the data preparation step.

tance was obtained by summing the AIC_c weights of all models in which the variable under consideration was present, and by calculating its model-averaged estimate and standard error (Burnham & Anderson, 2002). The variables FD, log PD and FD × log WP are well supported by the data (AIC_c weights 0.83–1.00, estimates > standard errors). We repeated the information-theoretic approach on the two subsets as outlined above. Analysis of the 'introduction year' subset confirmed the strong support for the variables FD, log PD and FD × log WP, and there was also some support for mean spring NDVI and year of introduction (AIC_c weights 0.62–0.65, Table 2), indicating an increase in establishment rate. The small 'introduction effort' subset yielded support only for FD, log PD, mean spring NDVI and, to a lesser extent, for year of introduction (Table 2).

Monk parakeet

Of the 58 monk parakeet introductions, 31 resulted in a breeding population, yielding an average introduction success rate of 53%. No variables were removed during the data preparation

steps (i.e. all univariate $P < 0.25$, Table 3). Monk parakeet establishment success decreased with FD, but increased with log PD (Fig. 4). The max-rescaled R^2 of this model was 0.28. WP and its interaction with FD were not included in the analysis of the introduction year subset because their univariate *P*-values were > 0.25. This analysis yielded only log PD and introduction year as significant variables, suggesting that establishment success may have increased towards the end of the 20th century (Table 3). Max-rescaled R^2 was 0.36. Not enough data were available to test the effect of introduction effort.

According to the information-theoretic approach, the highest-ranking model consists of the variables FD, GHF, mean winter NDVI, WP and FD × WP (AIC_c value = 73.2), but the AIC_c weight of this model is only 0.17. In order to construct the 95% confidence set, 34 models were needed, and variable importance was obtained as described above (summing AIC_c weights, calculating model-averaged estimates and standard errors). Results show strong support for the variables FD, log PD and mean winter NDVI (AIC_c weights ≥ 0.82, model-averaged estimates > standard errors, Table 4), and there was some evidence for GHF too. All other variables failed

Table 2 Results of logistic regression on the establishment success of ring-necked parakeets (*Psittacula krameri*) in Europe according to the information-theoretic model selection approach.

	All data ($n = 123$)				Subset introduction year ($n = 114$)				Subset introduction effort ($n = 36$)			
Variables	AIC_c	Estimate	SE	95% CI	AIC_c	Estimate	SE	95% CI	AIC_c	Estimate	SE	95% CI
FD	1.00	−1.68	0.39	−2.44 to −0.92	1.00	−1.68	0.46	−2.58 to −0.78	0.92	−3.05	1.69	−6.36–0.26
Log PD	1.00	1.16	0.38	0.42–1.90	1.00	1.40	0.46	0.50–2.30	0.98	2.81	1.35	0.16–5.46
GHF	0.42	−0.35	0.25	−0.84–0.14	0.42	−0.54	0.33	−1.19–0.11	0.21	−0.05	0.22	−0.48–0.38
FD × log WP	0.83	−0.56	0.29	−1.13–0.01	0.81	−0.46	0.29	−1.03–0.11	0.37	0.07	0.28	−0.48–0.62
Spring NDVI	0.48	0.18	0.15	−0.11–0.47	0.62	0.32	0.22	−0.11–0.75	0.85	1.45	0.79	−0.10–3.00
Winter NDVI	0.37	0.11	0.12	−0.13–0.35	0.26	0.03	0.07	−0.11–0.17	0.32	0.22	0.24	−0.25–0.69
Introd. year	n.a.	n.a.	n.a.	n.a.	0.65	0.40	0.28	−0.15–0.95	0.63	0.80	0.59	−0.36–1.69
Introd. effort	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.45	5.52	5.75	−5.75–16.79

FD, number of frost days; PD, human population density; GHF, Global Human Footprint; WP, mean winter precipitation; winter/spring NDVI, mean winter/spring NDVI. Probability being modelled is 1 (establishment).

Table 3 Results of logistic regression on the establishment success of monk parakeets (*Myiopsitta monachus*) in Europe according to the stepwise backward model selection.

