RESEARCH PAPER

The role of species traits and taxonomic patterns in alien bird impacts

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ABSTRACT

Aim To test whether the distribution of alien bird impacts varies across bird families and regions of origin, and to investigate whether species traits associated with successful introductions can predict which species will have negative impacts in the new area of introduction.

Location Europe and the Mediterranean Basin.

Methods Combining historical information and published literature about negative economic, biological and human health impacts, we compared the distribution of impacts among bird families and native origins of bird species for three major types of impact (economic, biodiversity and human health). We examined the relationships between ecological, biological and reproductive characteristics of species and the severity of the impacts.

Results The majority of alien species with reported impacts originated from the Afrotropical, Indo-Malayan and Palaearctic biogeographical regions. The distribution of alien bird species in Europe with reported impacts shows a taxonomic bias and largely mirrors patterns of establishment. While most species had primarily either economic or biodiversity impacts, several species in the Anatidae, Corvidae, Passeridae, Phasianidae and Sturnidae families were associated with moderate to serious negative impacts on both economic resources and native biodiversity. After controlling for taxonomic effects, species with the greatest overall impacts were habitat generalists and multi-brooded, while species with smaller bodies and the tendency to form large feeding or roosting flocks were linked with greater impacts on native biodiversity.

Main conclusions This study presents the first synthesis of published impact data for alien birds and provides a broad-scale perspective on factors that contribute to their impacts. The results show that accounting for both species traits and taxonomy improves our ability to predict the impacts of alien bird species. Because several species are currently in the early stages of establishment in Europe, there may be an opportunity to limit negative impacts with efforts that promote proactive strategies against species and families possessing the above characteristics.

Keywords

Alien birds, biological invasions, DAISIE, Europe, impacts, species traits.

INTRODUCTION

Introductions of alien species have increased dramatically in Europe since the 19th century (Shirley & Kark, 2006; Chiron *et al.*, 2009). Scientists and policy-makers are becoming increasingly aware that introductions of alien species can have serious negative impacts on the diversity of native species, economic resources and human health (Wilcove *et al.*, 1998; Williamson, 1999; Pimentel *et al.*, 2000). A growing number of studies have focused on the ability of species characteristics to explain patterns in biological invasions (Kolar & Lodge, 2001), but most have focused on the early stages of invasion (introduction

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and establishment) (e.g. O'Connor, 1986; Veltman *et al.*, 1996; Cassey, 2002; Sol *et al.*, 2002) rather than the outcome (impacts). While serious impacts have been reported for several alien birds (van Riper *et al.*, 1986; Pell & Tidemann, 1997; Barilani *et al.*, 2007), data on their effects on native bird populations and economic damages, such as those to agricultural resources, are often scarce (Parker *et al.*, 1999) or lacking in quantitative rigor. Thus, it often remains unclear whether the impacts of a species will be detrimental in a new location (Williamson, 1996). Overall impacts can be defined in a simplified way as the product of an alien species range size, abundance and the effect per capita (Parker *et al.*, 1999). However, this definition relies on impacts that are already apparent and measurable. Arguably the most important of these factors is the per-unit impact that incorporates particular aspects of the species biology.

It is now better understood which characteristics allow an alien bird species to become a successful invader (Blackburn & Duncan, 2001; Cassey, 2002; Duncan *et al.*, 2003; Cassey *et al.*, 2004), but not yet which traits are associated with its potential to cause negative impacts. Rather than wait until a species has spread enough for the evidence of impacts to become obvious, effective control would benefit from our ability to predict the probable impact of a given species based on its general biological, ecological and geographical characteristics.

Representing a first synthesis of impacts for alien birds at a continental scale, we use a database of successful European bird introductions across Europe and parts of the Mediterranean Basin that we generated as part of the EU consortium DAISIE (DAISIE, 2008) to examine the distribution of economic, biodiversity and human health impacts among alien birds. Because we are concerned with potential negative consequences of introductions often unknown to researchers and policy-makers, we focus on negative impacts. We test the hypothesis that the distribution of negative impacts varies across avian families and across birds from different native biogeographical regions of origin. Because biodiversity and economic impacts may be connected for certain species, we examine the relationships between types of impacts to investigate whether species with economic impacts are the same as those with negative impacts on species biodiversity.

