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What determines the impact of alien birds and mammals in Europe?

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Abstract An often-cited reason for studying the process of invasion by alien species is that the understanding sought can be used to mitigate the impacts of the invaders. Here, we present an analysis of the correlates of local impacts of established alien bird and mammal species in Europe, using a recently described metric to quantify impact. Large-bodied, habitat generalist bird and mammal species that are widespread in their native range, have the greatest impacts in their alien European ranges, supporting our hypothesis that surrogates for the breadth and the amount of resources a species uses are good indicators of its impact. However, not all surrogates are equally suitable. Impacts are generally greater for mammal species giving birth to larger litters, but in contrast are greater for bird species laying smaller clutches. There is no effect of diet breadth on impacts in birds or mammals. On average, mammals have higher impacts than birds. However, the relationships between impact and several traits show common slopes for birds and mammals, and relationships between impact and body mass and latitude do not differ between birds and mammals. These results may help to anticipate which species would have large impacts if introduced, and so direct efforts to prevent such introductions.

Keywords Bird · Clutch size · Diet breadth · Exotic · Habitat breadth · Invasion · Litter size · Mammal · Species traits

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Introduction

Considerable advances in understanding the invasion process have accrued from comparative analyses of historical data, particularly on alien birds (reviewed by Duncan et al. 2003; Sol et al. 2005a; Blackburn et al. 2009a) and alien mammals (Kraus 2003; Forsyth et al. 2004; Jeschke and Strayer 2005, 2006; Jeschke 2008; Sol et al. 2008; Bomford et al. 2009). These studies identify factors that determine which native bird and mammal species get introduced to novel environments,

and which of the introduced species subsequently establish self-sustaining alien populations. Far less attention, however, has been given to factors that influence the later stages of the invasion process, and specifically to the question of what determines the impact of invaders (Leung et al. 2012). This represents a significant gap in the literature, especially given that a primary motivation for studying the invasion process is to understand, and ultimately mitigate, these impacts (Leung et al. 2012).

Alien birds and mammals can have severe impacts on the economies and environment in areas to which they are introduced. For example, alien mammals are implicated in the extinctions of most bird species that have disappeared in the last 400 years (mostly on islands; Blackburn and Gaston 2005), and there is also evidence for negative impacts of alien bird species on extant bird species through competition, predation and genetic introgression (Holyoak and Thibault 1984; Thibault 1988; Rhymer and Simberloff 1996; Blanvillain et al. 2003; Smith et al. 2005; Hughes et al. 2008). Pimentel et al. (2000, 2001) estimated the economic losses to exotic species in six countries: the US, UK, Australia, South Africa, India, and Brazil. They attributed US$2.4 billion per year in damages to the impacts of alien birds, and US$80 billion per year in damages to the impacts of alien mammals, through such effects as damage to buildings, damage to crops, and the spread of diseases to livestock and humans. While the exact numbers for losses can be debated (e.g. Davis 2009), it is nevertheless true that alien species impose huge costs on societies worldwide. There is thus a strong imperative to predict which alien species will have impacts in their new ranges.

As far as we are aware, there are only two published comparative analyses of the correlates of impact in alien birds or mammals. Shirley and Kark (2009) compiled data on impacts to human health, agriculture and biodiversity in the native and alien ranges, of all bird species known to have been introduced to Europe according to the DAISIE (Delivering Alien Invasive Species Inventories for Europe) database (www. europe-aliens.org). They then assessed how species with impacts were distributed with respect to taxonomy and native biogeographic region, and correlated impact severity with a range of biological characteristics. They found that species with broad habitat tolerances tended to have higher economic impacts, while flock-forming and small-bodied species tended

to have higher impacts on biodiversity. Overall impacts (summed across categories) were positively associated with habitat breadth and number of broods per year. Nentwig et al. (2010) compared the impacts of 27 alien mammal species established in Europe to measures of life history, including body size, fecundity, diet, and habitat generalism. They found that economic and environmental impacts were related only to habitat generalism and impact elsewhere. Thus, there is a suggestion of a consistent effect of habitat generalism on the magnitude of impacts of alien birds and mammals, albeit not of body size or fecundity.

The extent to which conclusions about general correlates of the impacts of alien birds and mammals can be drawn is therefore limited by the paucity of studies assessing these effects. Moreover, the two studies to date have used very different metrics of impact and criteria for including species in the analysis. First, Nentwig et al. (2010) considered only impacts recorded from the alien range in Europe, whereas Shirley and Kark (2009) analysed impacts taken from anywhere the species occurs—native or alien ranges— and thus do not assess the actual impacts of the species in Europe. Second, Nentwig et al. (2010) assessed a much wider range of possible impacts of alien species than Shirley and Kark (2009). Thus, the metric for the severity of biodiversity impact used by Shirley and Kark (2009) integrates the effects of aggression, competition, predation and hybridization across three ordinal categories, while entry into the highest category is based only on the latter two processes. The metric of economic impact in Shirley and Kark (2009) is entirely based on damage to crops. In contrast, Nentwig et al. (2010) produced metrics based on five different categories of environmental impact, and a further five categories of economic impacts. Because of all these differences in the two studies, it is currently impossible to say how similar or dissimilar the life-history attributes correlated to impact are in alien mammals and birds. What is missing is a standardized assessment of impacts and traits in both taxa which will allow a direct comparative analysis.

In this paper, we close this gap by assessing determinants of the impact of alien bird and mammal species in Europe through a comparative analysis of the biological traits that relate to the magnitude of their environmental and economic impacts. Our analyses follow from the comparative approaches adopted by

Shirley and Kark ([2009](#)) and Nentwig et al. ([2010](#)), but build on them by analysing directly comparable data on the impacts of alien bird and mammal species, by restricting attention only to species with established alien populations in Europe, and by considering only impacts known from these alien distributions. Our definition of impact is given in Nentwig et al. ([2010](#)) and follows the framework established by Parker et al. ([1999](#)). Parker and colleagues defined overall impact, I, as the product of the range size R of a species, its average abundance per unit area A across that range, and E, the effect per individual or per biomass unit of the invader: $I_{total} = RAE$. For our analysis here, we only use the two latter components ($I_{local} = AE$), because the range size depends on the time since invasion and is thus not a species characteristic. Thus, our measure reflects the local impact of a species at its average population density. We compare the magnitude of documented local economic and environmental impacts (and their combination) against a set of species-level variables that should relate to the breadth of resources that a species can use (diet breadth, habitat breadth, native geographic range), and hence also how common it may become at any given site in the alien range, the amount of resources that a species is likely to use (body mass, clutch or litter size), and the likely similarity between native and alien ranges (the mean latitude of the native geographic range). We predict that large-bodied, wide-ranging, generalist species that are pre-adapted to high latitude regions, and that produce numerous offspring, should have larger impacts on the environment and economy of Europe.