Variables	All data ($n = 58$)			Subset introduction year ($n = 46$)		
	Estimate	SE	*P*-value	Estimate	SE	*P*-value
FD	**−1.07**	**0.38**	0.0044	−0.46	0.47	0.32
Log PD	**0.53**	**0.30**	0.07	**1.21**	**0.46**	0.0079
WP	−0.71	0.43	0.10	–	–	–
FD × WP	−0.53	0.41	0.20	–	–	–
GHF	0.05	0.35	0.88	−0.28	0.44	0.53
Spring NDVI	−0.41	0.39	0.29	0.02	0.37	0.95
Winter NDVI	0.55	0.34	0.11	–	–	–
Introd. date	n.a.	n.a.	n.a.	**1.38**	**0.61**	0.0232

FD, number of frost days; PD, human population density; GHF, Global Human Footprint,; winter/spring NDVI, mean winter/spring NDVI. Probability being modelled is 1 (establishment). Bold variables were included in the final model; '–' means that the variable was removed in the data preparation step.

to gain substantial support. Results from the introduction year subset supported log PD (AIC$_c$ weight = 0.96, estimate > standard error) and, to a lesser extent, FD (AIC$_c$ weight = 0.52), while indicating a tendency for monk parakeet establishment to have increased towards the end of the 20th century (AIC$_c$ weight = 0.95, Table 4).

DISCUSSION

Our results support both the climate-matching and the human-activity hypothesis. Ring-necked and monk parakeet establishment success is positively associated with log-human population density, and, both in the native and in the introduced regions, parakeet occurrence is negatively correlated with the number of frost days. Thus, parakeets are more likely to establish in warmer and human-dominated areas. In addition, ring-necked parakeets in Europe are negatively affected by the interaction between frost days and mean winter precipitation. Whereas ring-necked parakeet establishment success might be higher in areas with a higher spring NDVI, monk parakeets may benefit from higher mean winter

Figure 4 Success and failure of introduced monk parakeet (*Myiopsitta monachus*, $n = 58$) populations in Europe in relation to the log human population density and the number of frost days.

NDVI. For both species, there is a tendency for higher parakeet establishment success towards the end of the 20th century.

Climate matching

The ring-necked parakeet is the world's most widely distributed parakeet, occurring in most of tropical Africa north of the moist forest zone and in much of southern Asia (Juniper & Parr, 2003), and consequently it must have a broad tolerance of climatic and environmental conditions. However, the MAXENT response curve (Fig. 2) clearly shows that, in the native Asian range, ring-necked parakeet occurrence is negatively related to the number of frost days. In Europe, most introductions in areas with over 50 frost days have failed (Fig. 3) – a pattern which corresponds to a stark reduction in parakeet presence within the native area (Fig. 2). Essentially, the ring-necked parakeet is a bird of tropical and subtropical low latitudes (Cramp, 1985), and there are indications that ring-necked parakeets may suffer during cold European winters. In the Netherlands, Vergeer & van Zuylen (1994) mention the disappearance of several small populations after the harsh winter of 1984–85, and in Köln, Germany, there was a severe population crash after the very cold winter of 1978–79 (Schürmann, 1981). It is noteworthy that all established German populations are located in the Rhine valley, which has a milder climate than the rest of Germany (Krause, 2001). In addition, in several northern populations (e.g. Köln, Wiesbaden, Heidelberg and Brussels, but also New York, USA), it has been observed that the parakeets suffer from frostbite, resulting in the loss of toes, which can cause difficulties in foraging, mounting during copulation or in entering nesting cavities (D. Strubbe, personal observations; M. Braun, Institut für Pharmazie und Molekulare Biotechnologie der Universität Heidelberg, personal communication; Bull, 1973). Establishment failure in colder regions need not necessarily result from mass starvation of parakeets during harsh winters, but could be caused by a reduced breeding performance, for example as a result of a poorer body condition.
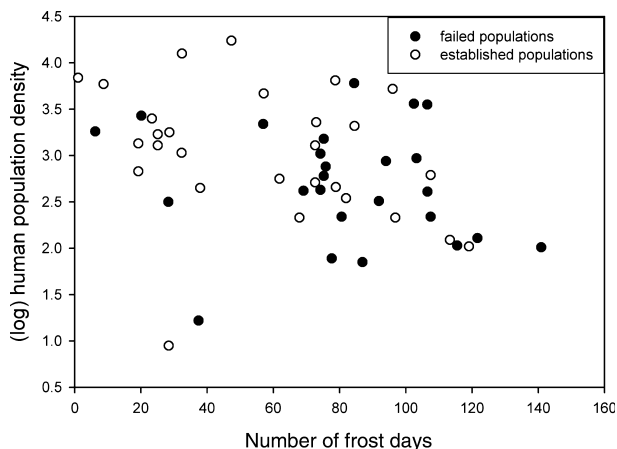
Table 4 Results of logistic regression on the establishment success of monk parakeets (*Myiopsitta monachus*) in Europe according to the information-theoretic model selection approach.