Successfully introduced alien bird species are characterized by several common features (e.g. Blackburn & Duncan, 2001; Duncan *et al.*, 2001, 2003; Cassey, 2002; Cassey *et al.*, 2004). These include: (1) non-random taxonomic affiliation and region of origin, (2) high reproductive success, often with multiple broods per year, (3) large body mass, (4) sedentary behaviour, (5) diet and habitat generalism, and (6) human commensalism. Several of these features are also important among other taxonomic groups (Kolar & Lodge, 2001; Sakai *et al.*, 2001; Hierro *et al.*, 2005; Hayes & Barry, 2008). There is little evidence on the nature of the relationship between success of establishment and impact. A recent study (Ricciardi & Cohen, 2007) found no evidence that alien species with high rates of establishment success and spread from a broad variety of introduced plants, invertebrates and vertebrates were more likely to have negative impacts than species with low rates. In this paper, we test the general hypothesis that traits associated with successful introductions in birds can also predict those species with negative impacts. In particular, we expect that characteristics of successfully introduced alien species, such as high reproductive productivity, habitat generalism and sedentary behaviour (e.g. O'Connor 1986; Veltman *et al.*, 1996; Kolar & Lodge, 2001; Cassey *et al.*, 2004), enabling species to achieve rapid population growth and permanently colonize a variety of habitats, will also be important predictors of negative impacts. We quantify the ability of species biological and ecological attributes to explain differences in the types and severity of impacts along with analytical techniques to control for taxonomic clustering to examine this hypothesis in birds.

MATERIALS AND METHODS

Sources of data

We used the European database of alien and invasive birds that we generated in the framework of the DAISIE consortium project (http://www.daisie.se/) (Shirley & Kark, 2006; Kark *et al.*, 2008), covering Europe and its associated islands. Alien introductions included species intentionally introduced by humans as well as unintended introductions arising from escapes or other factors. We identified and classified impacts on native bird species diversity, economic uses/resources and human health for alien species across Europe using published historical information. Here, we defined biodiversity impacts as those impacts on native bird species diversity (number of species and relative abundance). Economic impacts occur when an alien species leads to loss of monetary value of a given use or resource. Although we defined economic impacts a priori as losses occurring to a human use or resource, economic impacts in our data were overwhelmingly represented by damage to grain (including stored grain), vegetable and fruit crops. Human health impacts include the potential for disease transmission as well as fouling of structures with faecal droppings, noise and threats to air safety. Air safety impacts refer to airplane injuries caused because birds in flight have collided with planes and become lodged in engines.

Since information on impacts in alien ranges is poorly documented for most alien birds in Europe, we performed a review of the literature to find any reported impacts from areas other than Europe, where the species is present as a non-native, as well as from native ranges to represent the best currently available approximation of potential impacts (see Appendix S1 in Supporting Information). Because impacts in the introduced range where abiotic and biotic controls may be absent are likely to be more severe than in the native range (Long, 1981), our analyses present a conservative picture of potential impacts. Many described impacts are local, anecdotal case studies, although most reports include very little quantification of spatial extent. In cases where quantitative data exist, they are represented by a variety of different metrics including percentage of crop damaged, monetary value of losses, percentage area damaged or numbers of crop types with losses. We reviewed impacts from 99 studies (see Appendix S1) and, of these, 35 studies include some

Table 1 Criteria for ranking impacts reported for alien bird species in Europe based on published historical information. Impacts are ranked according to a general ordinal scale with the highest ranking representing the greatest impacts.