Methods

Data on the economic and environmental impacts of 26 alien bird species and 24 alien mammal species in Europe were taken from Kumschick and Nentwig ([2010](#)). These species are the subset of birds and mammals on the DAISIE database (www.europe-aliens.org) that were introduced by human agency after 1492 but at least before 1985 (as in Kumschick and Nentwig, [2010](#); after Gebhardt et al. [1996](#)), and currently have self-sustaining alien populations, but no native populations, within Europe. Europe here is defined as in Fauna Europaea ([2004](#)) as the European continent and its islands, including in the east Ukraine, Belarus, and the

European part of Russia. No species introduced less than 25 years ago (as of 2010, when the data were collated) was considered because the generation times of mammals and birds can be long, and so the status of species introduced after 1984 is difficult to establish with certainty. Species for which there is not yet evidence of establishment were excluded as estimates of their impact may be affected if their populations are actually transient. Species native to Europe were excluded to ensure that there is no uncertainty over the provenance (native or alien) of populations.

Here, we adopt the impact scoring system produced by Nentwig et al. ([2010](#)) and Kumschick and Nentwig ([2010](#)) for alien bird and mammal species. Parker et al. ([1999](#)) suggested that an integrative measure of the impact of alien species, I, should be a product of three factors: the alien range size, R, the mean abundance of the species across that range, A, and the per-individual effect on components of the native ecosystem, E, such that $I = RAE$. Kumschick and Nentwig's system integrates all negative environmental and economic effects known in the literature for the species in their alien range (in this case Europe) and it has been proven to be useful for scoring impacts in the native ranges of the respective species as well (Kumschick et al. [2011](#)). These impact scores represent a measure of "local impact" a species has at a site, which can be combined with alien range size R to produce a measure of "actual impact" (sensu Nentwig et al. [2010](#); Kumschick and Nentwig [2010](#)). Thus, actual impact equates to Parker et al.'s metric of total impact I, while local impact is an estimate of AE. Local impact is a sensible measure for interspecific comparison, as in practice R is likely to be a function of a species' residence time in a region (Wilson et al. [2007](#)), while it will be hard to estimate the impact of individual invaders, and hence E, at least for animals. Moreover, per-capita impact E is likely strongly related to body size (Peters [1986](#)) and therefore is on its own not a good indicator for interspecific comparison. The same is true for abundance, which also scales with body size, but negatively (White et al. [2007](#)). All our analyses are based on local impact, and hence are independent of the current distribution of a species.

Kumschick and Nentwig ([2010](#)) classified environmental and economic impacts into six sub-categories each. Environmental impacts were classified as being effected through competition, predation, hybridization, transmission of diseases, herbivory, or impact on

ecosystems. The last subcategory includes only impacts that are not already taken care of in the previous five categories (see Kumschick and Nentwig 2010). Economic impacts were classified as on agriculture, livestock, forestry, human health, infrastructure and human social life (e.g. noise disturbance, pollution of recreational areas). For each of the twelve different sub-categories, the minimum and maximum impacts were defined in the form of "scenarios". Scenarios are verbal descriptions of impacts and include variables that can be measured or quantified and that are indicative of the level of impact intended by the scenario. Scenarios are needed because different studies use different variables or indicators to measure impact, and thus cannot be directly compared. Then, a number of intermediate impact levels were defined (in our study 4), each also in form of a scenario. Thus, for each sub-category, impact values were scored in the range from zero to five, with zero denoting no impact known or detectable and five the highest impact possible at a site (Kumschick and Nentwig 2010). The resulting impact scores are ordinal, so that higher scores always indicate higher impact.

The impacts that have been measured in different studies describing alien bird or mammal impacts were then assigned to categories (and their associated scores) on the basis of their fit to the various scenarios. Where a range of impacts is known for a given sub-category for a given species, we assigned the species the highest recorded score, assuming that this denoted the potential impact that the species could achieve in this sub-category. The environmental or economic impact of a species is simply the sum of the scores in each sub-category, which can therefore take a value between zero and 30. The combined environmental and economic impact of a species is the sum of its environmental and economic impact scores, which can thus vary between zero and 60. More details on the scoring system are given in Nentwig et al. (2010) and Kumschick and Nentwig (2010). Adopting these measures ensures that we cover the widest possible range of impacts of alien species in their invaded European ranges.

Scoring systems are a firmly established and widely used tool in risk assessments for comparative purposes and prioritization (Leung et al. 2012), and their predictive value has been shown many times (e.g. Pheloung et al. 1999; Kŕivánek and Pyšek 2006;

Purvis et al. 2000; Fritz et al. 2009). Subjectivity in classification can be minimized by good descriptions of scenarios and a small number of categories, and Nentwig et al. (2010) found that results based on this scoring system were robust to uncertainties in classification. However, since scoring of impact is only a semi-quantitative method and impact scores therefore not linked to exact "values" of damage, it is to a certain degree subjective and the assessment dependent on the assessor (Strubbe et al. 2011). Independent reclassification of the impacts of the five highest-impact bird species resulted in practically the same rank order of species, albeit with lower impact scores (Strubbe et al. 2011; Kumschick and Nentwig 2011). Still, high-impact species received higher scores than low-impact species. Hence, we believe that our scoring system is a reasonable measure of the relative impacts of alien species and can be used in comparative analyses.

While it might appear preferable in the study of impacts to use quantitative indicators that can be objectively measured rather than ordinal scores, indicators also have significant shortcomings. First, it is not always clear how well a single indicator actually captures the relevant impact. For example, the impact of an introduced mammal species on native communities of ground-breeding birds through predation may be assessed by analyzing predator faeces composition with molecular methods to quantify diet, by quantifying differences in breeding success in areas with and without predators, or by assessing changes in bird population trends after the predator was introduced. Which of these indicators captures best "impact through predation" is impossible to say, unless the full scale of possible impacts through predation is defined and the observed impacts are then assigned to a pre-defined scenario, as in our scoring system.