Variables	All data (n = 58)				Subset introduction year (n = 46)			
	AIC$_c$	Estimate	SE	95% CI	AIC$_c$	Estimate	SE	95% CI
FD	0.98	−1.17	0.49	−2.13 to −0.21	0.52	−0.33	0.32	−0.96–0.30
Log PD	0.84	0.24	0.23	−0.21–0.69	0.96	1.31	0.55	0.23–2.39
GHF	0.56	0.32	0.24	−0.15–0.79	0.26	−0.03	0.15	−0.32–0.26
FD × WP	0.41	−0.28	0.35	−0.97–0.41	0.55	−0.02	0.30	−0.61–0.57
Spring NDVI	0.31	−0.10	0.14	−0.37–0.17	0.62	0.05	0.13	−0.20–0.30
Winter NDVI	0.82	0.85	0.44	−0.01–1.71	0.23	0.62	0.45	−0.26–1.50
Introd. date	n.a.	n.a.	n.a.	n.a.	0.95	1.44	0.67	0.13–2.75

FD, number of frost days; PD, human population density; GHF, Global Human Footprint; winter/spring NDVI, mean winter/spring NDVI. Probability being modelled is 1 (establishment).

For the monk parakeet as well, occurrence probability in the native range (Fig. 2) and establishment success in Europe (Fig. 4) correlate negatively with the number of frost days. Monk parakeets are native to South America, where their distribution extends from tropical Bolivia and Brazil into the temperate regions of Argentina. Monk parakeets occupy their communal stick-nests year-round (Forshaw, 1978), which considerably reduces the energy needed for maintenance during cold winter nights (Caccamise & Weathers, 1977). It has been suggested that the thermoregulatory benefits of their stick-nests enable them to survive in northern climates (Spreyer & Bucher, 1998). On the other hand, Weathers & Caccamise (1975) found that monk parakeets are relatively tolerant of low air temperatures, but that their metabolic rate rises sharply with decreasing temperatures. Abundant food is necessary to maintain these higher metabolic rates, and cold periods combined with limited food supplies could put the monk parakeets at risk. At first sight our data seem to suggest that the monk parakeet is less sensitive than the ring-necked parakeet to frost, as for frost days the (model-averaged) slope estimate for monk parakeets is lower than that for ring-necked parakeets (−1.17 vs. −1.68, Tables 2 and 4). However, the model-averaged 95% confidence intervals overlapped (−2.44 to −0.92 for the ring-necked parakeet, −2.13 to −0.21 for the monk parakeet), indicating that the estimates are not significantly different. Moreover, on average, ring-necked parakeets have been introduced into colder regions than have monk parakeets ($t = 4.9$, d.f. = 121.2, $P < 0.0001$). To test whether the two species differ in their sensitivity to frost, we reanalysed all parakeet introductions and included 'species' and the frost days × species interaction in the model. There is no marked difference in frost sensitivity between the two parakeet species, as the AIC$_c$ weight of the frost days × species interaction was only 0.14 and the interaction was also not included in the minimal model obtained by stepwise logistic regression ($P = 0.47$). Thus, although the MAXENT response curves suggest that in its native range the monk parakeet is more sensitive to frost than is the ring-necked parakeet (Fig. 2), the analysis of European introductions shows that the two species seem to be equally sensitive (Figs 3 & 4). In the native range, the presence probability of monk parakeets starts declining sharply from ± 15 frost days, whereas in Europe most failed introductions only occur in areas with more than 50 frost days, suggesting that the evidence for monk parakeet climate matching might be less persuasive. However, further research using a more extensive database on monk parakeet occurrence in the native region and taking into account other factors that might influence monk parakeet distribution is needed to clarify this.

Even though the nest-building behaviour of monk parakeets is not associated with a higher tolerance of cold, it may still protect them from the adverse effects of rain, particularly in combination with cold. For this species, neither mean winter precipitation nor its interaction with frost days was found to be important, in contrast to the case for the ring-necked parakeet, for which the model suggests that the combined effect of cold and rain is especially detrimental. Ring-necked parakeets spend the night at communal roost sites, and their roosting trees are usually very exposed (Pithon, 1998). Rain can soak the plumage so that its insulating air layer is lost and the birds may die of heat loss (Newton, 1998). In Brussels there is an anecdotal observation of ± 100 parakeets suffering from a combination of frost and fog that led to an ice layer on their plumage and tail and impeded their movements for several hours (Temara & Arnhem, 1996).