Ranking criteria for impacts		Examples from published literature
Biodiversity impacts		
1	Aggression or displacing at least one native bird species from feeding grounds	*Streptopelia decaocto*: aggression towards native doves in Florida (Romagosa & Labisky, 2000)
2	Competition with at least one native bird species resulting in local population decline	(1) *Psittacula krameri*: competition with nuthatches and great spotted woodpecker in Brussels (Strubbe, 2007), (2) *Acridotheres tristis*: displaced nesting of two native parrot species in Australia (Pell & Tidemann, 1997)
3	Predation on > 1 native bird species (generalist predator) or hybridization with at least one native bird species	(1) *Acridotheres tristis*: predation and decline of Tahiti flycatcher in Tahiti (Blanvillain *et al.*, 2003), (2) *Oxyura jamaicensis*: hybridization with rare native white-headed duck *Oxyura leucocephala* (Hughes *et al.*, 2006)
Economic impacts		
1	Minor feeding on crops	*Aratinga mitrata*: feeding on fruit and nut trees in southern California (Garrett *et al.*, 1997)
2	Light damage to crops from feeding	(1) *Nymphicus hollandicus*: generally minimal damage to sorghum and sunflower crops in Australia (Forshaw, 1973; Jones, 1987), (2) *Callipepla californica*: estimated 5% damage to wine grapes in California (Boudreau, 1972)
3	Considerable damage to crops through feeding and trampling	(1) *Columba livia*: US$1.1 billion in losses in large part due to feeding on grain (Pimentel *et al.*, 2000), (2) *Myiopsitta monachus*: US$0.6 million lost in 1974 in Uruguay; up to 64% of longan crop lost in Florida, USA (De Grazio, 1978; Tillman *et al.*, 2001)
Human health impacts		
1	Faecal droppings, low potential for disease transmission, noise	*Corvus splendens*: carrier of intestinal parasites in Aden, Yemen (al-Sallami, 1991)
2	Faecal droppings, moderate potential for disease transmission, potential threats to air safety	(1) *Columba livia*: fouling structures in urban areas with faecal droppings, facilitate the transmission of diseases in urban areas (Long, 1981 and refs therein), (2) *Branta canadensis*: air hazard in USA and UK (Allan & Feare, 1994; Watola *et al.*, 1996)
3	Potential for serious disease transmission to humans, avian flu	No published examples to date

measure of quantitative impacts. Therefore, we described impact severity using a rank category approach, useful for comparing data of varying quality (Kolar & Lodge, 2001; Ricciardi & Cohen, 2007). We classified impacts according to a general ordinal scale with the highest ranking representing major impacts causing serious effects to economic resources, biodiversity or human health and wellbeing (see Table 1 for specific impact criteria). Our categorization is consistent with the terminology used in the published literature (e.g. Long, 1981). Impacts for many species are often briefly described as 'minor' or 'major' (Long, 1981 also uses 'serious'). Impacts can vary in their severity across regions, so we used the maximum reported impacts for each species in our analyses.

Species trait associations

We examined the relationships between the ecological, biological and reproductive characteristics of species and the type and severity of impact using a number of factors hypothesized to directly influence impacts. We obtained data for each species on the location of their native range, degree of habitat and diet specialization, human commensalism, body mass, movement patterns, sociality and reproductive potential as measured by clutch size, number of broods per year and level of precociality from the published literature on global and regional avifauna (main sources: Macworkth-Praed & Grant, 1962–63, 1970–73; Forshaw, 1973, 1989; Cramp & Simmons, 1977; Long, 1981, and references therein; Dunning, 1993; del Hoyo *et al.*, 1994–2004; Veltman *et al.*, 1996). We defined the degree of a species' habitat specialization as the number of habitats occupied by the species in its native range, a simple measure that directly reflects the level of habitat specialization. Habitats were classified according to the European Nature Information System (EUNIS) system of habitat types (European Environment Agency, 2007, available at http://eunis.eea.europa.eu/habitats-code-browser.jsp). A species was classified as a human commensal if it was reported to use cultivated agricultural, horticultural, domestic habitats or constructed, industrial or other artificial habitats according to the EUNIS classifications. We categorized each species according to its diet (herbivorous, omnivorous, carnivorous), migratory patterns (sedentary, nomadic movements, partial migrant, migrant), precociality (precocial, semi-altricial, altricial) and degree of sociality (solitary/pairs, small flocks/parties, small flocks/parties with occasional large flocks, flocks/parties with large communal roosts).