Second, measurable indicators are difficult to compare. Different indicators are used in studies on different species, and it is harder still to compare indicators of different categories of impact (e.g. of predation vs. hybridization). Scoring systems allow comparisons among different indicators by assigning indicators to an impact scenario which in turn is given a score value. One can also compare impacts in different categories, because they are scored in the same way, from the least to the greatest impact. Thus, if an alien species scores an impact through predation

in the second level (= score 2) and an impact through hybridization in the fourth (= score 4), one can reasonably conclude that this species has a higher impact through hybridization than through predation.

We collated data on the following biological and biologically relevant geographical traits from the native ranges for all 50 species: body mass (g), clutch size (number of eggs per brood) or litter size (number of young per birth), breeding geographic range size (km^2), absolute mean latitude of the breeding geographic range (degrees from the equator), diet breadth, and habitat breadth. Diet breadth was estimated as the number of the following eight major food types included in the diet of a species: grasses/forbs, seeds/grains; fruits/berries; pollen/nectar/flowers; tree leaves/branches/bark; roots/tubers; invertebrate prey; vertebrate prey/carrion. Habitat breadth was estimated as the number of the following European Nature Information System habitat categories (http://eunis.eea.europa.eu) included in a species native range: Marine habitats, including littoral rock and sediment; coastal habitats; inland surface waters; mires, bogs and fens; grasslands and lands dominated by forbs, mosses or lichens; heathland, scrub and tundra; woodland, forest and other wooded land; inland unvegetated or sparsely vegetated habitats; regularly or recently cultivated agricultural, horticultural and domestic habitats; constructed, industrial and other artificial habitats. Data on diet and habitat breadth were coded on the basis of data in del Hoyo et al. (1992, 1994, 1997, 2009), Clement et al. (1993), Long (2003), the PanTHERIA database (Jones et al. 2009), www.ecologyasia.com and animaldiversity.ummz.umich.edu.

Data on the remaining variables came from the PanTHERIA database (Jones et al. 2009) for mammals. For birds, body mass data were taken from the compilation by Olson et al. (2009), and size and absolute mean latitude of the native breeding geographic range from the data used by Orme et al. (2005), where further details are given in each case. Clutch sizes came from Bennett (1986), with clutch sizes for species missing from this compilation estimated as the midpoint of the clutch size range given by del Hoyo et al. (1992). Body mass and geographic range size were both log$_{10}$-transformed for analysis.

All statistical analyses were carried out in R v. 2.14.1 (R Development Core Team 2006). We assessed the relationship between each of the specific traits and the environmental and economic impacts (separate and combined) of alien bird species in Europe using generalized linear mixed effects models using the lmer option in the lme4 package (version 0.999375, Bates and Maechler 2008). Impact was analysed as a binomial variable, out of 60 for combined and out of 30 for separate environmental and economic impacts, using a binomial error structure with an observation-level random effect to account for overdispersion in the data. We also included random effects for taxonomic order, nested within class, to account for autocorrelation amongst species due to taxonomy. All other response variables were included as fixed effects. For each continuous predictor variable, we identified the model with the lowest AIC out of four alternatives: the continuous predictor alone, taxonomic class alone (as a fixed effect), the continuous predictor + class, and the continuous predictor + class + their interaction. We included taxonomic class in the models to assess whether the effects of the continuous predictor variables on impact differed in birds and mammals, as might be expected. We do not present multivariate analyses as the low ratio of species to model degrees of freedom, as a result of the number of predictor variables, their interactions with taxonomic class, and the random effects of order and class, leads to problems of overfitting.

Results

The combined environmental and economic impact scores for alien bird and mammal species span similar ranges, but most birds have low impact scores relative to those for mammals (see Figs. 1, 2, 3). Combined environmental and economic impact values vary between 0 and 36 (out of a possible total of 60) for birds, with a median of 4, and between 1 and 37 for mammals, with a median of 16.5. Only one bird species has a combined environmental and economic impact score greater than the median value for mammals (the Canada goose, *Branta canadensis* 36). Median environmental impacts are 3.5 and 8.5 for birds and mammals respectively, and median economic impacts are 0 and 7.5. While the highest economic impact score relates to a bird (21 for *B. canadensis*), most bird species have low environmental and economic impacts.