Human-activity hypothesis

In support of the human-activity hypothesis, we found that the establishment success of both ring-necked and monk parakeets is correlated with measures of human activity. Human activity is a root cause of species introductions (Westphal *et al.*, 2008), but the actual pattern of introductions stems from a complex web of activities (Taylor & Irwin, 2004), and the exact role of human population density can vary with many potential factors such as spatial scale, geographic location and social factors (e.g. economy, policies). Human activity can act both as an event-level and as a location-level variable, and it can be notoriously difficult to

disentangle these effects (Chiron *et al.*, 2009). As a direct effect, human activity may enhance establishment success by increasing the introduction effort. However, after controlling for the number of parakeets released during the first introduction event, human population density was still an important predictor. This suggests that human activity influences establishment success (at least partly) independently of propagule pressure. It seems plausible, however, that there will be more parakeet escapes or releases in more heavily populated areas, and a positive effect of repeated introductions cannot be excluded, as we do not know whether more parakeets were introduced after the first (known) introduction event.

Bonier *et al.* (2007) found that birds successfully adapting to human-dominated areas have broad environmental tolerances. The native distributions of ring-necked and monk parakeets span a wide geographical area (Juniper & Parr, 2003), and as a species' geographical distribution provides a reliable index of environmental tolerance (Symonds & Johnson, 2006; Cofre *et al.*, 2007), the ecological flexibility implied by their wide distributions may enhance the parakeets' ability to tolerate a broad array of environmental conditions and predispose them to successful exploitation of anthropogenic habitat. This behavioural flexibility may include traits such as the ability to adjust behaviour in response to novel conditions or the use of novel resources such as food offered by humans (Lefebvre *et al.*, 2004; Sol, 2007). Increased food availability is recognized as one of the main indirect effects that human activity has on urban avian ecology (Robb *et al.*, 2008a,b), and abundant food could well explain the link between the parakeets' establishment success and human population density. People increase food availability by providing commercial wild bird foods, or by introducing a large number of (mostly exotic) plant species in urban parks and gardens (Chace & Walsh, 2006; Robb *et al.*, 2008a,b). Access to abundant food resources could be especially relevant for introduced species because, in their novel environment, they have to taste new foods or adopt novel foraging strategies (Møller, 2009). In addition, they are typically introduced in low numbers (Duncan *et al.*, 2006), and the increased survival and higher reproductive success facilitated by food provisioning (Chamberlain *et al.*, 2009) may increase their population growth rate and reduce the chance of stochastic extinction (Moulton & Pimm, 1986). Ring-necked parakeets are flexible foragers and often visit bird feeders, especially in the winter and during their breeding season (Dewinck, 2005). Pithon (1998) found that, in the UK, parakeet densities correlated best with densities of (semi)detached households inhabited by retired people, as they are most likely to provide bird food. Moreover, a recent telemetry study on breeding ring-necked parakeets in Brussels, Belgium, found that parakeets prefer to forage in city parks and gardens (rather than forest), where a wide variety of (often exotic) plant species are present (D. Strubbe, unpublished data). Although resource-matching theory predicts that high bird densities result from greater resource availability, Shochat (2004) argues that high food availability in cities leads to over-exploitation and that urban bird densities might exceed carrying capacity, impacting on body condition and/or life span. Urban bird populations might consist of a few successful, dominant competitors able to exploit urban food, and many losers, who might be able to survive, but whose contribution to the next generation will be negligible, unlike their contribution to the current population density (Shochat, 2004). However, Rodewald & Shustack (2008) found that the greater densities of northern cardinals (*Cardinalis cardinalis*) in urban habitats were consistent with resource-matching theory, as they were the result of higher food and nesting substrate availability. It thus remains to be seen to what extent the establishment probabilities of urban bird populations in general and invasive species in particular are affected by changes in population dynamics induced by food provisioning in anthropogenic habitats.

Apart from food availability, there are other reasons why human-dominated habitats can increase establishment success for invasive parakeets. In urban parks, old trees are often preserved for their aesthetic value and this increases nesting cavity availability, which is crucial for ring-necked parakeets. Exotic plantings can also offer nesting opportunities for monk parakeets, as Sol *et al.* (1997) showed that in Barcelona (Spain) the distribution and abundance of monk parakeets were determined mainly by the presence of exotic palms. Alternatively, large and densely populated cities can act as heat-islands (Arnfield, 2003), reducing the number of frost days, and this could also contribute to the positive relationship between parakeet establishment and human population density.