The native distribution ranges of species were classified into seven categories (Afrotropical, Australian, Holarctic, Indo-Malayan, Nearctic, Neotropical and Palaearctic) according to the global terrestrial biogeographical biomes developed by the World Wildlife Fund (WWF) (http://worldwildlife.org/science/

ecoregions/biomes.cfm). Clutch size was recorded as mean clutch size. If the mean clutch size was unavailable, we calculated a mean from the reported range of sizes. We took the maximum value for the reported number of broods fledged per season. Productivity was defined as the product of mean clutch size and the maximum number of broods. Body size was recorded for females to minimize any bias due to sexual selection (Veltman *et al.*, 1996; Cassey, 2002); where female body size was unavailable, unknown sex or male size were used in that order of preference.

Data analysis

We used a chi-square goodness of fit test to compare the distribution of impacts among families for total impacts and the different types of impacts (economic, biodiversity and human health). Nonparametric bivariate correlations using binary variables (0 = impact absent; 1 = impact present) were used to test for relationships between the three types of impacts. Similarities in the distribution and severity of impact types across species were assessed using ANOSIM in Primer 5.2.2 (Primer-E Ltd, 2001), which applies permutations to a similarity matrix. We used a multivariate general linear mixed model procedure in the SPSS 15.0 statistical software package to model the relationship between the response variable (impact severity) and the factors hypothesized to explain impacts. We fitted a model with a normal error distribution after using the Shapiro–Wilk statistic to test for normality of residuals. Homogeneity of variances was assessed using the Levene test. The clustering of species within higher taxonomic units where closely related species share many ecological and morphological characters has the potential to bias results by confounding associations with other variables. Several methods are used to account for taxonomic effects (see Sol *et al.*, 2008, for a review). To overcome difficulties associated with statistical non-independence if an observed effect is associated with traits that can be similar within the same family (Harvey *et al.*, 1995), we modelled family as a random effect (Blackburn & Duncan, 2001; Cassey *et al.*, 2004). We carried out analyses before and after including taxonomic information; however, only results after taxonomic effects were removed are shown. All other explanatory variables were included as fixed effects in the model. All first-order interactions were tested but were non-significant and removed from the model. The significance of parameter estimates was tested using the t distribution. We were unable to model human health impacts due to the small sample size (eight species); therefore, individual tests for each independent variable were performed. We set statistical significance at $\alpha = 0.05$ for all analyses.

RESULTS

Distribution of impacts across families and native ranges

The distribution of alien birds in Europe with reported impacts shows a taxonomic bias (Table 2). Economic impacts in particular differed across families ($\chi^2 = 53.62$, $P < 0.001$), with the Anatidae,

Table 2 The number of European alien species within avian families with reported biodiversity, health and economic impacts. The total number of species with reported impacts in each family includes species with more than one type of impact. Also shown is the percentage of successfully introduced species with reported impacts. Taxonomic classification and order follows that of Sibley and Monroe (1990, 1993).

Family	Biodiversity	Health	Economic	Total species with impacts	Percentage of species with impacts
Anatidae	6	1	8	11	38
Threskiornithidae	1			1	100
Numididae			1	1	100
Phasianidae	3	1	9	9	56
Meleagrididae			1	1	100
Columbidae	2	2	3	3	60
Psittacidae	4	2	13	13	72
Cacatuidae			2	2	100
Strigidae	1			1	50
Pycnonotidae	2		2	2	100
Timaliidae	1			1	25
Corvidae	4		4	4	100
Sturnidae	2	1	2	2	22
Passeridae	2	1	2	2	100
Ploceidae			3	3	23
Estrildidae			6	6	43
Fringillidae			3	3	100
Odontophoridae			1	1	100
Total	28	8	60	66	