Fig. 1 The relationship
between combined
environmental and
economic impacts and each
of the six different predictor
variables for birds (*filled
circles*, *dashed line*) and
mammals (*open triangles*,
solid line). Impact scores are
presented as proportions of
the maximum possible score
(= 60). The fitted curves in
each case are calculated
from the parameters of the
mixed models with random
effects for class and order
given in Table 1
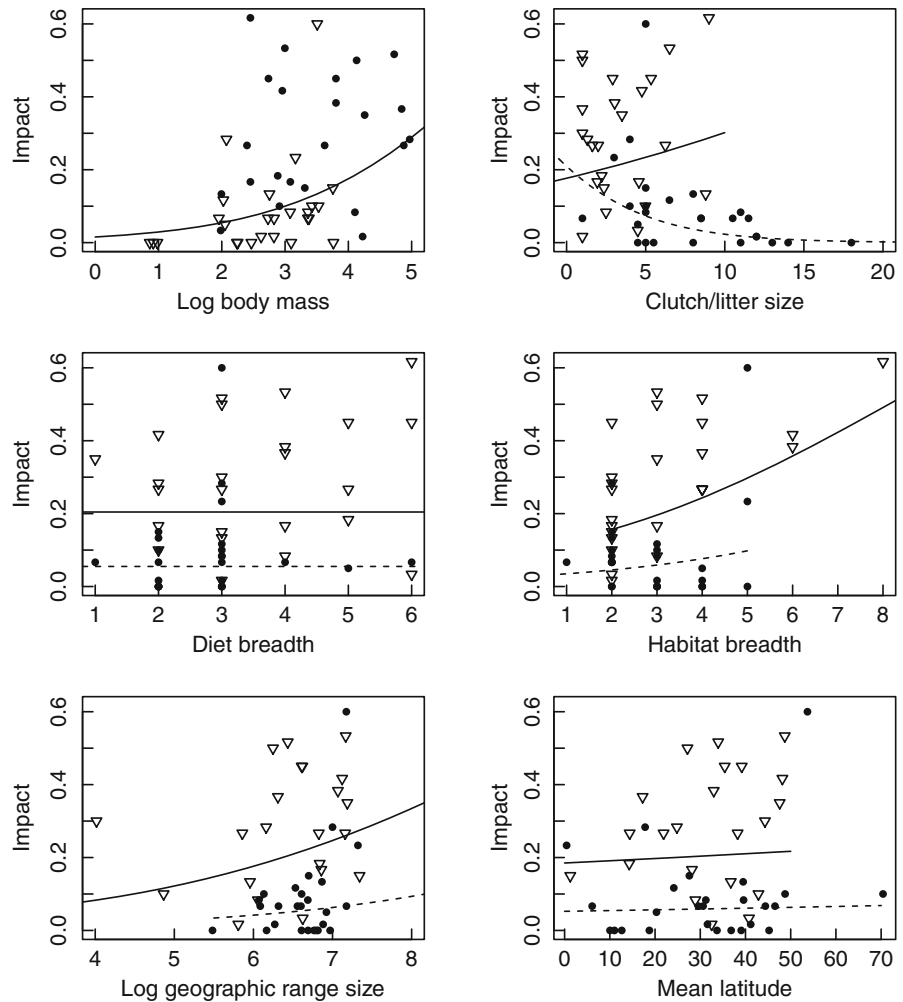
The relationships between each predictor variable and the combined environmental and economic impacts of established aliens tend to differ for birds and mammals (Fig. 1), such that the most likely model in five of the six cases includes a term for taxonomic class (Table 1). However, in only one of the six cases does the slope term differ between birds and mammals: combined environmental and economic impacts show common responses to changes in the predictor variables, albeit impacts are typically greater in mammals than birds for these variables within the range of variation common to both taxa (Fig. 1; positive estimate of class in Table 1). Combined environmental and economic impact increases with body mass, habitat breadth, geographic range size and native range latitude in both birds and mammals. The most likely relationship between body mass and

combined environmental and economic impact lacks a term for class, suggesting a common relationship across birds and mammals. Combined environmental and economic impact increases with litter size in mammals, but decreases with clutch size in birds. Finally, the most likely model for diet breadth and class does not include an effect of diet breadth, and therefore just returns the tendency for impacts to be greater in mammals than in birds.

The most likely models for the relationships between environmental impact and each predictor variable (Table 1, Fig. 2) once again show no effect of diet breadth for birds or mammals, a common positive relationship between body mass and impact for birds and mammals, and opposite effects of clutch and litter size on impact. The most likely model for latitude lacks a term for class, suggesting a common

Fig. 2 The relationship between environmental impacts and each of the six different predictor variables for birds (*filled circles, dashed line*) and mammals (*open triangles, solid line*). Impact scores are presented as proportions of the maximum possible score (= 30). The *fitted curves* in each case are calculated from the parameters of the mixed models with random effects for class and order given in Table 1
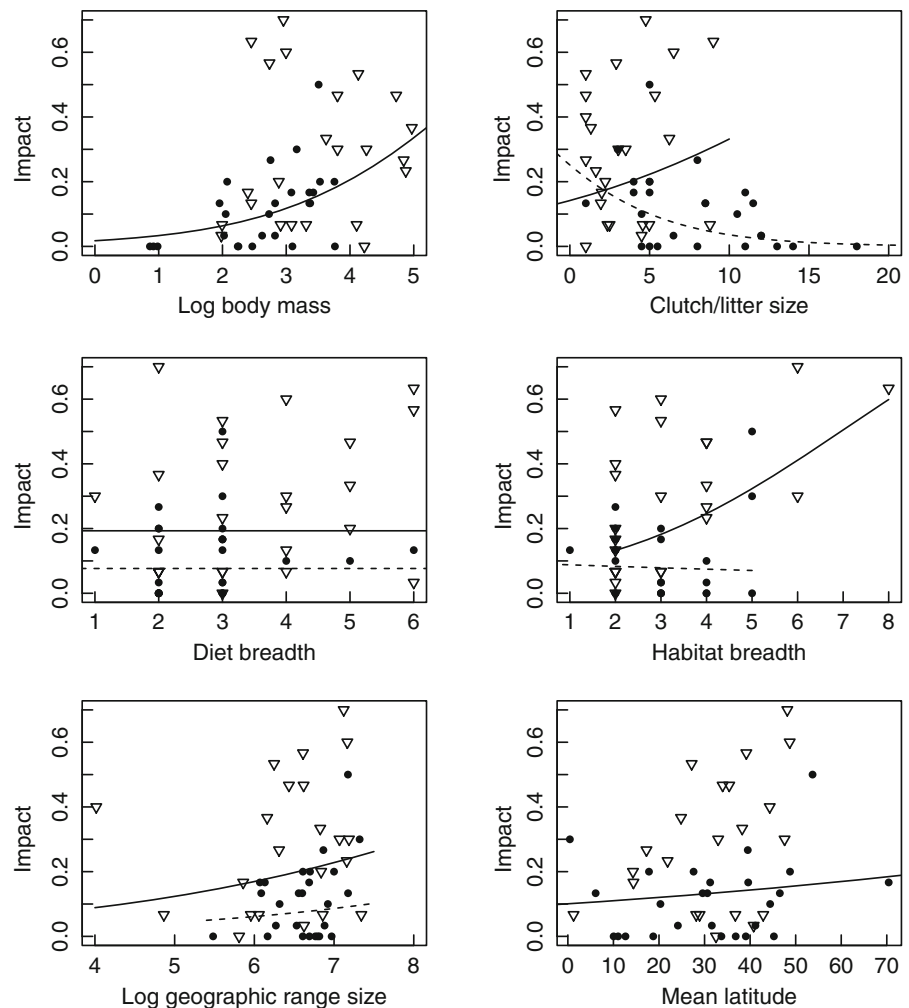

relationship between native latitude of origin and environmental impacts across birds and mammals. Conversely, the most likely model for habitat breadth suggests that it increases environmental impacts in mammals, but decreases it slightly in birds. Finally, geographic range size shows a common slope term for birds and mammals, but higher impacts for mammals for a given range size (Table 1, Fig. 2).