In Europe, ring-necked parakeets start breeding before the end of the winter, with the first eggs laid at the end of February (Butler, 2003; D. Strubbe, personal observations), and the correlation between parakeet establishment success and mean spring NDVI could indicate that, in regions with a higher plant production (and thus higher food availability), the breeding success and thus establishment probability of ring-necked parakeets are higher. However, mean spring NDVI appears as an important predictor only in the analyses on introduction date and effort subsets, and more research is needed to clarify the role of spring NDVI. For monk parakeets, Hyman & Pruett-Jones (1995) showed that in cold areas, such as Chicago, natural foods are not available and the parakeets depend exclusively on seeds provided at bird feeders for the whole winter. In view of this, the positive correlation between monk parakeet establishment and mean winter NDVI could mean that in more productive areas more food is available for monk parakeets, enabling them to survive the winter period better. However, these results should be interpreted with caution, as an analysis of the monk parakeet introduction year subset yields no support for mean winter NDVI as an important predictor. Characteristics of disturbed ecosystems often positively influence establishment, but, in this study, establishment success correlated only with human population

density, and not with the Global Human Footprint, suggesting that parakeet establishment success relates directly to human presence, and not so much to the ecosystem disturbance caused by humans (Sanderson *et al.*, 2002). Human presence and (exotic) species richness may both be responding positively to energy availability, generating a positive but non-causal correlation (Evans & Gaston, 2005). However, in our analyses, we included rough measures of energy availability (frost days and NDVI; Evans *et al.*, 2006), and, even after accounting for the possible influence of energy availability, human population density remains an important predictor of parakeet establishment success.

Results are suggestive of a possible role for year of introduction, as there is a tendency for ring-necked and monk parakeets to have a higher establishment probability when introduced more recently. This could signify that environmental conditions have recently become more suitable for the establishment of parakeets (e.g. because of warming as a result of climate change). This result is probably not an artefact caused by the inclusion in the database of recently introduced populations consisting of non-reproducing parakeets, whose presence may give the false impression of an established population, leading to an apparent increase in establishment success over time. We did not include introduction events after the year 2000, and because monk parakeet mortality is ± 20% per year (Spreyer & Bucher, 1998; Butler, 2003), the chances that, after 7 years, a population of non-reproducing parakeet will still be present is small, especially because introductions typically involve a low number of individuals being released. Ring-necked parakeet mortality rates have not been determined, but are thought to be more or less comparable to those for monk parakeets (Butler, 2003).

Most studies on bird establishment success rely on large databases of species introductions, but the number of independent introductions per species is often low (Veltman *et al.*, 1996; Duncan *et al.*, 1999, 2001; Blackburn & Duncan, 2001a,b). Consequently, hypotheses such as climate matching or human activity are most often invoked to explain broad-scale patterns in exotic species richness or ranges (Forsyth *et al.*, 2004; e.g. Chown *et al.*, 2005). This study is, to our knowledge, the first in which these hypotheses have been tested at the species level using a large number of independent introductions. We show that climate/environment-matching and the human-activity hypotheses offer insight into the invasion process of both monk and ring-necked parakeets, and parakeet establishment success is thus influenced by local geographical factors such as climate and human population density. Our results suggest that parakeet establishment probability may increase even further in the future because global warming will cause a decrease in the number of frost days (IPCC, 2007) and because urbanization and human populations are still increasing (Kasanko *et al.*, 2006). On the other hand, as time advances and more parakeets are introduced, it is possible that locations suitable for parakeet establishment could become saturated, leading to an apparent decline in parakeet establishment rates. However, a recent GIS-based niche modelling study showed that, at least in northern Belgium, suitable locations remain plentiful (Strubbe & Matthysen, 2009b). A further factor that could influence future establishment success is the recent EU decision to permanently ban the wild bird trade. This could affect not only the number of introduction events of parakeets (and other birds), but also establishment success itself, as Carrete & Tella (2008) suggest that most successful invasions involve wild caught birds, as captive-bred birds seem to have lost the capacity to cope with new environments.

Clearly, more research is needed to elucidate the mechanisms that determine the establishment probability of invasive species. Future studies should include more accurate data on introduction effort and should focus on the manner in which human population density influences the establishment success of invasive species. The large dataset available for parakeet introductions obviously results from their conspicuousness in combination with the presence of many amateur bird observers. However, exotic species are typically not well covered in bird atlas publications, and hence we had to consult local or regional publications and in many cases had to resort to personal contacts. We suggest that monitoring studies should collect data on invasive species, even if anecdotal, in a more consistent way, in order to provide more accurate data on introduction events and their success or failure.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Appendix S1 Ring-necked and monk parakeet introductions in Europe.

Appendix S2 Correlations between the explanatory variables in all datasets used.

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BIOSKETCHES

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