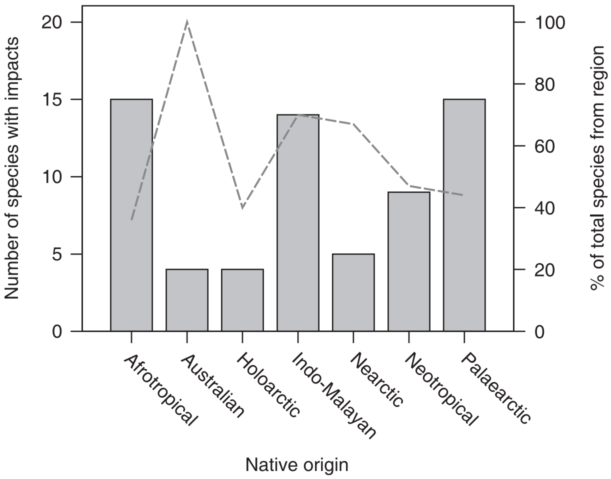

Figure 1 Distribution of native ranges for European alien bird species with reported impacts (histogram) and percentage of total established species originating from each region (dashed line). Native range categories are based on global biogeographical regions, as described in the text.

Estrildidae, Phasianidae and Psittacidae families having greater numbers of species with economic impacts. Biodiversity and human health impacts did not differ significantly across families ($\chi^2 = 9.71$, $P = 0.467$, $\chi^2 = 1.00$, $P = 0.963$, respectively). Alien species originating from the Afrotropical, Indo-Malayan and Palaearctic biogeographical regions had the majority of reported impacts ($\chi^2 = 18.15$, $P < 0.006$) (Fig. 1). This pattern was generally consistent for both biodiversity ($\chi^2 = 13.00$, $P < 0.043$) and economic ($\chi^2 = 18.75$, $P < 0.005$) impacts. The proportion of species from these regions with reported impacts ranged from approximately 40% (Afrotropical and Palaearctic) to 70% (Indo-Malayan). The number of species with reported impacts from a region was not related to the percentage of total species with impacts from the same region ($r = -0.421$, $P = 0.347$). For example, although the number of species originating from Australia was small, all had reported impacts.

Associations between different types of impacts

Overall, we found that species with reported economic impacts were not similar to those species with impacts on native biodiversity ($r = -0.370$, $P = 0.002$). No correlation was observed between economic and human health impacts ($r = 0.115$, $P = 0.352$), but there was a positive association between biodiversity and human health impacts ($r = 0.341$, $P = 0.005$). The type and severity of reported impact was distributed differently across species (analysis of similarity (ANOSIM) $R = 0.153$, $P = 0.016$). Species in the Columbidae, Estrildidae, Ploceidae and Psittacidae families had negative impacts on grain and fruit crops while species in the families Pycnonotidae and Threskiornithidae had negative impacts on biodiversity. Species in several families including the Anatidae, Corvidae, Passeridae, Phasianidae and Sturnidae were associated with moderate to serious negative impacts on both native biodiversity and economic resources (Table 2).

Species attributes associated with impacts

After accounting for the significant taxonomic effects for all impact categories (all P values < 0.04), there were several attributes that were associated with the degree of impact severity. The degree of habitat generalism and location of native range were significant predictors of total and economic impacts (Table 3). Species from Indo-Malayan, Afrotropical and Palaearctic regions had high-severity total impacts and economic impacts. Species with greater habitat generalism had greater overall impacts, specifically economic impacts, than those using three or fewer habitats. While human commensalism was a factor strongly associated with the presence of impacts of all types (binomial tests, all Ps < 0.01), it was not a significant predictor of the degree of impact severity for any impact type. There were no significant predictors of human health impacts, probably due to the small number of species with reported impacts (results not shown).

Although migratory status was not a statistically significant predictor of total impacts (Table 3), sedentary and partially migratory species had a tendency towards greater impacts than nomadic or migratory species. We found a significant association between sociality and total impacts ($F = 3.86$, $P = 0.014$), whereby species forming large roosting flocks had greater impacts. However, this relationship disappeared once family (taxonomy) was considered in the model, especially for the families Corvidae, Estrildidae and Passeridae. In contrast, taxonomic correction did reveal significantly greater biodiversity impacts for species with large feeding or roosting flocks or low body mass. The number of broods was positively related to overall impacts, whereby the severity of total impacts increased with brood number (Table 3).