The economic impacts of birds are low relative to their environmental impacts (Wilcoxon rank sum test, $W = 198$, $P < 0.01$), and hence to their combined environmental and economic impacts. In contrast, there is no difference in the level of economic and environmental impacts for mammals ($W = 293.5$, $P = 0.92$). The most likely models for all six variables include terms for taxonomic class, which in all cases is

the result of higher average impact scores for mammals than birds for any given trait value. The models for geographic range size, habitat breadth and clutch size also include interaction terms with class. For the first two of these variables, impact increases more slowly with respect to the predictor variable in mammals than in birds (negative estimate of the interaction term), while there are again opposite effects of clutch and litter size on economic impact (Fig. 3).

The variance estimates for the random effects in the impact models were consistently high for taxonomic order, but low for taxonomic class. For example, the standard deviations of the random effects for order varied between 0.79 and 1.03 for the combined environmental and economic impact models, whereas

Fig. 3 The relationship
between economic impacts
and each of the six different
predictor variables for birds
(*filled circles*, *dashed line*)
and mammals (*open
triangles*, *solid line*). Impact
scores are presented as
proportions of the maximum
possible score (= 30). The
fitted curves in each case are
calculated from the
parameters of the mixed
models with random effects
for class and order given in
Table 1
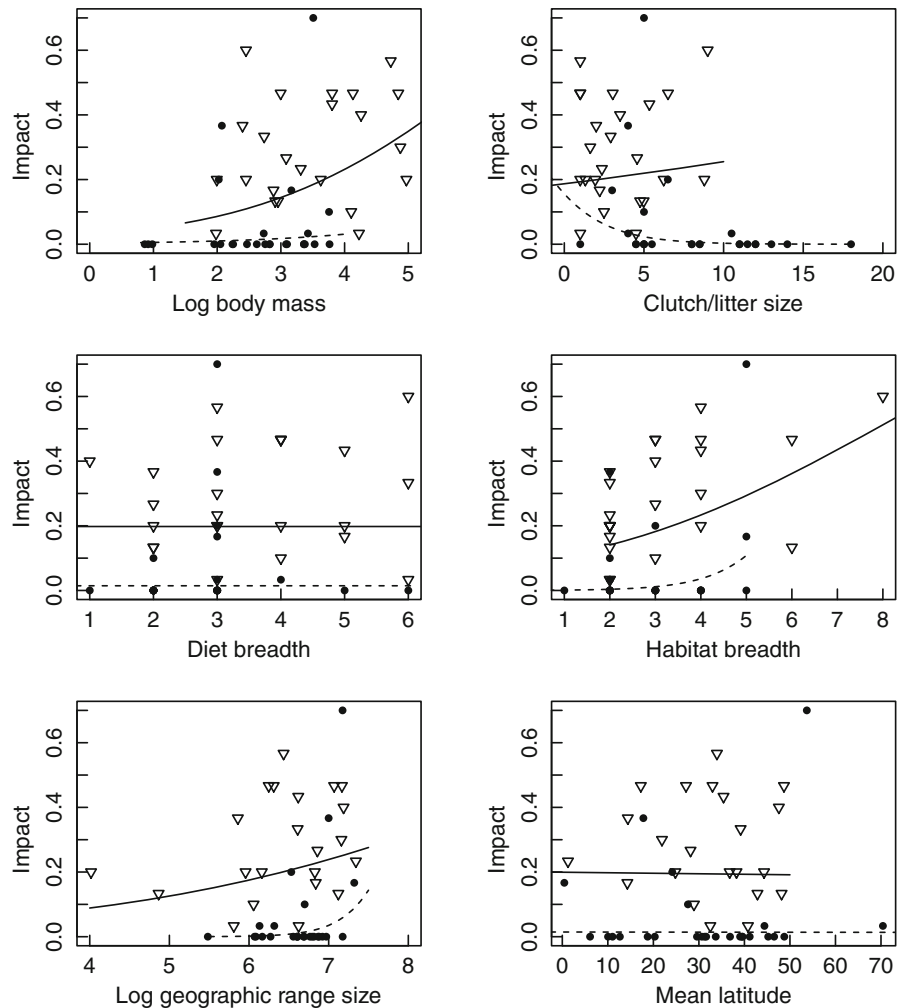
those for class were always less than 0.001 for the same models. Impacts tended to be high for species in the Rodentia, Carnivora and Psittaciformes, and low for Galliformes (e.g. Fig. 4).

Simple Pearson correlations between the six predictor variables were generally weak (Table 2). The only significant relationships were for mammals, between habitat breadth and log body mass, litter size and log body mass, and litter size and absolute mean latitude. Only one correlation coefficient exceeded 0.5 in absolute magnitude, and none of the relationships for birds exceeded 0.4. Economic and environmental impacts were positively correlated across species (Spearman rank correlation, rho = 0.68, $P < 0.001$), and also in a mixed effects model that included class and order as random effects (estimate ± s.e. = 0.581 ± 0.106, t = 5.47).

Discussion

This study considerably expands on previous findings on the relationship of impacts and species traits in birds (Shirley and Kark 2009) and mammals (Nentwig et al. 2010). We confirmed earlier results of habitat generalism as a predictor of impact in mammals and birds, species with broader habitat tolerances have higher levels of economic and combined environmental and economic impacts in Europe, and higher environmental impacts in alien mammals. In addition, our analyses showed that, as predicted, traits related to the breadth of resources that a species can use and traits related to the amount of resources that a species is likely to use both were significantly related to impact, with the exception of diet breadth. Although mammals tend to have broader diets and higher

Table 1 The relationship between environmental and economic (combined and separate) impact metrics and the variables in the first column, for 26 species of alien bird and 24 species of alien mammal in Europe