DISCUSSION

In the past 10 years a growing number of studies have described those attributes contributing to the success of alien birds; however, there has been little effort to synthesize the widely dispersed literature on alien bird impacts to examine broad-scale patterns. This study presents a first synthesis of published impact data for birds and provides a broad-scale perspective on factors that may contribute to impacts of alien bird species. As predicted, the distribution of alien bird species in Europe with reported impacts shows a taxonomic bias driven largely by species with economic impacts and largely mirrors patterns of establishment ($r = 0.77$, $P < 0.001$) (Shirley & Kark, unpublished). Families with greater numbers of established species in Europe generally have greater numbers of species with reported negative impacts. This taxonomic pattern among avian families is also found for successfully introduced (established) birds at a global scale (Lockwood, 1999; Cassey, 2002), in which the Anatidae, Phasianidae and Psittacidae families are among those with the

Table 3 Parameter estimates and statistics of a general linear mixed model for factors hypothesized to explain total, biodiversity and economic impacts. Only factor levels significant at $P \leq 0.10$ are shown. Values for n are the number of species with reported impacts in each category of impact type.

	All impacts (n = 66)		Biodiversity (n = 28)		Economic (n = 60)	
Variables	Parameter estimate	*t*	Parameter estimate	*t*	Parameter estimate	*t*
Habitat factors						
Number of habitats						
(two)	1.850	**1.710**	–0.223	0.218	**1.066**	**1.680**
(three)	1.755	1.642	–0.310	0.324	**1.156**	**1.894**
(four)	2.652	2.584*	0.606	0.601	1.380	2.360*
(five)	4.162	3.762**	0.996	0.915	1.940	3.010**
(six)	4.080	2.353*	–	–	**1.880**	**1.885**
Human commensalism	0.315	0.648	1.144	1.778	0.334	1.133
Ecofunction	0.259	0.534	0.914	1.649	0.035	0.118
Native range						
(Afrotropical)	1.922	2.147*	0.131	0.124	1.085	2.037*
(Indo-Malayan)	2.579	2.575*	–0.558	0.447	1.431	2.411*
(Palaearctic)	1.767	2.044*	0.379	0.288	0.568	1.147
Biological factors						
Migratory status (partial)	1.101	**2.201**	–0.098	0.199	0.270	0.590
Sociality (small flocks)	–0.672	1.170	–0.802	2.653*	–0.025	0.081
Body mass	0.002	1.282	–0.000	2.138*	0.001	0.688
Reproductive factors						
Clutch size	0.173	1.058	0.096	0.414	0.100	1.162
Brood number	1.696	2.179*	0.798	1.032	0.535	1.346
Productivity	–0.161	1.357	–0.028	0.171	–0.062	1.033

$^*P \leq 0.05$, $^{**}P \leq 0.01$. Results in bold are trends noted as $0.05 \leq P \leq 0.10$.

highest introduction success (Blackburn & Duncan, 2001; Cassey, 2002). This suggests that similar traits may lead to both establishment success and impact. Thus, understanding why some species are successfully introduced into non-native locations may also help to explain their potential to exhibit negative impacts.

It is still unknown which specific factors explain why patterns of non-randomness among taxa for establishment and impacts are strongly linked. We hypothesize that these reasons relate to intrinsic taxonomic traits (e.g. those associated with species abundance such as reproductive productivity), introduction effort or the ability to adapt to environments influenced by human use. Introduction effort, though widely believed to be among the strongest predictors of establishment (e.g. Veltman *et al.*, 1996; Blackburn & Duncan, 2001; Duncan *et al.*, 2001; Cassey *et al.*, 2004), would not explain the impact patterns noted in this study, since most impacts were reported for species ranges outside Europe. Furthermore, the approach used to compile the data was both taxonomically and geographically neutral, including impacts for all species established in Europe. Because species abundance is often a major factor in determining whether impacts will occur, further research to elucidate those factors most important in determining species abundances is needed.

Several ecological and life-history traits explained variation in the severity of impacts. Species with greater habitat generalism, Afrotropical, Indo-Malayan and Palaearctic native ranges, sedentary or partially migratory tendency, large feeding or roosting flocks, small body mass and/or a greater number of broods were associated with greater overall impacts. In support of our second hypothesis, several of these traits have also been associated with greater introduction success (Blackburn & Duncan, 2001; Cassey, 2002; Duncan *et al.*, 2003; Cassey *et al.*, 2004). The ability of a species to use a variety of habitats in their introduced range has been associated with both high introduction success (Duncan *et al.*, 2003; Cassey *et al.*, 2004) and serious negative impacts (Williamson, 1998). This ability may reflect a greater variety of habitats used by individuals or populations in the native range, phenotypic plasticity and/or the potential for a species to evolve and adapt to novel habitats (Sol *et al.*, 2002; Lambrinos, 2004; Strayer *et al.*, 2006).

The positive association between increasing habitat generalism and economic impacts suggests that these species may be able to adapt to new habitats. There are several examples of dietary evolution in invasive birds (Ralph, 1984; Lahti, 2003) and mammals (Michaux *et al.*, 2007). For example, village weavers (*Ploceus cucullatus*) have been reported eating cactus (Lahti, 2003), and house sparrows (*Passer domesticus*), along with several other species, became nectivorous when introduced to Hawaii (Ralph, 1984). Although not directly addressed in this study, species have greater establishment success in areas with climates or latitudes similar to their native range (Blackburn & Duncan, 2001; Duncan *et al.*, 2001). Species arrive in Europe from nearby Palaearctic, Indo-Malayan and Afrotropical regions either intentionally through trade routes or unintentionally by escapes (Shirley & Kark, unpublished data). The association between these regions of origin and economic impacts suggests that economic resources in climatically suitable habitats in Europe may be vulnerable to exploitation by alien birds. High rates of successful establishment found in the Mediterranean Basin (Kark & Sol, 2005) may reflect the ability of Afrotropical and Indo-Malayan species to thrive in these relatively warm areas where food resources are available all year round. There was no relationship between the number of species with reported impacts from a given region and the proportion of the total species with impacts from the same region. For several regions having a number of species with impacts, these species represented a fraction of the overall numbers of established species. Conversely, all established species from Australia had reported impacts suggesting that alien birds from Australia may represent a high risk.

Migratory tendency is negatively associated with establishment success in some studies (Veltman *et al.*, 1996; Duncan *et al.*, 2003; Cassey *et al.*, 2004). This has been explained by the failure of individuals with low population densities to find each other during the breeding season (Veltman *et al.*, 1996). However, once established, we found that partially migratory species (having both sedentary and migratory populations) have a tendency towards greater overall impacts. Sedentary populations of a given species spend more time in an area compared to migratory species, and therefore may have a higher impact on both agricultural crops and native species. At the same time, those populations of the same species that are migratory may have restricted ranges and so may avoid difficulties encountering other individuals during breeding. Species with high population growth potential reflected in large clutch sizes and multiple broods might be expected to exhibit greater impacts. Similar to studies that found no relationship between clutch size and establishment success (Veltman *et al.*, 1996; Duncan *et al.*, 2001), we found no relationship between clutch size and impacts. However, the positive association with number of broods suggests that species with several broods can have high population growth, producing not only higher establishment success (O'Connor, 1986; Veltman *et al.*, 1996; Cassey, 2002) but also greater overall impacts. For some birds such as parrots, the number of broods is a better predictor of pest potential than clutch size (Bucher, 1992). Species may be able to produce a greater number of broods annually near human-modified habitats where food sources are plentiful, even in northern areas if 'urban heat island' (Oke, 1995; McDonnell *et al.*, 1997) effects exist.