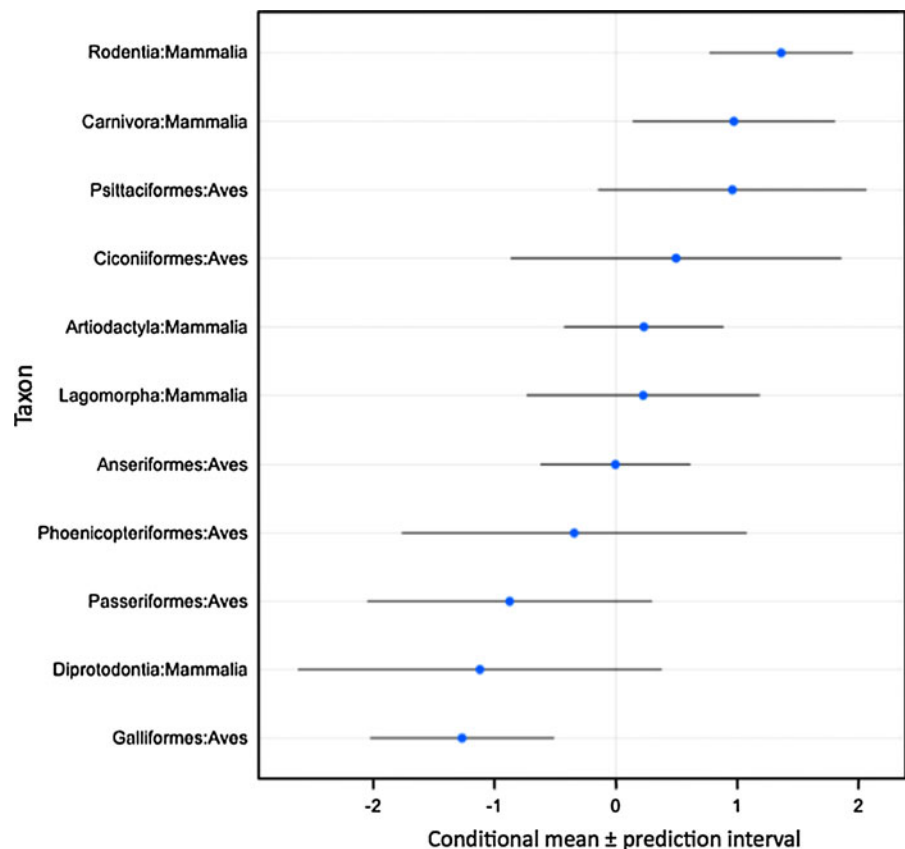|	Environmental and economic		Environmental		Economic	
	Estimate	s.e.	Estimate	s.e.	Estimate	s.e.
Intercept	−4.15	0.82	−4.03	0.81	−5.76	1.30
Log mass	0.65	0.24	0.67	0.24	0.58	0.36
Class					2.24	1.21
Interaction						
Intercept	−2.84	0.45	−2.49	0.44	−4.22	0.81
Diet breadth						
Class	1.48	0.65	1.06	0.63	2.82	1.11
Interaction						
Intercept	−3.59	0.53	−2.28	0.74	−7.96	1.42
Habitat breadth	0.28	0.11	−0.06	0.21	1.17	0.30
Class	1.36	0.61	−0.36	0.95	5.53	1.71
Interaction			0.44	0.25	−0.86	0.33
Intercept	−5.70	1.81	−4.95	1.99	−24.81	8.42
Log geog. range size	0.43	0.26	0.37	0.29	3.07	1.22
Class	1.59	0.61	1.14	0.60	20.92	8.70
Interaction					−2.68	1.27
Intercept	−2.89	0.46	−2.19	0.392	−4.22	0.82
Absolute latitude	0.004	0.01	0.01	0.01	−0.001	0.01
Class	1.41	0.65			2.83	1.11
Interaction						
Intercept	−1.39	0.63	−1.09	0.66	−1.69	1.12
Clutch size	−0.24	0.08	−0.22	0.08	−0.41	0.18
Class	−0.26	0.83	−0.71	0.88	0.22	1.34
Interaction	0.32	0.13	0.33	0.14	0.45	0.22

The models presented are those with the lowest AIC out of four alternatives in each case: the continuous predictor alone, class alone, the continuous predictor + class, and the continuous predictor + class + their interaction. The interaction term represents the difference in slope for mammals in comparison to birds. All parameters presented in this table except those for diet breadth derive from generalized linear mixed models with the explanatory variables as fixed effects, taxonomic order nested within class as a random effect, a species-level random effect, and binomial error structures. The parameters for diet breadth derive from general linear models with binomial error structures, as there is no reason to include random effects for taxonomy when class is the only predictor variable (the most likely model for diet breadth was nevertheless derived using the same mixed modelling approach as for all other variables)

Table 2 The correlations between each of the six predictor variables for mammals (above the diagonal) and birds (below the diagonal)

	Log mass	Clutch/litter size	Diet breadth	Habitat breadth	Log geog. range size	Mean latitude
Log mass		**−0.614**	−0.318	0.026	−0.260	−0.058
Clutch/litter size	0.012		0.284	0.379	0.194	**0.473**
Diet breadth	0.177	0.139		0.219	0.169	0.011
Habitat breadth	−0.133	0.058	0.046		**0.448**	0.206
Log geog. range size	−0.079	−0.192	0.076	0.250		−0.172
Mean latitude	0.376	0.208	−0.222	−0.082	−0.217	

Sample sizes are 24 for mammals and 26 for birds. Significant correlations ($\alpha < 0.05$) are in bold

Fig. 4 A caterpillar plot of the conditional means and their associated 95 % prediction intervals for the order-level random effects for the model of combined environmental and economic impacts as a function of log body mass (see Table 1 for the fixed effect parameters), produced using the dotplot function in R. The prediction intervals for Rodentia, Carnivora and Galliformes all fail to overlap zero, indicating significant positive or negative effects, and also justifying the inclusion of random effects in this model

impacts than birds, there is no tendency for the species with broader diets to have greater impacts in either birds or mammals, or across the two classes. This is true for environmental and economic impacts, separately and combined.

Most of the traits analysed show qualitatively similar relationships to impact across both birds and mammals. The clear exception is clutch/litter size. Impacts increase with litter size in mammals, as predicted, but decrease with clutch size in birds, contrary to our a priori expectation. Interestingly, the opposing patterns shown by clutch and litter size occur despite the fact that large-bodied species in both groups have higher impacts (Table 1), and despite a strong negative correlation between body mass and litter size in mammals (Table 2). Thus, impacts are greater for birds with large body mass and small clutches, as might be expected given a general negative correlation between body mass and clutch size (Blackburn 1991; albeit not significantly so in our data), but for mammals impacts increase with both large body mass and large litters, even though large

mammals tend to bear small litters. The results for birds suggest that impacts are greater for species with "slower" life histories, as species with small clutches and large body masses also have higher adult survival rates and ages at first breeding (Bennett and Owens 2002). Our results run counter to the analyses of Shirley and Kark (2009), who found that overall impact was positively associated with number of broods per year (which is negatively correlated with adult survival rate: Bennett and Owens 2002). The results for mammals suggest that impacts are high for both "fast" species bearing large litters and "slow" species with large body mass. This is in contradiction to Nentwig et al. (2010) who found no correlation of any parameter associated with "slow" or "fast" life histories (body mass, age at maturity, longevity, litter size) and impact in mammals. This may be due to the use of simpler models in the latter study. A multivariate mixed model with log mass, clutch/litter size and class identifies a most likely model with mass, clutch/ litter, class, and the interaction between class and clutch/litter size as predictors (results not shown).