Database approaches combined with analyses of species traits have been successfully used to identify general patterns from empirical data (e.g. Blackburn & Duncan, 2001; Kolar & Lodge, 2001; Cassey *et al.*, 2004; Cadotte *et al.*, 2006). We found that impacts were associated with a combination of taxonomic relationships and species traits. This approach can provide many benefits for the management of exotic species over large jurisdictions. Detailed information on impacts of exotic species in a given geographical area, while highly desirable for risk assessment and management, is rarely available at country or continental scales (Parker *et al.*, 1999; Coluatti & MacIsaac, 2004; Vilà *et al.*, in press). Given that early efforts can be critical for the control of new aliens (Simberloff, 1997), explanatory models that incorporate the impact history from other areas where they have been introduced can be a valuable guide to predicting consequences (Ricciardi, 2003). For those species in the early stages of invasion, impact history in the native ranges would be useful (Sakai *et al.*, 2001). Although not necessarily a reliable predictor of impacts outside a species' native range, there are several examples of bird species regarded as minor pests in their native range that subsequently became serious pests in introduced ranges (Long, 1981). Long (1981, p. 18), in his pivotal work, states 'those species which cause damage, however minor, to agricultural crops in their native habitats will cause similar or worse damage in those into which they have been introduced'.

Poor predictions about impacts of alien species can result from time lags between the initial introduction and detectable impacts (Williamson, 1999; Ricciardi, 2003). These lags are generally poorly understood for introduced avian species, but may be shorter than those for some other taxa because of their mobility and the high prevalence of human commensalism among alien birds introduced into highly modified landscapes (Holzapfel *et al.*, 2006). Understanding how certain characteristics influence a species' ability to produce negative impacts elsewhere would provide information before impacts become apparent. Although impacts of alien species are often largely dependent on abundance, the relationship is not necessarily linear and may involve complex dynamics such as thresholds or nonlinear effects (Byers *et al.*, 2002; Ricciardi, 2003). There are also important exceptions, such as hybridization effects, that can occur at very low abundances (Hughes *et al.*, 2006).

A major goal in dealing with impacts of alien species is to distinguish those species with large effects in order to focus efforts at national and international scales (Parker *et al.*, 1999; Vilà *et al.*, in press). The strong taxonomic structure of impacts among alien bird species in Europe suggests that additional effort directed towards specific families could be beneficial. Several species with potentially serious negative impacts are in the early stages of establishment with limited distributions and abundances (Shirley & Kark, unpublished) and efforts should be considered to prevent the establishment and spread of these species. In some cases, early efforts are already proving successful (Hughes *et al.*, 2006; S. Saavedra, pers. comm.). We restricted ourselves to those species introduced into Europe, so our sample size somewhat limits the generality of our results. More work is needed to understand whether the taxonomic and species trait relationships are retained in other regions and at a global scale. Although our approach has synthesized historical knowledge of impacts based on sparse and often localized studies, we believe this preliminary information is nevertheless critical because it represents a potential for negative effects at some unknown local level of abundance. Greater quantification of impacts in both the introduced and native ranges, and particularly their relationship to abundance, is necessary and would facilitate biogeographical comparisons (Hierro *et al.*, 2005). In the meantime, for agencies that will have to make decisions quickly, sometimes at a continental scale and before more refined information is available, consideration of species characteristics may provide an opportunity to limit negative impacts.

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SUPPORTING INFORMATION

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

Appendix S1 Sources of data for reported impacts.

BIOSKETCHES

Susan Shirley was a post-doctoral researcher on the European Union DAISIE project. Her research interests include analyses of factors underlying the spatial and temporal distribution of alien bird species in Europe, examining the local and landscape effects of habitat alteration on riparian food webs, and investigating species characteristics of birds responding to climate change.

Salit Kark's interests are in the patterns and processes shaping biodiversity in natural and human-dominated landscapes, and the effects of global changes on these patterns. She works on species distribution ranges, ecological gradients, urban and alien species, as further described in http://biodiversity-group.huji.ac.il/.

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