Thus, there may be independent and opposing effects of body size and litter size on the impacts of alien mammal species in Europe.

Mammals tend to have higher impact scores on average than birds at a given value for every trait analysed (Figs. 1, 2, 3), which is also reflected in the preponderance of positive terms for class in the most likely models (Table 1): 15 of these 18 models include class terms, of which 12 are positive. Nevertheless, two-thirds of the most likely models show no inter-action term between class and the trait concerned, indicating a common slope of the relationship between the trait and impact. In three cases, the similarity between birds and mammals in relationships between traits and impact is such that the most likely model of impact includes common estimates of slope and intercept for the two taxa: the relationships between environmental and combined environmental and eco-nomic impact and body mass, and between environ-mental impact and latitude, are shared across birds and mammals. This is surprising given that the different demands of avian versus mammalian lifestyles lead to very different body mass distributions for the two taxa, and very different suites of life histories in general. Models with an interaction term between class and the trait concerned are most frequent for economic impacts (Table 1), which is perhaps to be expected given that the economic impacts of birds are notably low relative to mammals – indeed, the median economic score for the former group is zero.

The early stages of the invasion process have been well studied in birds, and relatively well so in mammals. Current evidence from these taxa suggests that introduction is more likely for widespread, abundant species, which are more readily available for capture and transport, and which as a result are also released in larger numbers (Blackburn and Duncan 2001; Cassey et al. 2004a; Jeschke and Strayer 2006; Blackburn et al. 2009a). Establishment is more likely for, amongst other things, populations of generalist and behaviourally flexible species released in larger numbers (Cassey et al. 2004b; Forsyth et al. 2004; Sol et al. 2005b, 2008; Jeschke and Strayer 2006; Blackburn et al. 2009a, b). What determines the extent of spread following establishment is poorly under-stood, although data for alien birds in New Zealand and alien mammals in Australia show that species with higher population growth rates and released in larger numbers end up with wider distributions (Duncan et al.

1999; Forsyth et al. 2004; but see Duncan et al. 2001). We can now add to this catalogue the traits relevant for the magnitude of alien bird and mammal impacts. Thus, it is large-bodied, widespread in their native range, habitat generalist bird and mammal species that have the greatest impacts on the environment and economy in their alien European ranges.

Our results have important implications for the management of current and future invasions. They show that the impacts of mammal and bird species relate to a wide range of biological traits. If these relationships were shown to hold for alien mammals and birds in regions other than Europe, then presum-ably they would be of use in anticipating which introductions would also have large impacts, and so in preventing such introductions. They would also be of use in assessing which currently established species may have the largest actual impacts in the future. It would be a great step forward in the management of invasive pests if biological traits could help us to identify species with large impacts on the environment and economy before they have spread enough for their impacts to be felt, when control will be substantially easier (Pluess et al. 2012).

References

Bates D, Maechler M (2008) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375. http://CRAN.R-project.org/package=lme4

Bennett PM (1986) Comparative studies of morphology, life history and ecology among birds. Ph.D. thesis, University of Sussex

Bennett PM, Owens IPF (2002) Evolutionary ecology of birds: life histories, mating systems, and extinction. Oxford University Press, Oxford

Blackburn TM (1991) An interspecific relationship between egg size and clutch size in birds. Auk 108:973–977

Blackburn TM, Duncan RP (2001) Determinants of establish-ment success in introduced birds. Nature 414:195–197

Blackburn TM, Gaston KJ (2005) Biological invasions and the loss of birds on islands: insights into the idiosyncrasies of extinction. In: Sax DF, Gaines SD, Stachowicz JJ (eds) Exotic species: a source of insight into ecology, evolution, and biogeography. Academic Press, New York, pp 85–110

Blackburn TM, Lockwood JL, Cassey P (2009a) Avian invasions. The ecology and evolution of exotic birds. Oxford University Press, Oxford

Blackburn TM, Cassey P, Lockwood JL (2009b) The role of species traits in the establishment success of exotic birds. Glob Change Biol 15:2852–2860

Blanvillain C, Salducci JM, Tutururai G, Maeura M (2003) Impact of introduced birds on the recovery of the Tahiti Flycatcher (*Pomarea nigra*), a critically endangered forest bird of Tahiti. Biol Conserv 109:197–205

Bomford M, Darbyshire RO, Randall L (2009) Determinants of establishment success for introduced exotic mammals. Wildlife Res 36:192–202

Cassey P, Blackburn TM, Russell GJ, Jones KE, Lockwood JL (2004a) Influences on the transport and establishment of exotic bird species: an analysis of the parrots (Psittaciformes) of the world. Glob Change Biol 10:417–426

Cassey P, Blackburn TM, Sol D, Duncan RP, Lockwood JL (2004b) Global patterns of introduction effort and establishment success in birds. Biol Lett 271:405–408

Clement P, Harris A, Davis J (1993) Finches and sparrows. An identification guide. Christopher Helm, London

Davis MA (2009) Invasion biology. Oxford University Press, New York

del Hoyo J, Elliott A, Sargatal J (1992) Handbook of the birds of the world, vol 1. Ostrich to ducks. International Council for Bird Preservation, Cambridge

del Hoyo J, Elliott A, Sargatal J (1994) Handbook of the birds of the world, vol 2. New World vultures to guineafowl. BirdLife International, Cambridge

del Hoyo J, Elliott A, Sargatal J (1997) Handbook of the birds of the world, vol 4. Sangrouse to cuckoos. BirdLife International, Cambridge

del Hoyo J, Elliott A, Sargatal J (2009) Handbook of the birds of the world, vol 14. Bush-shrikes to Old World Sparrows. BirdLife International, Cambridge

Duncan RP, Blackburn TM, Veltman CJ (1999) Determinants of geographical range sizes: a test using introduced New Zealand birds. J Anim Ecol 68:963–975

Duncan RP, Bomford M, Forsyth DM, Conibear L (2001) High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. J Anim Ecol 70:621–632

Duncan RP, Blackburn TM, Sol D (2003) The ecology of bird introductions. Annu Rev Ecol Evol Syst 34:71–98

Fauna Europaea Web Service (2004) Fauna Europaea version 1.1. Available from www.faunaeur.org. Accessed September 2011

Forsyth DM, Duncan RP, Bomford M, Moore G (2004) Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. Conserv Biol 18:557–569

Fritz SA, Bininda-Emonds ORP, Purvis A (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecol Lett 12:538–549

Gebhardt H, Kinzelbach R, Schmidt-Fischer S (1996) Gebietsfremde tierarten—auswirkungen auf einheimische lebensgemeinschaften und biotope—situationsanalyse. Ecomed, Landsberg, Germany

Holyoak DT, Thibault JC (1984) Contribution à l'étude des oiseaux de Polynésie orientale. Memoirs du Museum National d'Histoire Naturelle (France). Nouvelle Serie. Serie A. Zoologie 127:1–209

Hughes JB, Martin GR, Reynolds SJ (2008) Has eradication of feral cats *Felis silvestris* halted the decline in the Sooty Tern *Onychoprion fuscata* population on Ascension Island, South Atlantic? Ibis 150(1):122–131

Jeschke JM (2008) Across islands and continents, mammals are more successful invaders than birds. Divers Distrib 14:913–916

Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. PNAS 102:7198–7202

Jeschke JM, Strayer DL (2006) Determinants of vertebrate invasion success in Europe and North America. Glob Change Biol 12:1608–1619

Jones KE, Bielby J, Cardillo M et al (2009) PanTHERIA: a species-level database of life-history, ecology and geography of extant and recently extinct mammals. Ecology 90:2648

Kraus F (2003) Invasion pathways for terrestrial vertebrates. In: Ruiz GM, Carlton J (eds) Invasive species: vectors and management strategies. Island Press, Washington, DC, pp 68–92

Krívánek M, Pyšek P (2006) Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe). Divers Distrib 12:319–327

Kumschick S, Nentwig W (2010) Some alien birds have as severe an impact as the most effectual alien mammals in Europe. Biol Conserv 143:2757–2762

Kumschick S, Nentwig W (2011) Response to Strubbe et al. (2011): Impact scoring of invasive birds is justified. Biol Conserv 144:2747

Kumschick S, Alba C, Hufbauer RA, Nentwig W (2011) Weak or strong invaders? A comparison of impact between the native and invaded ranges of mammals and birds alien to Europe. Divers Distrib 17:663–672

Leung B, Roura-Pascual N, Bacher S, Heikkilä J, Brotons L, Burgman MA, Dehnen-Schmutz K, Essl F, Hulme PE, Richardson DM, Sol D, Vilà M (2012) TEASIng apart alien species risk assessments: a framework for best practices. Ecol Lett (in press)

Long JL (2003) Introduced mammals of the world: their history, distribution and influence. CSIRO Publishing, Collingwood, Australia

Nentwig W, Kühnel E, Bacher S (2010) A generic impact-scoring system applied to alien mammals in Europe. Conserv Biol 24:302–311

Olson V, Davies RG, Orme CDL et al (2009) Global biogeography and ecology of body size in birds. Ecol Lett 12:249–259

Orme CDL, Davies RG, Burgess M et al (2005) Global biodiversity hotspots of species richness, threat and endemism are not congruent. Nature 436:1016–1019

Parker I, Simberloff D, Lonsdale W, Goodell K, Wonham M, Kareiva P, Williamson M, Von Holle B, Moyle P, Byers J (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Peters RH (1986) The ecological implications of body size. Cambridge University Press, Cambridge

Pheloung PC, Williams PA, Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. J Environ Manage 57:239–251

Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53–65

Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. Agric Ecosyst Environ 84:1–20

Pluess T, Cannon R, Jarošík V, Pergl J, Pyšek P, Bacher S (2012) When are eradication campaigns successful? A test of common assumptions. Biol Invasions 14:1365–1378. doi: 10.1007/s10530-011-0160-2

Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. Proc R Soc Lond B 267:1947–1952

R Development Core Team (2006) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rhymer JM, Simberloff D (1996) Extinction by hybridization and introgression. Annu Rev Ecol Evol Syst 27:83–109

Shirley SM, Kark S (2009) The role of species traits and taxonomic patterns in alien bird impacts. Glob Ecol Biogeogr 18:450–459

Smith GC, Henderson IS, Robertson PA (2005) A model of ruddy duck *Oxyura jamaicensis* eradication for the UK. J Appl Ecol 42:546–555

Sol D, Blackburn TM, Cassey P, Duncan RP, Clavell J (2005a) The ecology and impact of non-indigenous birds. In: del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the birds of the world, vol 10, cuckoo-shrikes to thrushes, vol 10. Lynx Ediçions and BirdLife International, Cambridge, pp 13–35

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L (2005b) Big brains, enhanced cognition, and response of birds to novel environments. PNAS 102:5460–5465

Sol D, Bacher S, Reader SM, Lefebvre L (2008) Brain size predicts the success of mammal species introduced into novel environments. Am Nat 172:63–71

Strubbe D, Shwartz A, Chiron F (2011) Concerns regarding the scientific evidence informing impact risk assessment and management recommendations for invasive birds. Biol Conserv 144:2112–2118

Thibault J-C (1988) Menacés et conservation des oiseaux de Polynésie Française. In: Thibault JC, Guyot I (eds) Livre rouge des oiseaux menacés des regions françaises d'outremer. Conseil International pour la Protection des Oiseaux, Saint Cloud

White EP, Ernest SKM, Kerkhoff AJ, Enquist BJ (2007) Relationships between body size and abundance in ecology. Trends Ecol Evol 22:323–330

Wilson JRU, Richardson DM, Rouget M, Proches S, Amis MA, Henderson LS, Thuiller W (2007) Residence time and potential range: crucial considerations in modelling plant invasions. Divers Distrib 13:11–22